

Fossil *Comptonia difformis* (Sternberg) Berry (Myricaceae) from the type area in North Bohemia with comments on foliage anatomy and associated fruits

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Type specimens and other material of *Comptonia difformis* (Sternberg) Berry (Myricaceae) from the Most Basin, North Bohemia, have been re-investigated in order to obtain more complete information on the leaf morphology, epidermal structure and co-occurring fruits. The history, paleoecology and comparisons with similar fossils from Eurasia and extant *Comptonia* have been discussed including additional notes on associated pollen and wood anatomy. • Key words: *Comptonia*, leaf, fruit, pollen, wood, morphology, ecology, Paleogene, Neogene, Bohemia, Europe.

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Foliage of fossil angiosperms has presented difficulties in determining natural affinities since the very beginning of scientific paleobotany. Among first fossils of this kind, Sternberg (1821, 1825) described a fossil angiosperm foliage and incorrectly assigned it to ferns as *Asplenium* or *Aspleniopteris*. Only a few years later Brongniart (1828) recognized Sternberg's erroneous interpretation and, correctly suggested this plant fossil to belong to *Comptonia* L'Hér. ex Aiton. Consequently, paleobotanists studying fossil angiosperms reported fossil foliage of the genus *Comptonia* many times. After Sternberg (1821) and Brongniart (1828) who described firstly fossil *Comptonia* from the lower Miocene of the Most Basin in the Czech Republic (see in Kvaček & Straková 1997, Kvaček 2004), this typical fern-like foliage has been recorded from sediments of the upper Cretaceous to Cenozoic of the Northern Hemisphere (e.g., Berry 1906, Florin 1920, Bůžek 1971, Rufflé 1976, Zhang 1976, Zhilin 1980, Mai 1995, Bůžek *et al.* 1996,

Manchester 1999, Tao 2000, Erdei & Rákosi 2009, Kvaček *et al.* 2015). Similarly, fossil fruits of *Comptonia* have been reported from the upper Cretaceous to Pliocene of Russia (e.g., Budantsev & Gladkova 1963, Budantsev 1994) and from the upper Eocene to Miocene of Europe (e.g., Friis 1974, 1979; Mai & Walther 1978, 1991; Mai 1997; Bůžek *et al.* 1996; Kvaček & Teodoridis 2007).

The present study is focused on the numerous records so far known from the Bohemian Massif with a particular reference to the type area of *C. difformis* in the Most Basin in North Bohemia to facilitate comparisons with those known from other sites elsewhere. We aimed at the whole plant concept of the *Comptonia difformis* plant and its paleoecology adding geological and geochemical data as well as associated plant assemblages. A wider comparison with other fossil records of *Comptonia* is only partially attempted, although some preliminary suggestions express our views on species diversity of fossil *Comptonia* in Eurasia.

Geological setting

The studied fossil material originates from Cenozoic sediments of two sedimentary basins – the Most and Cheb basins. Both basins (Fig. 1), together with the Sokolov Basin, Zittau Basin and volcanic complexes of the Doupovské hory Mts. and the České středohoří Mts., are considered primarily to be a part of the Ohře Rift (Eger Graben) one of ECRIS (European Cenozoic Rift System *sensu* Ziegler 1994) structures, located in the NW part of the Bohemian Massif (Rajchl *et al.* 2009). They arose during the Oligocene by volcano-tectonic activity. However, the main phase of their sedimentary fill ran during the early Miocene. In the case of the Cheb Basin a younger reactivation of the basin occurred during the Pliocene, when the basin was enlarged within tectonic activation of the Domažlice-Tachov tectonic structure (Špičáková *et al.* 2000).

The Most Basin

The sedimentary fill of the Most Basin (Fig. 1) started after intensive volcanic activity during the Oligocene (Střezov Formation). It was designated as the Most Formation (Domáci 1975, Mach *et al.* 2014, Matys Grygar *et al.* 2014). The oldest part of the Most Formation is represented by the Duchcov Member – a very varied formation of alluvial and proluvial sediments (up to 70 m in thickness), formed both by local, and by great regional sources (Central River – Pešek & Spudil 1986, Mach *et al.* 2014) of clastics. The Duchcov Member passes upwards into the Holešice Member (thickness up to 250 m), which is characterized by products of alluvial, swampy and local lacustrine to deltaic conditions – sands, clays, coals. The main coal seam is a dominant geologic formation of this lithostratigraphic unit. The peat-forming swamp was supplied by water and clastic material coming from South by the “Central River” (in the Žatec area) and drained northward near the Jirkov City. The clastic material, formed a system of alluvial sediments usually called the “Žatec Delta”, is splitting the main coal seam and a forming system of lacustrine delta sediments of the Bílina Delta on the top of the seam in the Bílina Mine area (Mach *et al.* 2014). The next unit – the Libkovice Member (thickness 250 m), is formed exclusively by lacustrine clays, distinguished by the content of illite-smectite clay mineral and thin phosphate rich layers (Matys Grygar *et al.* 2014). A special facies within the Lib-

kovice Member near the northern border of the basin is called the Mica (micaceous) facies. It is characterized by abundance of visible hydromuscovite in clay. Changing of lacustrine conditions led in the end of the early Miocene to the origin of another coal seam (the Lom Member – thickness 40 m) and the youngest formation – the Osek Member (thickness up to 100 m), built of monotonous lacustrine clays again. The extent of the Lom and Osek members are limited only to the deepest part of the Most Basin. Although many researchers tried to specify exactly the age of the Most Basin sedimentary fill, there are only three relevant dating milestones until now. The first one is an occurrence of the mammal fauna in the lower third to the half of the Holešice Member belonging to the MN3a zone (Fejfar & Kvaček 1993), which corresponds to the time interval of 18–20 Ma. The second one is an application of the paleomagnetic/cyclostratigraphic dating methods within the Libkovice Member (Matys Grygar *et al.* 2014), which predicted a time slice of 17.5–16.5 Ma for these sediments. These two milestones have defined the age of the Holešice and Libkovice Members to the 20–16.5 Ma time interval. Additionally, the K-Ar age data of the basanites penetrating the Holešice, Libkovice and Lom members have limited the top of the Most Formation by the time interval of 10–12 Ma (Malkovský *et al.* 1985). Unfortunately, older paleomagnetic data of Bucha *et al.* (1987) used for the Most Formation dating cannot be accepted, because they are in contradiction with new results of Matys Grygar *et al.* (2014) and the definition of the MN3a zone (see above).

