Research papers

Comptonia naumannii (Myricaceae) from the early Miocene of Weichang, China, and the palaeobiogeographical implication of the genus

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ARTICLE INFO

ABSTRACT

Newly collected material of *Comptonia* leaves and fruits (*C. naumannii* and *C. tymensis*, respectively) from the lower Miocene of Weichang, China, are studied in detail. The leaves show great similarities in morphology and cuticular structures to those of the single extant species *C. peregrina*. It suggests a close genetic relationship between *C. numannii* and *C. peregrina*. *Comptonia* was widespread over the Northern Hemisphere during most of the Cenozoic, and obviously migrated into Asia from North America via a continental connection in the Eocene. Due to the cooling of global climate, it may have later gradually evolved into two ecotypes (thermophilous and cold tolerant). In the early Miocene *C. naumannii* was recorded from Northeast Asia and Alaska, but it disappeared from Alaska in the latest Miocene. The records suggest that plant exchange between Northeast Asia and North America may have ceased after the early Miocene.

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1. Introduction

Comptonia L'Héritier de Brutelle ex Aiton (Myricaceae) today is a monotypic genus, with a single species *Comptonia peregrina* (Linnaeus) Coulter including, besides the typical variety (*C. peregrina*), two varieties, *C. peregrina* var. *tomentosa* A. Chevalier and *C. peregrina* var. *aspleniifolia* (L.) Fernald. This species is presently restricted to North America ranging from Ontario and Nova Scotia (Canada) in the north to Georgia and South Carolina (USA) in the south (Berry, 1906; Elias, 1971; FNAEC, 1997; Fig. 1).

Since the first record of a fossil leaf of *Comptonia* (*C. difformis* (Sternberg) Berry) from the lower Miocene of the Most Basin (Bohemia, Czech Republic) by Sternberg in 1821 (Berry, 1906; Kvaček and Straková, 1997; Kvaček, 2004), this characteristic foliage was abundantly found from the Upper Cretaceous of North America, Europe, and Greenland (e.g., Berry, 1906), and from the Cenozoic of the Northern Hemisphere (e.g. Arnold, 1955; Baghai and Jorstad, 1995; Berry, 1906; Budantsev, 1994; Boyd, 1985; Chen et al., 1983; Christensen, 1975; Denk et al., 2005; Dillhoff et al., 2005; Ferguson, 1998; Friis, 1979; Greenwood et al., 2005; Grímsson and Denk, 2007; Hably, 2006; Hably and Fernandez Marron,

1998; Hably et al., 2001; Huzioka, 1961; Iljinskaja et al., 1976; Ina, 2004; Kvaček, 1998; Kvaček and Walther, 2004; Mai, 1995; Manchester, 1999; McClaughry and Gaylord, 2005; McIver and Basinger, 1999; Matthews and Ovenden, 1990; Millar, 1996; Momohara, 2005; Tao, 2000; Teodoridis, 2003; Teodoridis and Kvaček, 2006; WGCPC, 1978; Walther, 1999; Wilde and Frankenhäuser, 1999; Wolfe, 1966, 1972; Wolfe et al., 1966; Yasuno, 2003, 2005; Zhang, 1976; Zhilin, 1989; Zhilin and Vikulin, 1986). Fossil fruits of *Comptonia* were recorded from the Late Cretaceous, Late Eocene, Oligocene, Miocene and late Pliocene in Russia (Budantsev, 1994), from the Miocene of Denmark (Friis, 1979), and from the Oligocene to Miocene in Germany (Mai in Mai and Walther, 1978) and elsewhere in Europe. In China, leaves of *Comptonia* were previously recorded from the Upper Eocene of Fushun (Florin, 1920; WGCPC, 1978), Yilan (Tao, 2000), Litang (Chen et al., 1983), Xiangxiang (WGCPC, 1978) and Zhangjiakou (WGCPC, 1978), from the Miocene of Chifeng (Tao, 2000), and the Pliocene of Liangcheng (Zhang, 1976).

The Weichang District is a region where clay deposits are sandwiched between late Cenozoic basalts (Teilhard de Chardin, 1927). The flora there was initially described to be composed of *Pinus*, *Carpinus*, and *Betula* and was regarded as Oligocene to Miocene in age (Depape, 1932). Based on palynological studies, Gan (1982) and Li et al. (2009) regarded the predominant gymnosperms to have grown under a warm and humid climate in the early Miocene.

In this work, we investigated the leaves of *Comptonia naumannii* (Nathorst) Huzioka collected from the Hannuoba Formation, early

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Fig. 1. Distribution of *Comptonia peregrina* in North America (grey colour) drafted according to http://www.efloras.org/object_page.aspx?object_id=5965&flora_id=1.

Miocene in age, at Meiyaoling near to Guangfayong Village, Weichang County, Hebei Province, China. Based on the data obtained from this study, we compared *Comptonia naumannii* with the extant species *C. peregrina* (L.) Coulter with respect to gross morphology and epidermal anatomy, and considered the palaeogeography of the genus. In addition, the co-occurring fruits of *Comptonia* were also investigated from Weichang.

2. Locality and stratigraphy

The studied section is situated in the Meiyaolin coal mine (42°07′ 34″N, 117°50′27″E, 1396 m high) near to the village of Guanfayong (Fig. 2). The respective sediments mostly consist of mudstone, lignite, conglomerate, and shale, are similar to those of the Wuluogong section (Hannuoba Formation), and their geological age is early Miocene (about 22.1 Ma) by K–Ar dating method (Li and Xiao, 1980).

3. Material and methods

Fossil leaves and fruits of *Comptonia* for the present study were collected from the 8th layer of the section (see Li et al., 2009), which consists of mudstone and lignite horizons. Extant materials of *Comptonia peregrina* were taken from the Peking Herbarium, Institute of Botany, Chinese Academy of Sciences, Beijing, China (No. 1341432 collected near Eastbrook, Hancock County Maine; No. 2042933 from Cape Cod Peninsula, Massachusetts; No. 1343171, collected in Middlesex County, Massachusetts). In addition, Late Eocene leaves of *C. anderssonii* Florin were studied for comparison from the collections of the Museum of Plant History of China, which is part of the same Institution (No. 153937 and 153850, from Fushun and Yilan, respectively). European fossil records have been studied during previous research activities by V. Wilde and Z. Kvaček and employed also for comparison (Kvaček, 1985; Wilde, 1989; Wilde and Frankenhäuser, 1999).

Fossil and extant leaves were prepared for light microscopy following the method described by Krings and Kerp (1997). The fruits were isolated from the sediment following the procedure of Wellman and Axe (1999).

The palaeogeographic maps were prepared from the base maps of Scotese (1997), for the Cretaceous (90 Ma), Palaeocene (60 Ma), Eocene (40 Ma), Oligocene (30 Ma), early Miocene (20 Ma), late Miocene (10 Ma), Pliocene (3 Ma), and present (0 Ma). The distribution of megafossils of *Comptonia* including fruits (endocarps) and leaves is taken from the literature of the authors.

4. Systematics

Order MYRICALES
Family MYRICACEAE Blume 1829, *nom. cons.*
Genus **Comptonia** L'Héritier ex Aiton (1789).

Species *Comptonia naumannii* (Nathorst 1888) Huzioka (1961)
(Plates I, II, III)
1888 *Comptoniphyllum naumanni* Nathorst, Paläontologische Abhandlungen, 4, p. 8, pl. 2, fig. 2.
1888 *Comptoniphyllum japonicum* Nathorst, Paläontologische Abhandlungen, 4, p. 13, pl. 4, figs. 2–3.
1932 *Comptoniphyllum naumanni* Nathorst; Endo & Morita, p. 43 (3), pl. 5(1), figs. 3–16.
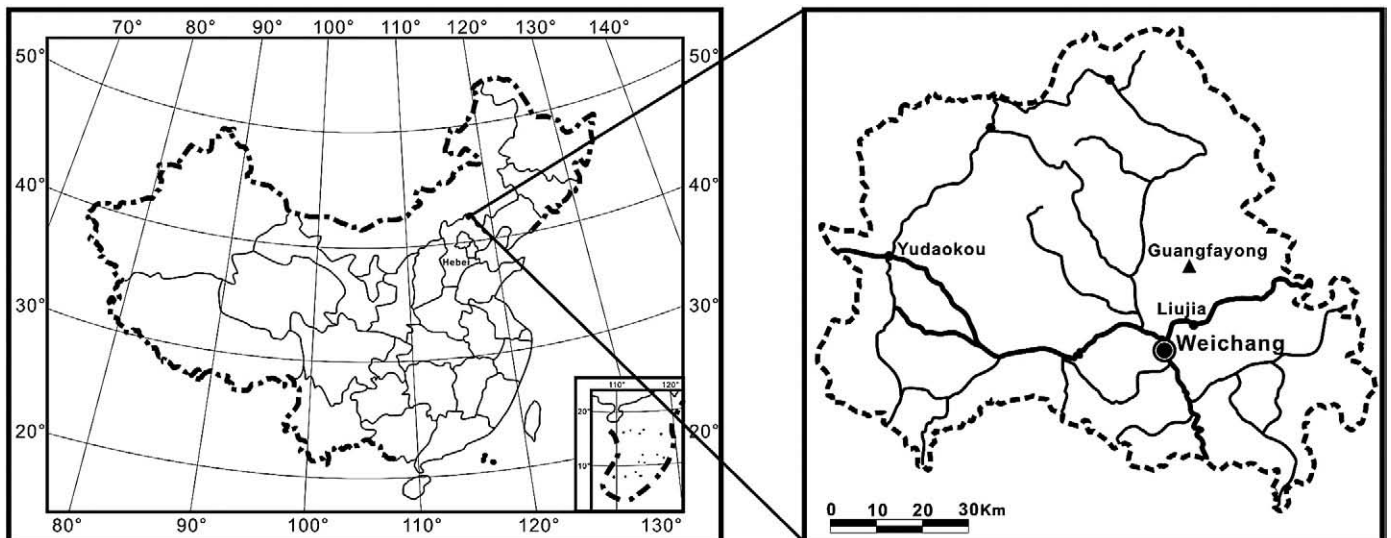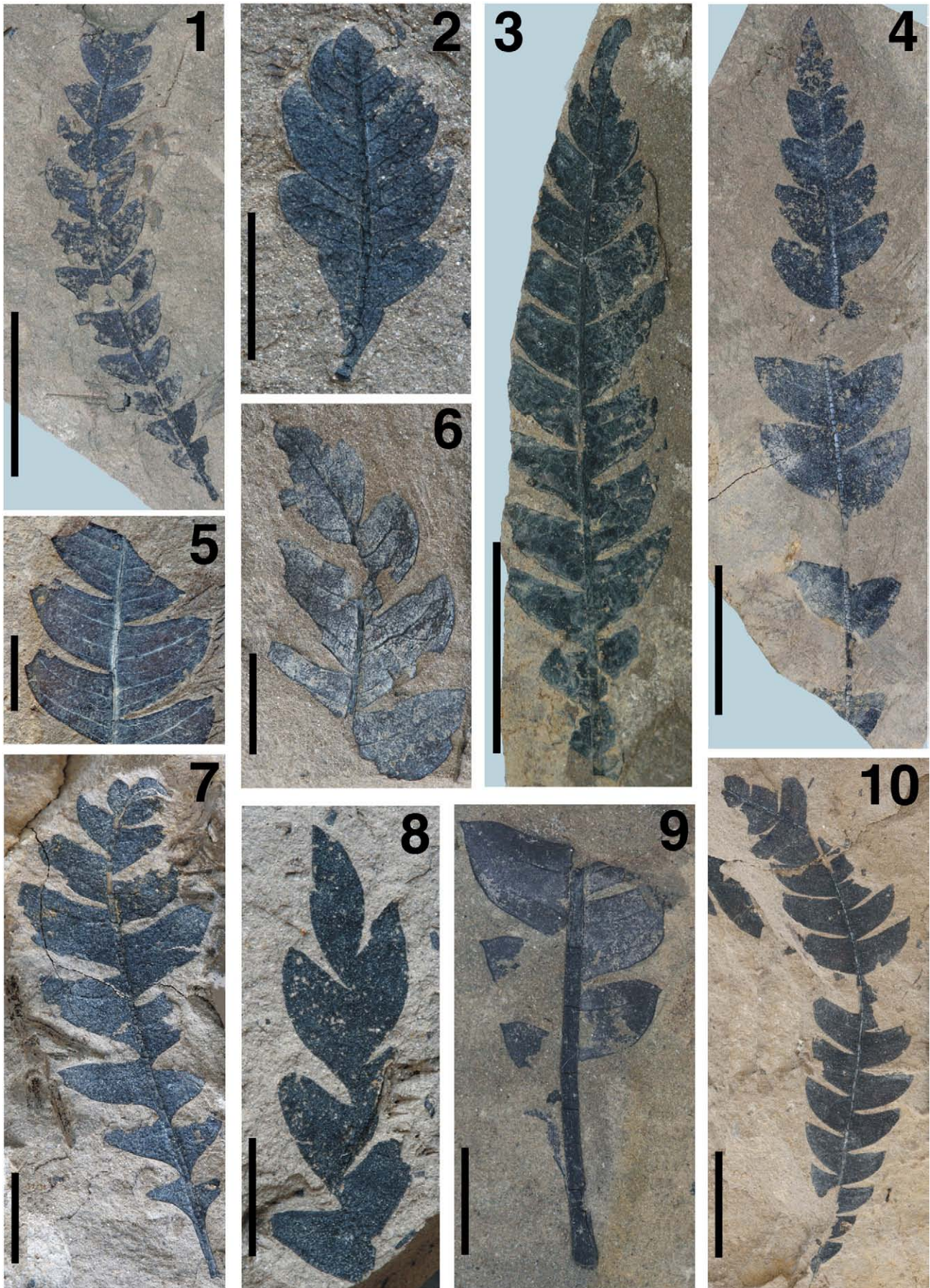1961 *Comptonia naumanni* (Nathorst) Huzioka, p. 65, pl. 3, figs. 6, 8.

Fig. 2. The map of China indicating the position of new early Miocene records of *Comptonia* at Guanfayong, Weichang (▲).