The Cheb Basin

The sedimentary fill of the Cheb Basin (Fig. 1) starts with locally very limited sediments of the Staré Sedlo Formation. According to paleobotanical findings, this formation is considered to be of late Eocene age and is represented by sands, clays and coaly clays. The overlying unit is informally called the Lower Clayey-Sandy Formation. The age of this unit is estimated from the Oligocene to the early Miocene. Its distribution is irregular reaching the maximum thickness of 75 m. The main portion of sediments of this unit is formed by clayey sands to conglomerates probably of proluvial to deluvial origin. The source for these sediments were prevalently local outcrops of granites Also the so-called lower seam and some volcanic products are referred by Václ (1979) as a part of this unit. This unit passes without hiatus to an informal unit of the Main Coal

Figure 1. Position of studied samples/localities within geological units of NW Bohemia. Stratigraphic column of the Most Basin modified after (Matys Grygar *et al.* 2014). Stratigraphic column of the Cheb Basin constructed after Pešek (2010). Symbols: the Most Basin – CV (Chomutov), TU (Tušimice), KU (Kundratice, boreholes KU 115, KU 127), BM (Bílina Mine), BS (Břešťany), BZ (Břežánky), JU (Jenišův Újezd, borehole JU 399), HD (Holedeč),

Seam Formation. The dominant geological unit within this formation is the coal seam (up to 32 m thick from 50 m of the unit). Below the bottom of the seam and above its roof layers of brown kaolin clays occur. The main river bringing water and clastic material to the swamp entered the basin from its northern side and left it on the eastern side. In some areas, the coal seam is split by these river sediments. The uppermost unit of Miocene age is called the Cypris Formation. Similarly, as in the neighboring Sokolov Basin, this formation is represented mainly by lacustrine clays (thickness up to the 170 m). Monotonous lacustrine clays on some basin margins can be facially changed by coaly or sandy clays. According to stable isotope analysis of abundant carbonates and sulfates, Šmejkal *in* Malkovský *et al.* (1985) assumed higher salinity of the lake water. After 12 my lasting hiatus the youngest sedimentary unit called the Vildštejn Formation was formed. It is of late Pliocene to Pleistocene age, up to 100 m thick and the most spread unit in the Cheb Basin. It is usually divided into two subunits – the Vonšov Member (usually 8–12 m thick, up to 60 m) and the Nová Ves Member (thickness up to 80 m). Both members were formed in lacustrine to deltaic conditions from prevalently local material – kaolin clays, *i.e.*, products of neighboring granite and mica schist weathering. The Vonšov Member is usually represented by a bluish grey clay layer. The Nová Ves Member starts on its bottom from a layer of coaly kaolin clays called “overburden coal seam” covered by a layer of kaolin sandy clays. The upper part of the Nová Ves Member was deposited after a hiatus and it is represented by brown sandy clays, to sands, sandstones, gravels and conglomerates. The Pliocene formations are covered by a discontinuous sheet of Pleistocene gravels and sands. In the area of the basin and its vicinity three small Quaternary volcanic complexes are known – Železná Hůrka, Komorní Hůrka and Mýtina Maar.

Dating of the Cheb Basin has been done by the mammal fauna recovered in Dolnice and Františkovy Lázně localities. The clays from these localities are considered to being a marginal facial equivalent of the lowermost part of the Cypris Formation. Fossil mammals occurring plentifully in green clays with calcareous oncolite nodules were classified as representing the MN5 zone (15–17 Ma) by Fejfar (1974). This is in contradiction with the published paleomagnetic data of the Cypris Formation corresponding to the time interval of 17–23.5 Ma (Bucha *et al.* 1990).

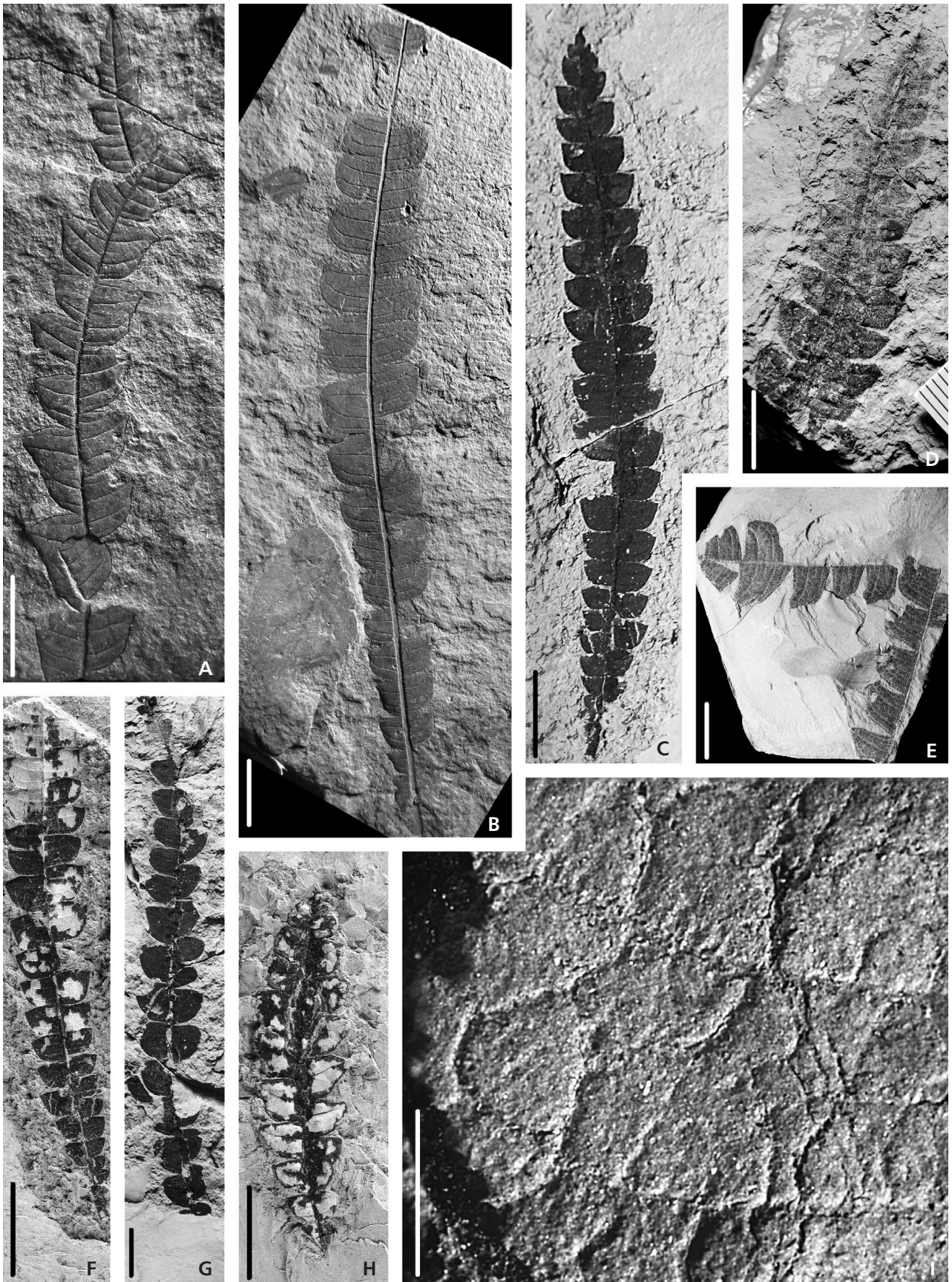
Material and methods

The studied material comprises numerous collections housed in the National Museum in Prague (NM), in the Czech Geological Survey (CGS) and the North Bohemian Mining Enterprise in Bílina (DB). A few of the samples were selected for a detailed study of geochemistry, leaf anatomy and carpology. Much effort has been laid to show variation from different sites within the type area in the Most Basin, namely Chomutov (Komotau in German), Bílina (Bilin in German), and the adjacent occurrences of *Comptonia* in the Cheb Basin and the České středohoří Mountains.

Geochemical analysis of several samples for fixing the stratigraphic position has been made to determine lithostratigraphic units of the Most Basin. The chemical composition of clay material from the sample has been analyzed by XRF method and a Cation exchange capacity method (Grygar *et al.* 2009) using Cu(II) complex with triethylenetetramine has been used to quantify the content of expandable minerals.

The leaf fossils studied are preserved both as impressions and compressions with cuticle remains preserved. Hydrofluoric acid was applied to clean inorganic particles. The lamina fragments of fossil and modern leaves of *Comptonia* were macerated in Schulze solution and immersed in 5% solution of KOH. Cuticle preparations are kept at the National Museum in Prague (NM). The fossil carpological material is compressed, carbonaceous and three-dimensionally preserved and was obtained from the drill-cores by washing. Fresh pollen of *Comptonia peregrina* (Linnaeus) J.M. Coulter was obtained from plants cultivated at the Dendrological Garden of the Silva Tarouca Research Institute for Landscape & Ornamental Gardening in Průhonice. The samples were macerated via acetolysis (Erdtman 1960) and observed in light microscope as well as electron microscope (SEM) for detailed studies and documentation. The carpological material was examined using a HITACHI S-3700N scanning electron microscope at 15 kV (NM, Horní Počernice). The comparative leaf and pollen material was partly obtained also from the herbaria of the Institute of Botany of the Academy of Sciences of the Czech Republic in Průhonice (PRA) and the carpological samples were studied from the W. Szafer Institute of Botany, Polish Academy of Sciences,

Figure 2. *Comptonia difformis* (Sternberg) Berry, leaf compressions and impressions from the Chomutov (Khomotau in German) area, the Most Basin, early Miocene. • A – apical part of leaf impression, syntype not illustrated but included in the type collection by Sternberg, NM G 7672, Chomutov. • B – lower part of leaf impression, holotype, NM G 2113, Chomutov. • C – complete leaf compression, NM G “no.55”, Tušimice. • D – apical part of leaf compression with cuticle structure (see Fig. 3C), NM G 12127 Tušimice. • E – compression of fractured leaf with cuticle structure (see Fig. 3E), NM G 12128, Tušimice. • F – lower part of leaf compression/impression with areolation details (see Fig. 2I), NM G 12047 Tušimice. • G – lower part of leaf compression/impression with cuticle structure (see Fig. 3D), NM G 12120, Tušimice. • H – complete leaf compression/impression, NM G 12125a. • I – detail of areolation from leaf compression/impression figured in 1F, Tušimice. Scale bars A–H = 10 mm, I = 1 mm.