Plate I. Various leaf forms of *Comptonia naumannii* from the lower Miocene of Weichang. Scale bar: 1, 3, 4 = 1.5 cm; 2, 5–9 = 0.5 cm; 10 = 1 cm.

1961 *Myrica* (*Comptonia*) *naumanni* (Nathorst) Tanai, p. 271, pl. 5, figs. 1–3, 6–10, 13, 14, 16, 18.

1976 *Comptonia naumanni* (Nathorst) Huzioka; Iljinskaja et al., p.104, pl. 17, figs. 3, 4; pl. 51, fig. 3.

Description: leaves are simple, narrow elliptical to mostly lanceolate, 1.2–7 cm long, 0.7–1.8 cm wide. Their petioles are short, expanding towards the base (Plate I, 2, 9). Laminas are deeply lobed to dissected, with alternate to opposite lobes (Plate I). Sinuses between the lobes regularly reach the midvein. Individual lobes are triangular (Plate I, 1, 8; Plate II, 1), falcate (Plate I, 10; Plate II, 2) or rounded, and half-oval (Plate I, 2, 4, 5, 9; Plate II, 3, 4) with rounded (Plate I, 7) or acute (Plate I, 3, 5, 6 and 10) tips. Apical side of lobes is almost straight to slightly convex, and the basal side convex (Plate I; Plate II). The basal pair of lobes is sometimes shortly decurrent on the petiole (Plate I, 2, 7, 9). Venation is pinnate. Midrib is 0.4–0.8 mm wide in the middle of the leaf length and tapers towards the apex. Two to four secondary veins per lobe diverge from the midrib at an angle of 55°–85° and extend into the apex of the respective lobes (Plate I, 2, 5, 6; Plate II). Tertiary veins branch from secondary veins at an angle of 30°–48° (Plate I, 5–6).

Unicellular simple trichomes appear on both sides of leaves, about 50–120 μm long and tapering (Plate III, 1, 4), and their unicellular bases are surrounded by 7–8 cells (sometimes two of the unicellular bases fused: Plate III, 3). Glandular trichomes are capitate with the originally globular balloon-shaped head. The heads are disc-shaped compressed due to fossilisation, and 60 μm in diameter attached to a unicellular circular base. The base is 12 μm in diameter and also surrounded by 7–8 cells (Plate III, 4). Anomocytic broadly elliptical stomata are $20–25 \times 15–18$ μm in size (Plate III, 2).

Comments: Leaf shape and venation of *C. naumannii* are shared by Late Eocene *C. anderssonii* Florin (1920) from Fushun, China. Iljinskaja et al.

(1976) even attributed the latter species to *C. naumannii*. In our opinion, the leaves of *C. naumannii* are specifically distinct having a short and relatively thick petiole, while the leaves of *C. anderssonii* are characterized by a long petiole (Endo and Morita, 1932). Furthermore, the present study revealed some differences in the epidermal anatomy. Although the stomata of *C. naumannii* and *C. anderssonii* are similar (Plate III, 2, 5), the bases of the glands in the latter species are often composed of two, three, or four cells (Plate III, 6–8) while they are always single-celled in *C. naumannii*. In this case, we prefer to keep the two species separate. Leaves, described as "*Comptonia*" *difformis* (Sternberg) Berry from the Middle Eocene of Eckfeld, Eifel, Germany (Wilde and Frankenhäuser, 1999), have frequently additional secondary teeth on the lobes, and more complex bases of glands. The material from Eckfeld is also specifically different from *C. naumannii*. Leaves of *C. columbiana* Dawson from the Palaeogene of North America (Wolfe and Wehr, 1987; Meyer and Manchester, 1997) have teeth, and are different from those of *C. naumannii*.

Berry (1906) described the variability of leaves in extant *Comptonia peregrina* in detail and documented the leaves from the Cretaceous to the Miocene. He thought that the leaves of *C. naumannii* are similar to those of *C. dryandroides* Unger (1850) from Sotzka, though the leaves of the latter species are larger than those of the former and have strongly falcate lobes recalling *C. longirostris* Jarmolenko (see Zhilin, 1980) from the upper Oligocene of Ashutas Mountain. Since details of the cuticles of the two species are unknown, and *C. dryandroides* was described from the Eocene of Europe in contrast to *C. naumannii* from the Miocene of East Asia, we prefer to keep these species separate.

Apart from the above comparison, *C. naumannii* resembles in its leaf morphology *C. difformis* (Sternberg) Berry from Europe. The latter is synonymous with *C. acutiloba* Brongniart (Berry, 1906; Kvaček, 2004). Nathorst (1888) even regarded *C. naumannii* as a variety of *C. acutiloba* when describing it as a new taxon, but the former is distinguished by lobes completely separate from each other (cf. figures in Nathorst, 1888; Endo and Morita, 1932), a trait which is in contrast to the conditions found in the type specimen of *C. difformis* as figured by Kvaček and Straková (1997). Some leaves of *C. difformis* from the lower Miocene of Bohemia (Kvaček, 1998; Hably et al., 2001; Teodoridis and Kvaček, 2006; Kvaček and Teodoridis, 2007) may appear morphologically similar to those of *C. naumannii*. Nevertheless, most specimens differ from *C. naumannii* in incomplete dissection of the laminae. Leaves of *C. difformis* from the Libkovice Member in the Most Basin have globular glands with a polycellular head, which is 70 to 80 μm in diameter attached to the invariably simple rounded base (Kvaček, 1985). On the other hand, the glands of *C. naumannii* have a unicellular head (Plate III, 4). Christensen (1975) obtained similar epidermal features from the middle Miocene material from the Søby-Fasterholt area, Denmark and assigned it to the same species (*C. acutiloba* = *C. difformis*). *Comptonia* from the Oligocene of Germany is more diversified morphologically and displays subtle differences in the epidermal structure (Walther, 1999). Therefore, we prefer for the present to keep these species separate.

Species — *Comptonia tymensis* Dorofeev (1966)
(Plate V)

1994 *Comptonia tymensis* Dorofeev, Budantsev, p. 33, pl. 70, figs. 1–19.