Kraków (KRA). Currently accepted morphological terminology follows Ellis *et al.* (2009) for leaf morphology and Dilcher (1974) for fossil cuticles. Symbols and abbreviations for distinguishing vegetation storeys in environmental reconstruction and climatic parameters are: E1 (herbs and vines), E2 (shrubs and lianas), E3 (trees under 25 m high) and E4 (trees over 25 m high).

Systematic part

Family Myricaceae Richard ex Kunth

Genus *Comptonia* l'Hérhier ex Aiton

Comptonia difformis plant

The holistic concept combining detached foliage, fruits and other organs co-occurring in the same area follows suggestions to complement characteristics of fossil angiosperms from various systematically important views (Kvaček 2008). Because the organs have not been found interconnected, the fossil species based on individual organs are maintained below in the sense of the current nomenclature rules.

Comptonia difformis (Sternberg) Berry (leaves)

Figures 2–6

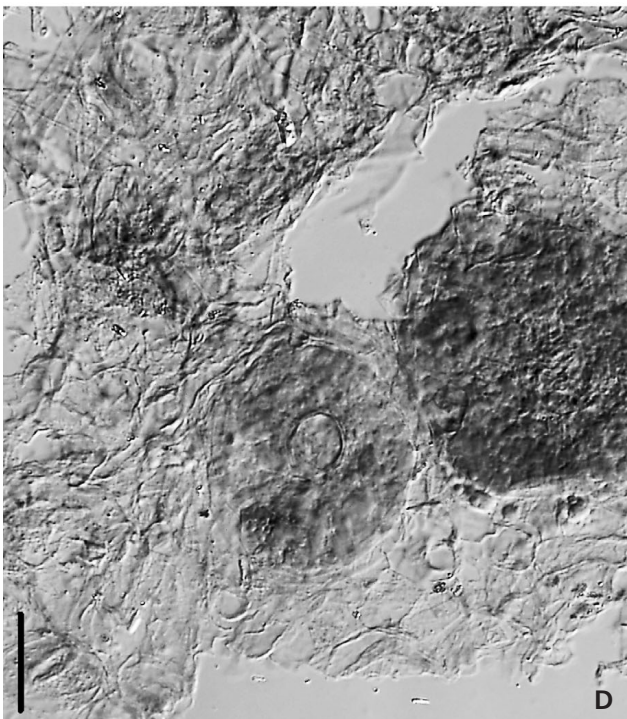
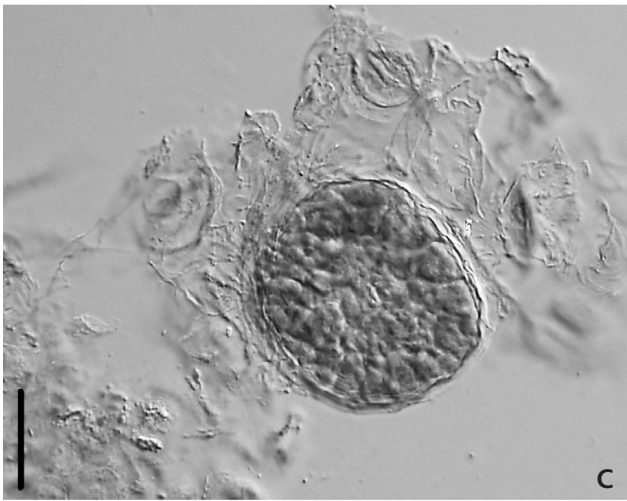
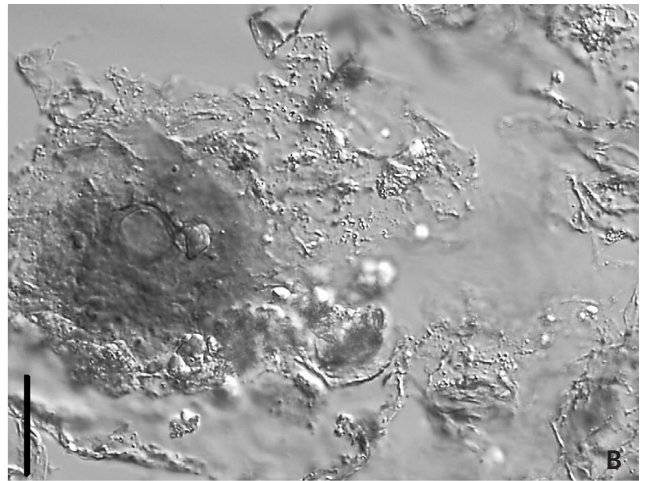
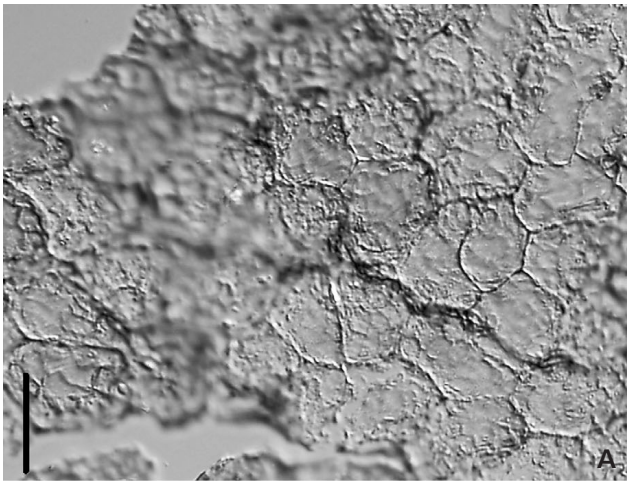
- 1821 *Asplenium difforme* Sternberg, pp. 29, 33, pl. 24, fig. 1. *nom. illegit* (non R. Brown).
- 1825 *Aspleniopteris difformis* Sternberg, p. 21.
- 1828 *Comptonia acutiloba* Brongniart, pp. 141, 143, 209. *nom. illegit*.
- 1833 *Zamites difformis* (Sternberg) C. Presl in Sternberg, p. 198.
- 1851 *Dryandra acutiloba* (Sternberg) Ettingshausen, p. 27 (735), pl. 4 (33), figs 2–3. *nom. illegit*.
- 1872 *Myrica acutiloba* (Brongniart) Schimper, p. 560. *nom. illegit*.
- 1877 *Myrica (Comptonia) tschernowitziana* Engelhardt, p. 375, pl. 4, fig. 14.
- 1877 *Myrica credneri* Engelhardt, p. 376, pl. 4, fig. 13.
- 1906 *Comptonia difformis* (Sternberg) Berry, p. 495.
- 1997 *Comptonia difformis* (Sternberg) Berry; Kvaček & Straková, pp. 12, 63, pl. 17, fig. 3.

Description. – To show diversity in the foliage record of *Comptonia difformis* we describe separately several plant populations based on the leaf morphological features within the Most and Cheb basins during the early Miocene. Similarly, the early Oligocene records from the České středohoří Mts. are separately described because they belong to chronologically separated plant populations. The treatment of the first population of *C. difformis* from the Most Basin characterized below was divided in two parts. Firstly, the holotype of the taxon from Chomutov as well as foliage from the adjacent Tušimice area characterized also by epidermal structure expand the protologue of the species. The second part of the description deals with other populations from other sites within the Most Basin based on leaves lacking preservation of epidermal features.

Foliage – population of *C. difformis* from the Most Basin (early Miocene): *Material.* – Chomutov and Tušimice areas, the Libkovice Member of the Most Formation (Sternberg 1821, p. 29, 33, pl. 24, fig. 1, as *Asplenium difforme*, Sternberg 1825, Tentamen and p. 21, as *Aspleniopteris difformis*; Zhilin 1980, p. 17, 117, as *Comptonia acutiloba*, pl. 3, figs 1–2; Kvaček & Straková 1997, p. 63, pl. 17, fig. 3, as *Asplenium difforme*), Kundratice (drill-cores KU 115/95–99.2 m depth, KU 115/90–95 m depth, KU 108/71.2–76.7 m depth, KU 127/64–69 m depth, KU 127/70–79 m depth – micaceous facies).

Description. – The holotype (Fig. 2B) see Sternberg (1821, p. 29, 33, pl. 24, fig. 1) represents a narrow obovate leaf without its apex much over 140 mm long and maximum 17 mm wide showing the pinnatifid to pinnatisect lamina dissected into alternate or opposite half oval entire-margined lobes/leaflets broadly attached to the midrib, oriented mostly perpendicularly and completely separated by sinuses reaching up to the midrib. Only in the basal part shorter lobes are slightly falcate. The craspedodromous-semicraspedodromous venation of lobes consists of the slightly curved main secondary vein reaching the lobe apex, another thicker vein curved along the margin and three thinner parallel eucamptodromous secondary and intersecondary veins. A syntype not yet illustrated from the Sternberg's collection (Fig. 2A) is the apical part of another 10 mm wide slender leaf, which ends by a narrow triangular apex, where dissections sometimes do not reach to the midrib. Newly collected compressions from the same area (Fig. 2C–I) match in gross morphology the holotype

Figure 3. *Comptonia difformis* (Sternberg) Berry, cuticle structure of leaf compressions from the Most Basin. • A – adaxial cuticle with traces of slightly curved anticlinal walls and tiny spots left by crystals, Horní Jiřetín, NM G 12130b (drill core KU 115). • B – abaxial cuticle with a glandular peltate trichome and corroded anomocytic stomata, Horní Jiřetín, NM G 12130b (drill core KU 115). • C – abaxial cuticle of compression illustrated in figure 2D showing cell structure of the peltate trichome and stomata, Tušimice, NM G 12127b. • D – abaxial cuticle with peltate trichome on unicellular base and anomocytic stoma of leaf compression illustrated in figure G, Tušimice, NM G 12129b. • E – densely hairy weakly macerated abaxial epidermis of leaf compression shown in Fig. 2E, Tušimice, NM G12128b. Scale bars = 20 µm.



but are usually smaller. Details of areolation (Fig. 2I) are similar to those of *C. peregrina* (Chevalier 1901, text-fig. 6; Fig. 9F). Adaxial cuticle (Fig. 3A) reflects polygonal straight-walled cells and a few rounded trichome bases. Dense, simple to paired (or stellate) trichomes 30–60 µm long up 5 µm thick, and peltate, disc-shaped glandular trichomes are attached to the abaxial cuticle (Fig. 3B–E). Heads of glands show in less macerated samples (Fig. 3C) numerous radially disposed ovoidal cells *ca.* 10 µm in diameter and uniseriate rounded stalks *ca.* 10–12 µm in diameter. Stomata are anomocytic, broad oval, 15–20 µm long and 15–20 µm wide, stomatal ledges thin, reaching to the poles and forming wide spindle-shaped outer stomatal cavity. The stomatal pores are slit-like.