Description: Nutlets are 3.1–5.8 cm long and 1.8–2.9 cm wide, and ovoidal, with an apex tapering into a distinct tip and a knob-like blunt scar at the base (Plate V, 1–2). External surface has 4–6 conspicuous longitudinal ribs extending from the basal scar into the apical part of the endocarp. Sometimes a shorter and less developed rib between two adjacent ribs (Plate V, 1). Endocarp with one locule and two valves separates along a marginal suture, spongy in cross section (Plate V, 2, 7). It is about 0.3–0.8 mm thick in the plane of dehiscence (Plate V, 2). Locule is oval to obovate in longitudinal section, tapering into an apical stylar canal (Plate V, 2, 7). Cells of locule surface are more or less
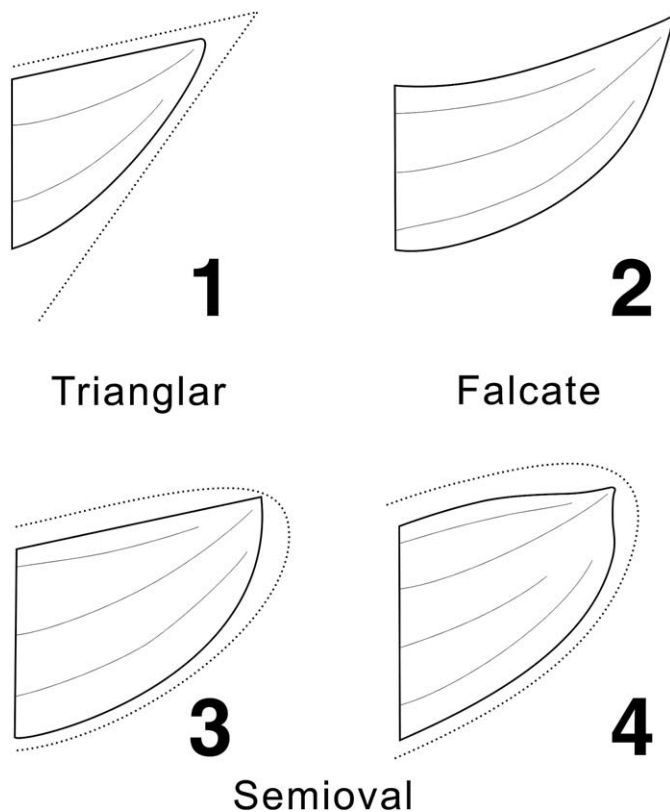

Plate II. Line drawings showing variation of lobe shape in leaves of *Comptonia naumannii*.

1.   Triangular lobe.
2.   Falcate lobe.
3-4.   Half-oval lobe. Dotted lines imply the outline of lobe.
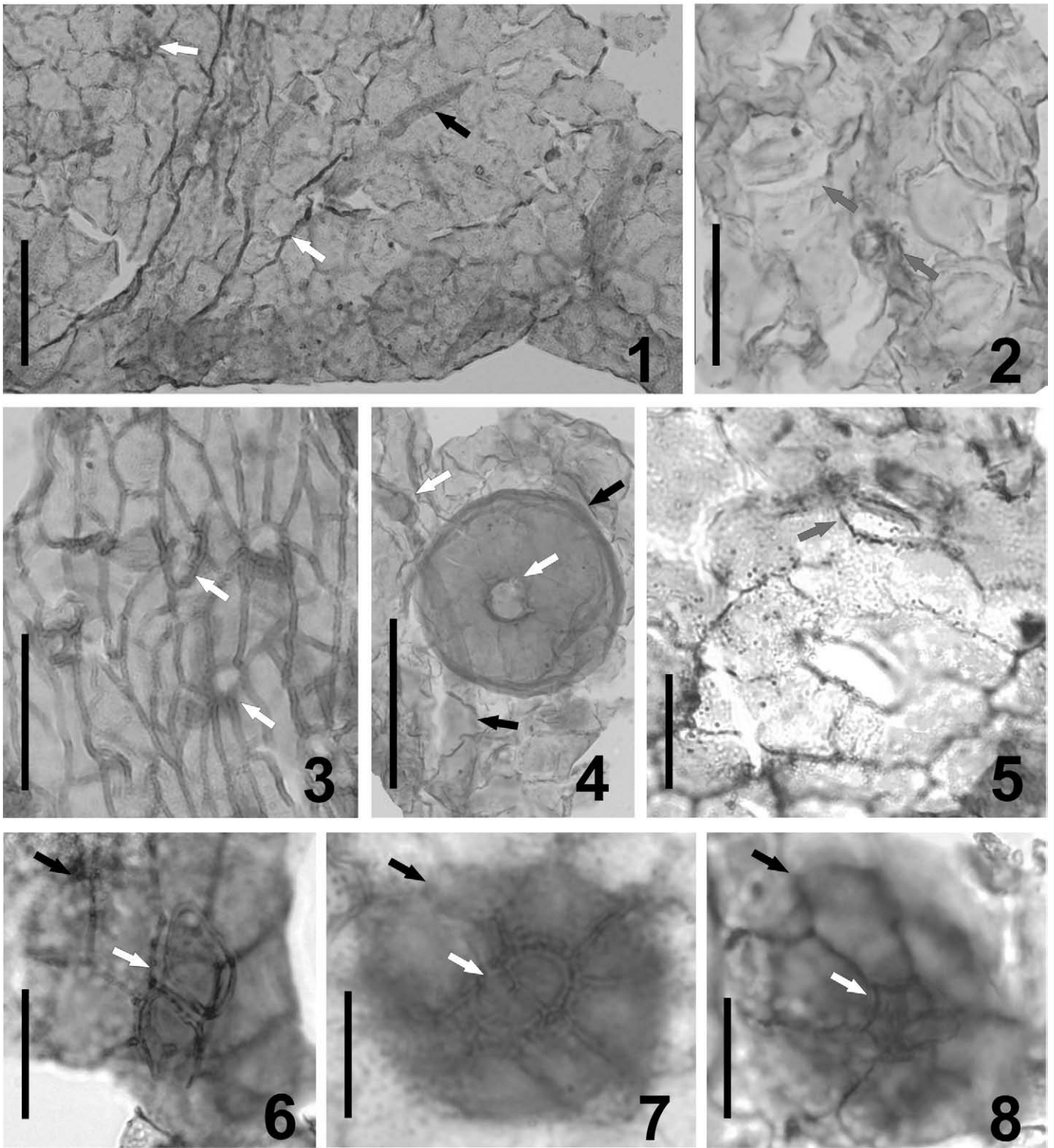
Plate III. Cuticles of *Comptonia naumannii* and *C. anderssonii*. 1–4: *C. naumannii*.

1.   Cell structure of the upper epidermis.
2.   Lower epidermis.
3.   Upper epidermis.
4.   That of lower epidermis with stomata.
5–8.   *C. anderssonii.*
5.   Anomocytic stomata.
6.   A two-celled base of the gland.
7.   A three-celled base of the gland; 8: a four-celled base of the gland. Black arrows show unicellular trichomes and a disc-shaped gland, grey arrows indicate stomata and white arrows show unicellular base of trichomes and a globular gland. Scale bar: 1, 3, 4 = 50 μm; 2, 5–8 = 25 μm.
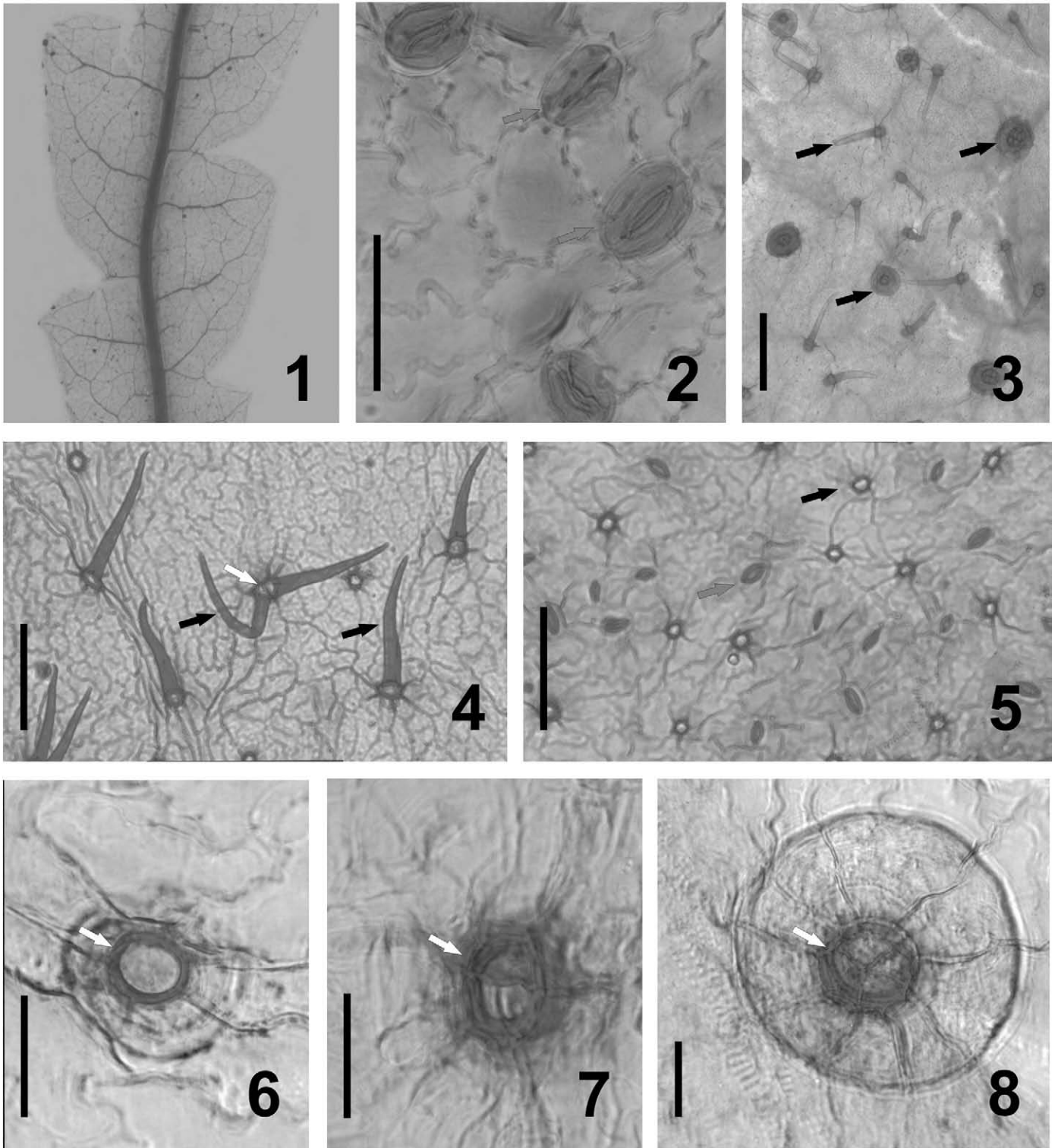
Plate IV. Details of lamina and cuticle of leaf of *Comptonia peregrina.*

1. Pinnate venation and pinnate lobes.
2. Anomocytic stomata.
3. Cellular structure of upper epidermis with unicellular trichomes and a globular ("balloon-shaped") gland.
4. Unicellular trichomes, some of them fusing together in pairs.
5. Lower epidermis with unicellular trichomes.
6. A one-celled base.
7. A two-celled base.
8. A four-celled base of globular gland. Black arrows show the unicellular trichomes and glands, grey arrows indicate stomata and white arrows show bases of trichomes and globular glands. Scale bar: 2 = 50 μm; 3 = 200 μm; 4, 5 = 100 μm; 6–8 = 25 μm.

Comptonia naumannii   other species of Comptonia
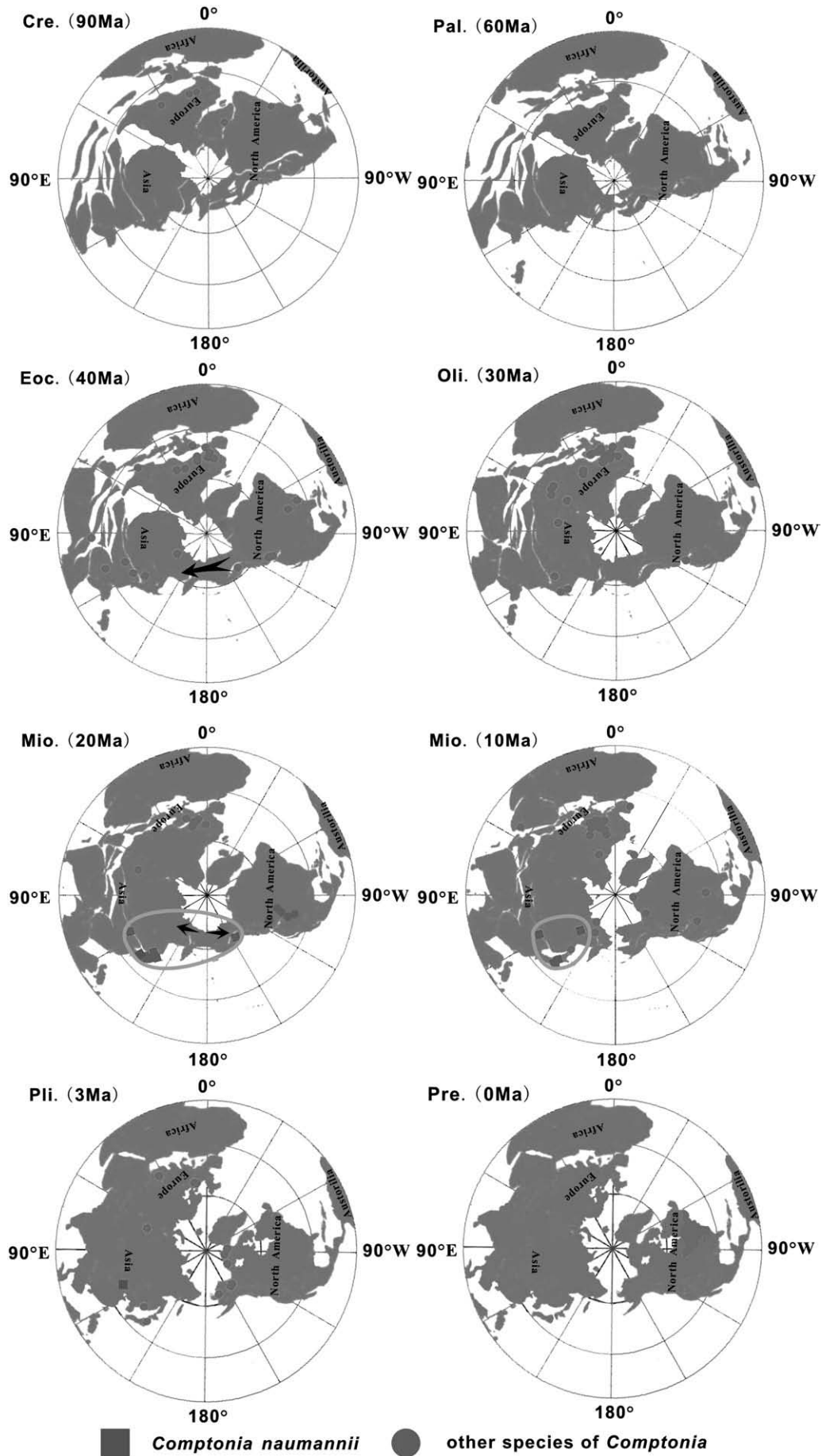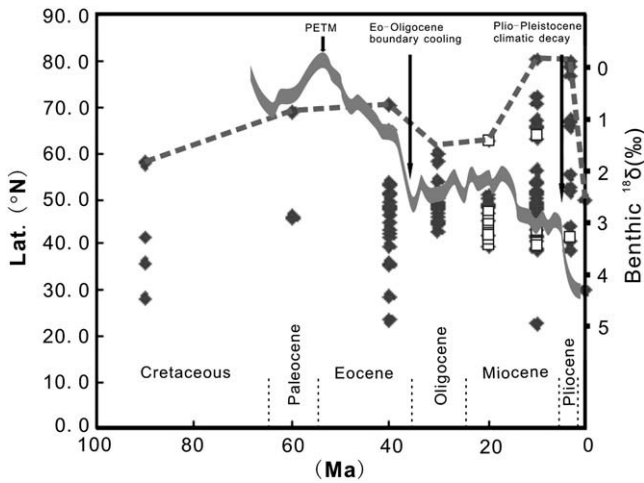
Fig. 4. Northern Hemisphere latitudinal distribution of *Comptonia* from the Late Cretaceous to the present based on fossil occurrences in our database of 131 localities. Open squares indicate sites of *C. naumannii*. Black rhombuses represent the occurrences of other species of *Comptonia*. Grey dotted line shows the maximum northern latitudinal distribution of *Comptonia* in time. Grey line reflects trend of MAT (mean annual temperature) change in Northern Hemisphere from 65 Ma to the present based on marine oxygen isotope data (Zachos et al., 2001). Major Cenozoic climatic events including the Palaeocene–Eocene Temperature Maximum (PETM), Eocene–Oligocene boundary cooling event and Plio-Pleistocene climatic decline are noted.