Material. – Bílina Mine (previously Maxim Gorkij Mine – horizons Nos 1, 2, 4, 5, 33, 36, 41, 65, 66, 71), the Holešice Member of the Most Formation (Bůžek *et al.* 1992, p. 124, 128, 133, pl. 3, fig. 5, as *Comptonia acutiloba*; Kvaček *et al.* 2004, p. 118–9, figs a, d), Holedeč and Nesuchyně (Teodoridis 2002, p. 115, pl. 3, fig. 3, pl. 4, fig. 6, text-fig. 3.9), Čermníky, Dolany (Bůžek 1971, pp 41–42, pl. 9, figs 1–8), Záhoví u Žatce (Teodoridis 2003, p. 264, pl. 2, figs 11–12, text-fig. 2.15); Břeštiny Clay – exploited in former clay pits at Břeštiny (formerly Preschen in German) in the Bílina Mine area, Břežánky (Priesen in German), Jenišův Újezd (Langaujezd in German, JÚ 399/36–55 m), the Libkovice Member of the Most Formation [*Dryandra acutiloba* (Brongniart) Ettingshausen 1851, 735, pl. 33, figs 2–3; Ettingshausen 1868, p. 17, pl. 35, figs 18–26; Hably *et al.* 2001, p. 50, pl. 57, fig. 5, pl. 58, figs 1–6, pl. 59, fig. 4; *Myrica acutiloba* (Brongniart) Schimper 1870–1872, p. 560; Brabenec 1909, p. 95, text-figs 73–74], Čermníky and Dolany, Nechranice

(Bůžek 1971, pp 41–42, pl. 9, figs 1–8), Přívlaky (Teodoridis 2006, p. 167, pl. 1, figs 6, 8, text-fig. 2.15).

Description. – Leaves petiolate (Figs 4A–C, 5A–I), petiole 3 to 9 mm long, thickened at base, lamina linear to narrow elongate to obovate, rarely narrow elliptical, pinnatifid to pinnatisect, 95–140 mm long and 10–20 mm wide, base cuneate to rounded, apex acute or acuminate to truncate, segments (lobes or leaflets) opposite to alternate, per 10–25 on either side of the midrib, half oval to subtriangular, entire-margined, rarely dissected into a secondary lobe, apical segment short triangular or ovate, sometimes truncate, rarely elongate, venation of the same kind as in the holotype specimen (Fig. 5J). Aberrant reduced leaves shortly petiolate, lamina obovate, only incompletely dissected or lobed, 11–16 mm long and 6–10 mm wide, long acuminate to bluntly short acute to almost truncate at apex, cuneate or rounded, symmetrical at base (Fig. 4G, H).

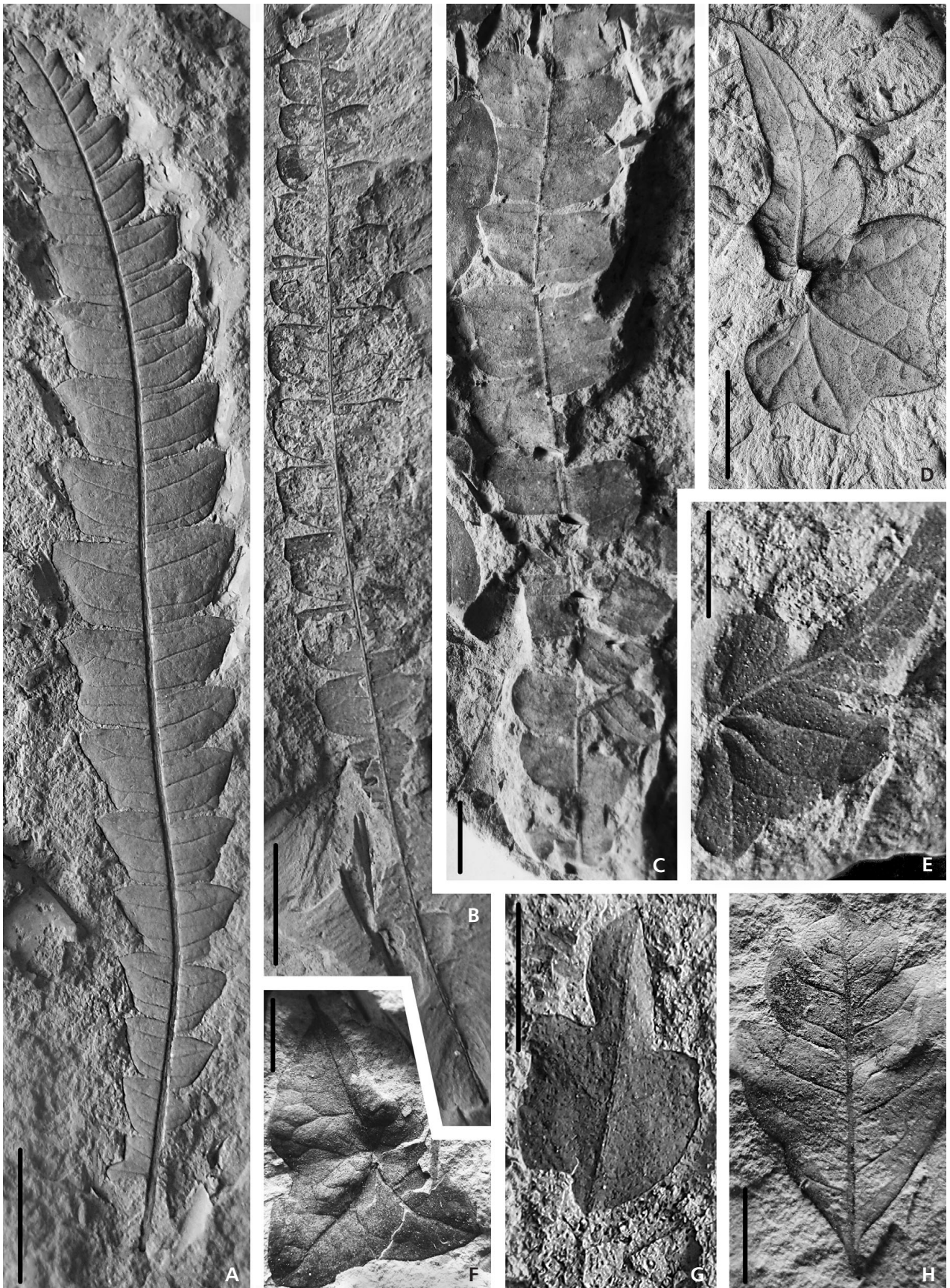
Stipules (Fig. 4D–F) co-occurring in the same area, but always detached, strongly asymmetrical, elongate, 10–15 mm long, 4–8 mm wide, sessile, semicordate, *i.e.*, deeply cordate, shallow bluntly coarsely dentate on one side and cuneate-rounded to narrow cuneate on the other side, at apex long acute, midrib straight to curved apically, secondary veins craspedodromous to semicraspedodromous, at an angle of 40–60°, fan-like disposed and curved, of variable thickness, intersecondary and tertiary veins forked and looping.