polygonal to rounded-polygonal, with irregular walls (Plate V, 4). Mesocarp is about 14 μm thick, consisting of two or three layers of cells (Plate V, 5). Epicarp, about 25 μm thick, consists of elongate-rectangular cells (Plate V, 6, 8). and its surface is pitted (Plate V, 3).

Comments: Except for its slightly larger size, the fruits from Weichang are similar to those of *C. tymensis* Dorofeev from the Oligocene of Western Siberia that attain at most 2.1–5.0 × 1.4–2.5 mm in size. Fruits of *C. tymensis* are different from the fruits of extant *C. peregrina* since the former are obovoidal, with the apex and base tapered (Plate V, 1–2), while the shape of the latter is ovoidal, with a rounded apex and base (Plate VI, 1). The epicarp cells of the former are square with 7 cells per 100 μm (Plate V, 8), while those of the latter are elongate-rectangular with 3 cells per 100 μm (Plate VI, 2, 3, 5). The endocarp of *C. tymensis* (Plate V, 2) is thicker (0.3–0.8 mm) than that of *C. peregrina* (ca. 0.25 mm) (Plate VI, 4, 7). Although the endocarp in both species is spongy (Plate V, 5; Plate VI, 4), the meshwork is more regular throughout in *C. tymensis* while the part next to the mesocarp in *C. peregrina* has the appearance of cotton wool (Plate VI, 4, 7).

Leaves of *C. naumannii* and fruits of *C. tymensis* were both collected from the same site in Weichang. Therefore, it is very likely that these fruits and leaves formed parts of the same natural species, but organic connection between the two still needs to be confirmed.

Fossil endocarps co-occurring with leaves of *C. difformis* are variously assigned to *C. longistyla* (Nikitin) Dorofeev, *C. srodoniowae* Friis and *C. goniocarpa* Mai (Friis, 1979; Bůžek et al., 1996; Teodoridis and Kvaček, 2006) and differ generally from *C. tymensis* in their smaller size.

5. Discussion

5.1. Relationship between Comptonia naumannii and C. peregrina

Foliage remains of *Comptonia naumannii* resemble leaves of the single extant species *C. peregrina* in most characters, like their simple, narrow elliptical to mostly lanceolate leaves with deeply dissected laminae, pinnate venation and diverging secondary veins (Berry, 1906; Plate I; Plate IV, 1), unicellular trichomes, and globular glands (Plate III, 1, 4; Plate IV, 3–8). Matsuo (1965) found that two distinct shapes of the lobes in *C. naumannii*, triangular and rounded, can also be observed in the extant *C. peregrina*. Therefore, variation in shape of the leaves and their lobes may be regarded as a character common to both the extinct and the extant species (Nathorst, 1888; Huzioka, 1961; Tanai, 1961). The globular glands of the fossil species *C. naumannii* are characterized by a consistently unicellular base (Plate III, 4), while in those of extant *C. peregrina* four-celled bases were observed in addition (Wilde and Frankenhäuser, 1999; Plate IV, 3, 8). The fact that no distinct differences between the unicellular bases of simple glandular trichomes in *C. naumannii* and *C. peregrina* can be observed may also support a close relationship between the fossil and the extant species.

5.2. Palaeobiogeographic implications of Comptonia naumannii

Leaves of *Comptonia naumannii* have been recorded in the Miocene of Japan (Nathorst, 1888; Huzioka, 1961; Tanai, 1961; Matsuo, 1965; Yasuno, 2003, 2005; Momohara, 2005), East Siberia (Iljinskaja et al., 1976), Northeast China (Tao, 2000; this study), and Alaska (USA: Wolfe et al., 1966), and in the Pliocene of Liangcheng, China (Zhang, 1976). *C. naumannii* occurred during the early Miocene both in Northeast Asia and Alaska, but was restricted to Northeast Asia in the late Miocene and Pliocene (Fig. 3). This occurrence suggests that *C. naumannii* may have migrated freely between Northeast Asia and the Alaska Peninsula during the early Miocene, but was later separated by the Bering Strait, which originated for the first time during the late Miocene (Marincovich and Gladenkov, 2001; Fig. 3).