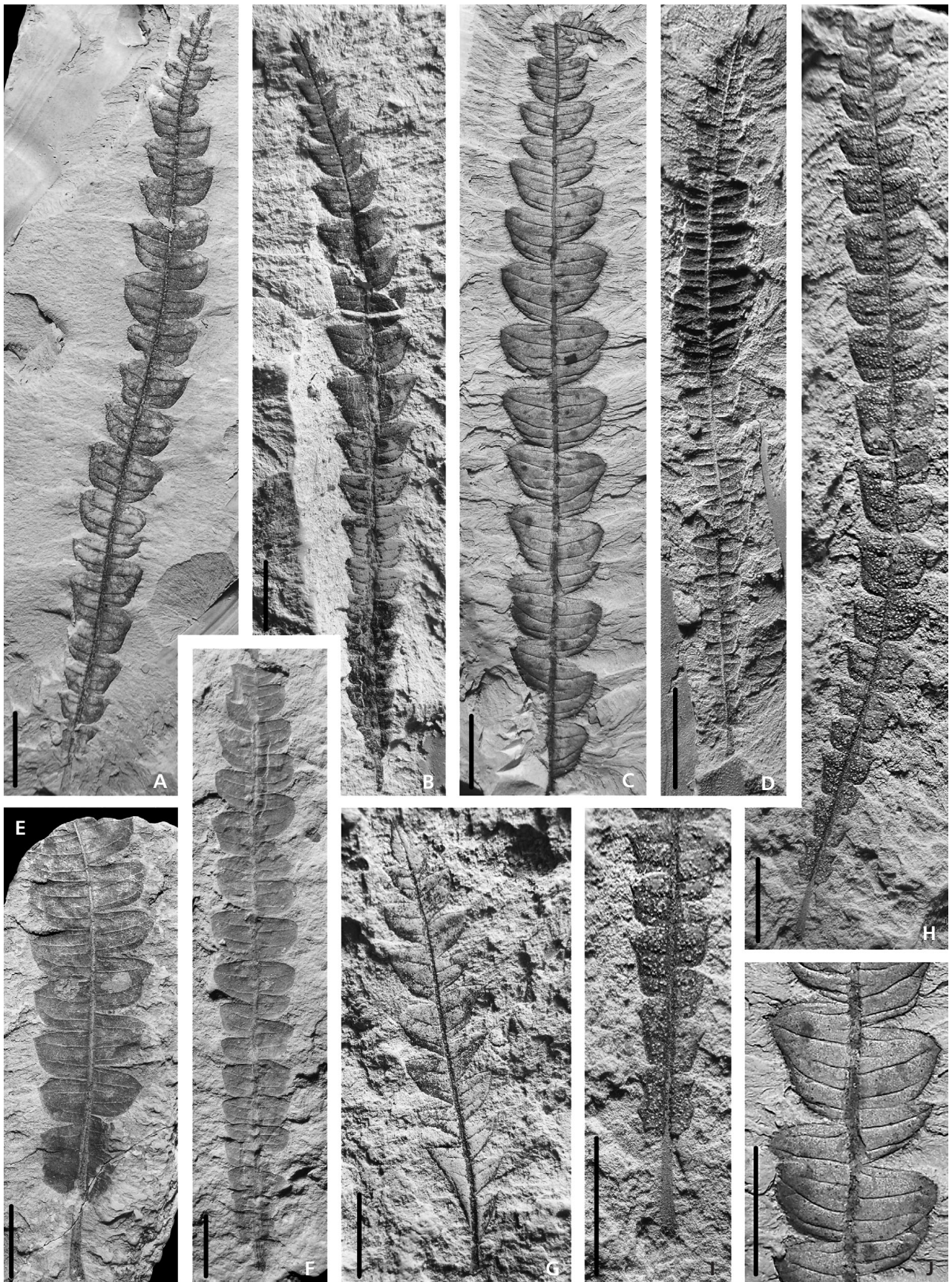
Foliage – population of *C. difformis* from the Cheb Basin (early Miocene): Material. – The Lower Clays and Sands, the Main Lignite Seam and the Cypris Formation (Bůžek *et al.* 1996, p. 16, pl. 5, figs 5–6, as *Comptonia acutiloba* Brongniart) Františkovy Lázně (core BJ1/73–75 m) and Libá u Chebu (cores 4393/62–68 m,