5.3. Palaeobiogeography of Comptonia

The oldest remains of *Comptonia* is from the Albian of New Jersey; Cenomanian of Greenland, Transylvania and Bohemia; Senonian of Westphalia; and Upper Cretaceous of Novopokrovka (Berry, 1906; Budantsev, 1994). These reports, including the systematic identity of remains and their Cretaceous age, are questionable and need to be re-investigated in more detail. The genus spread throughout the Northern Hemisphere during the Palaeogene and Neogene (Arnold, 1955; Baghai and Jorstad, 1995; Berry, 1906; Budantsev, 1994; Boyd, 1985; Chen et al., 1983; Christensen, 1975; Denk et al., 2005; Dillhoff et al., 2005; Ferguson, 1998; Friis, 1979; Greenwood et al., 2005; Grímsson and Denk, 2007; Hably, 2006; Hably and Fernandez Marron, 1998; Hably et al., 2001; Huzioka, 1961; Iljinskaja et al., 1976; Ina, 2004; Kvaček, 1998; Kvaček and Walther, 2004; Mai, 1995; Manchester, 1999; McClaughry and Gaylord, 2005; McIver and Basinger, 1999; Matthews and Ovenden, 1990; Millar, 1996; Momohara, 2005; Tao, 2000; Teodoridis, 2003; Teodoridis and Kvaček, 2006; WGCPC, 1978; Walther, 1999; Wilde and Frankenhäuser, 1999; Wolfe, 1966, 1972; Wolfe et al., 1966; Yasuno, 2003, 2005; Zhang, 1976; Zhilin, 1989; Zhilin and Vikulin, 1986), but its distribution changed with the changing climate (Fig. 3). There are only a few records from the Palaeocene. With the gradual onset of cooling in the Eocene it appeared in East Asia and the western part of North America at latitudes of 20–70°N (Figs. 3 and 4). However, it moved from 70° to 60°N with the cooling climate during Eocene and Oligocene (Fig. 4). In the Oligocene and early Miocene, it was at latitudes of 39–63°N and was widespread in Asia, Europe and North America with *C. naumannii* appearing for the first time in the early Miocene of Northeast Asia and Alaska (Figs. 3 and 4). In the late Miocene some species (e.g. *Comptonia* spp. (Matthews and Ovenden, 1990)) may have migrated to high latitudes of 70–80°N with climate continuously cooling (Figs. 3

Fig. 3. Distribution of *Comptonia* during the Cretaceous to Present. "Cre.", "Pal.", "Eoc.", "Oli.", "Mio.", "Pli." and "Pre." are Cretaceous, Paleocene, Eocene, Oligocene, Miocene, Pliocene and present. Arrows show the migration directions of the genus and grey lines indicate the possible distribution of *C. naumannii*.

and 4). The area of distribution for *Comptonia* was reduced in the Pliocene due to the cooling of the climate, but some species (e.g. *Comptonia* spp. (Matthews and Ovenden, 1990)) still occurred at latitudes as high as 65–80°N (Figs. 3 and 4).

The present data may suggest that:

– the plants of *Comptonia* evolved into two eco-types after the early Miocene, one became a thermophilous plant (e.g. *C. naumannii*), while another developed cold tolerance (e.g. *Comptonia* spp. (Matthews and Ovenden, 1990)). During the period of Eocene, the thermophilous plant − *Comptonia* appeared in the high latitude (70°N) (Fig. 4), for the temperature was higher than present (Zachos et al., 2001; Fig. 4). At the Eocene–Oligocene boundary, the thermophile could not tolerate the cooling climate, and migrated southwards into mid-latitude (60°N) (Figs. 3 and 4). From Oligocene to early Miocene, the plants of *Comptonia* evolved in the cooling climatic regime and developed a new type adapted to the cooling. In the late Niogene, the thermopilous species of the genus (e.g. *C. naumannii*) still maintained their original ecological range and kept moving further south, as Global Climate became colder and colder, while the new type (e.g. *Comptonia* spp. (Matthews and Ovenden, 1990)) adapted to and tolerate the colder climate and remained at high latitudes (Figs. 3 and 4). However, the species suitable for a cold climate finally disappeared, when the extreme conditions of the icehouse climate controlled the Earth in the Pleistocene.

– *Comptonia* may have migrated into East Asia from North America via the continental connection in the Eocene (Fig. 3). Since the Turgai Strait, which separated Europe from western Siberia, acted as an effective barrier for the migration of plants (and animals) from mid-Mesozoic until Late Eocene times (Tiffney, 1985), the Bering land connection possibly remained the only route for the migration of plants between East Asia and western North America until the Oligocene. In this case, many plants (e.g. *Pseudolarix*, *Amerisinia*, *Eucommia*, *Paliurus*, and *Florissantia*) were shared by both continents from the Eocene to early Miocene (Manchester, 1999; Fig. 3).

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Plate V. Fruits of *Comptonia tymensis* from lower Miocene of Weichang.

1.	Fruits of *C. tymensis* with exposed endocarps.
2, 4.	Surface of locule.
3.	Outside of epicarp.
5.	Section of mesocarp and endocarp.
6.	Section of epicarp.
7.	The dehiscent apex of locule tapering into an apical stylar canal.
8.	Inside of epicarp. "ct", "cw", "ec", "mc", "pt", and "sc" are cuticle, cell wall, endocarp, mesocarp, pit, and stylar canal, respectively. Scale bar: 1 = 2.5 mm; 2 = 2 mm; 3, 8 = 50 µm; 4, 5 = 100 µm; 6 = 20 µm; 7 = 500 µm.

Plate VI. Fruit and its anatomy of *Comptonia peregrina*. (see on page 62)

1.	nutlet
2.	cuticle of epicarp
3.	fruit surface
4.	section of endocarp
5.	inner part of epicarp
6.	inside of endocarp
7.	section of epicarp and mesocarp. "cw", "ec", "ep", "mc", and "pp" are cell wall, endocarp, epicarp, mesocarp, and protoplast, respectively. Scale bar: 1 = 2.5 mm, 2–6 = 100 µm, 7 = 50 µm.
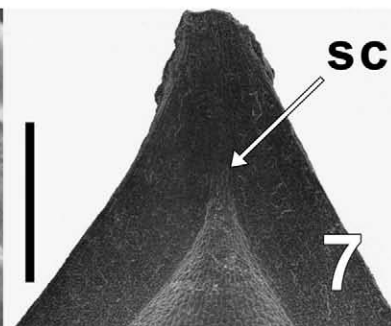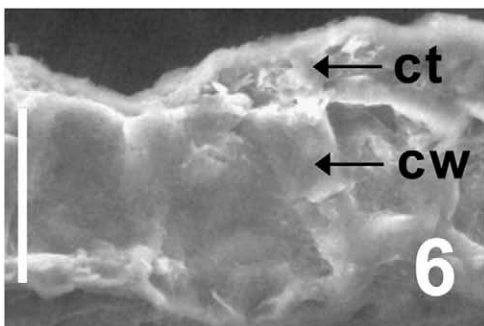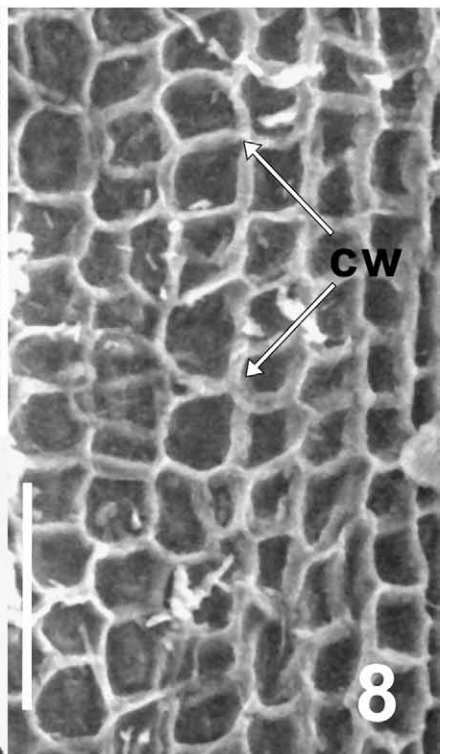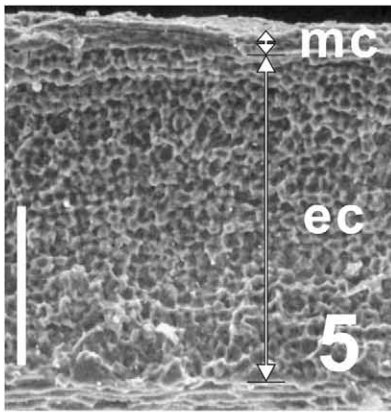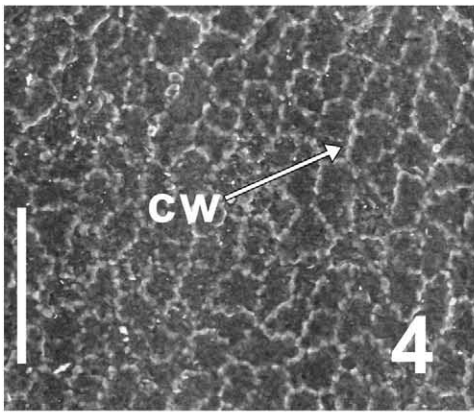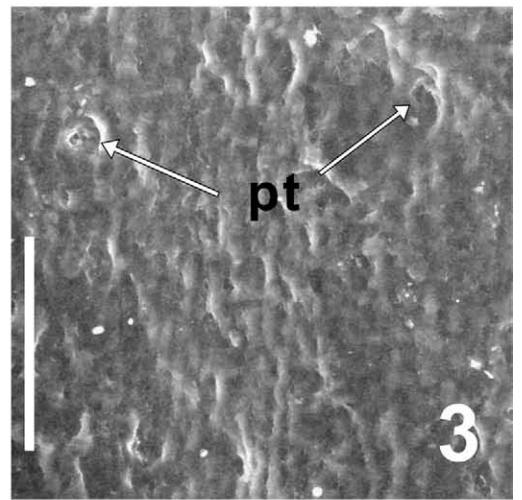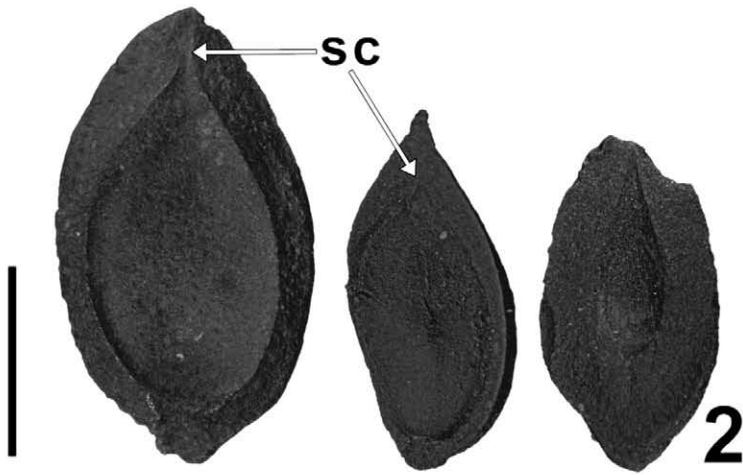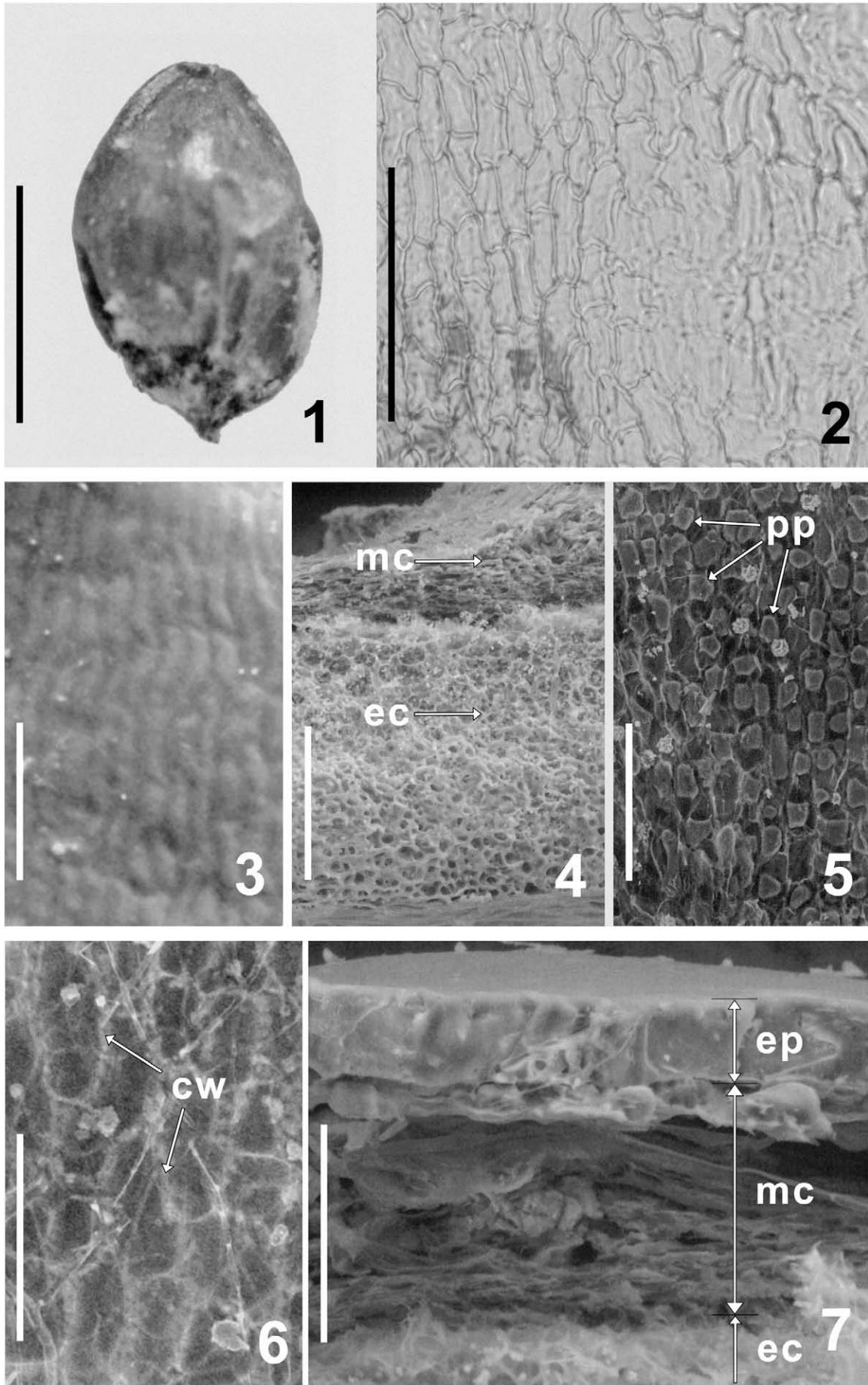
Plate V.

Plate VI. (*caption on page 60*).

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