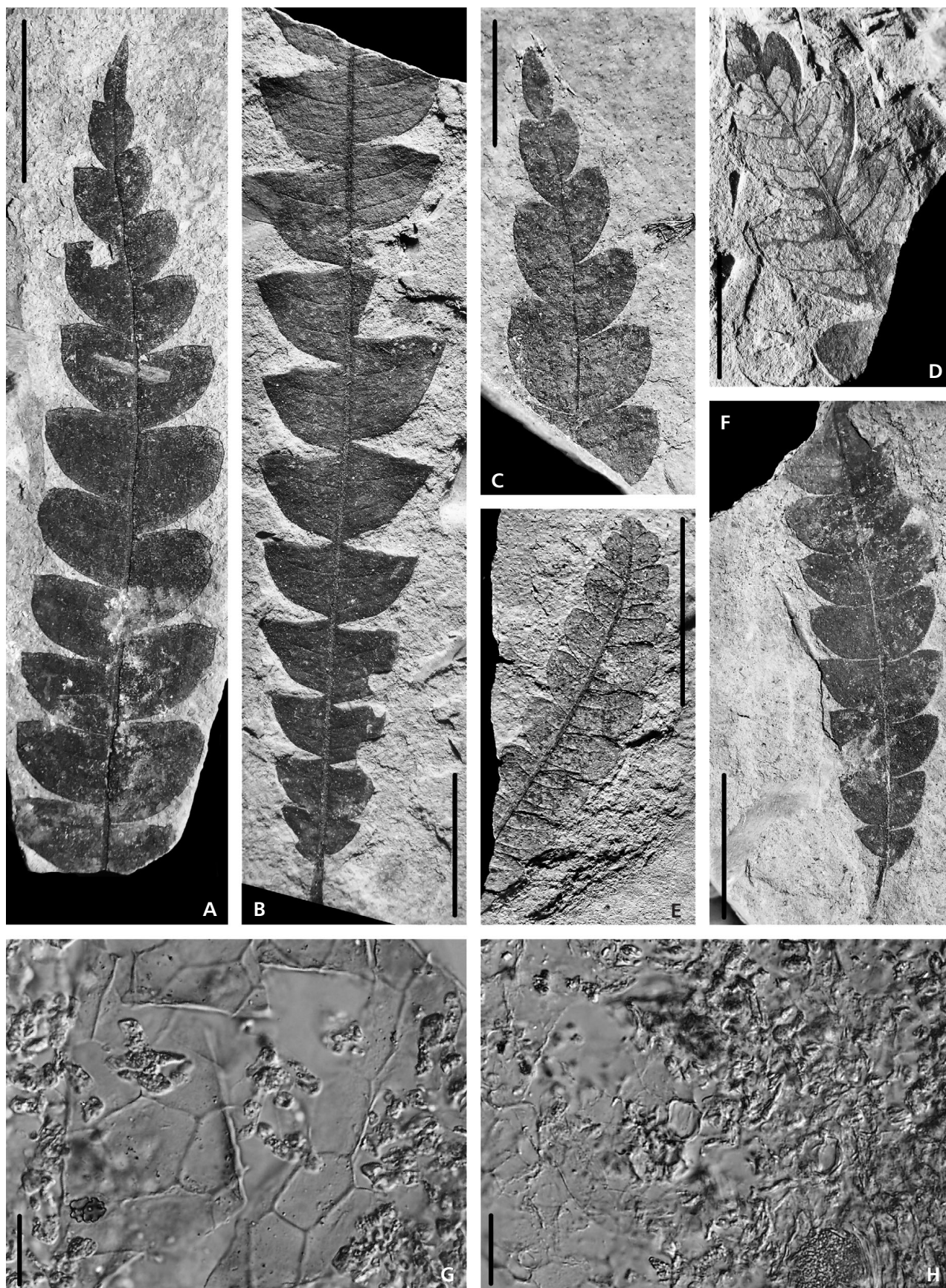
Figure 4. *Comptonia difformis* (Sternberg) Berry, impressions of leaves and stipules from the Bílina area. • A – complete leaf. • B – almost complete leaf with leaf segments shed in the basal part. • C – fragment of an unusually broad leaf. • D–F – stipules. • G–H – abnormally reduced leaves. Collections of the Bílina mine except D housed in NM G 7878 – see Bůžek *et al.* (1992, pl. 3, fig. 5). Scale bars A–C = 10 mm, D–H = 5 mm.

Figure 5. *Comptonia difformis* (Sternberg) Berry, impressions of leaves from the early Miocene Břeštiny Clay. Historical collections in NM. • A – complete leaf with distinct venation, NM G 2656. • B – complete leaf with less distinct venation, NM G 12131. • C – complete leaf impression with solitary secondary teeth on lobes, NM G 4683. • D – small complete leaf impression, NM G 2677. • E – petiolate leaf base, NM G 2616. • F – leaf impression with truncate apex, NM G 2641. • G – smaller leaf with acute apex, NM G 2636. • H, I – incomplete leaf impression with distinctly petiolate base, NM G 2626. • J – detail of figure C. Scale bars A–I = 10 mm, J = 5 mm.

Figure 6. *Comptonia difformis* (Sternberg) Berry, impressions of leaves from the Hrazený Hill, early Oligocene. • A – incomplete leaf with elongate apex, CGS. • B – lower part of petiolate leaf, NM G 2826. • C – leaf apex, CGS. • D – leaf apex with insect traces, NM G 2831. • E – upper part of a small leaf with short apex, NM 2987. • F – petiolate leaf base, CGS. • G – adaxial cuticle with straight anticlinal walls NM G 11502b. • H – abaxial cuticle showing rounded peltate glandular trichome on simple base, NM G 11502b. Scale bars A–F = 10 mm, G–H = 20 µm.







4395/58 m); HV 11/88–93 m, HV 19a/78–79 m, V 3a/75–76.5 m, D 7 23.5–24.3 m, A 28/91–92 m, A 42/18–19 m (the Cypris Formation).

Description. – The fragmentary specimens recovered in this population differ from the normal foliage of *C. difformis* known from the Most Basin in narrower and longer lobes (Bůžek *et al.* 1996). The newly obtained only poorly preserved epidermal structure shows polygonal epidermal cells 15–20 µm in diameter with straight or slightly curved anticlinal walls and peltate glandular trichomes with simple stalks 10 µm in diameter and 50 µm large heads. The structure of stomata has not been discerned.

Foliage – population of *C. difformis* from the České středohoří Mountains (early Oligocene): Material. – Hrazený Hill (Pirskenberg in German) at Knížecí near Šluknov (Kvaček *et al.* 2015, pl. 6, fig. 6, pl. 13, figs 1–8).

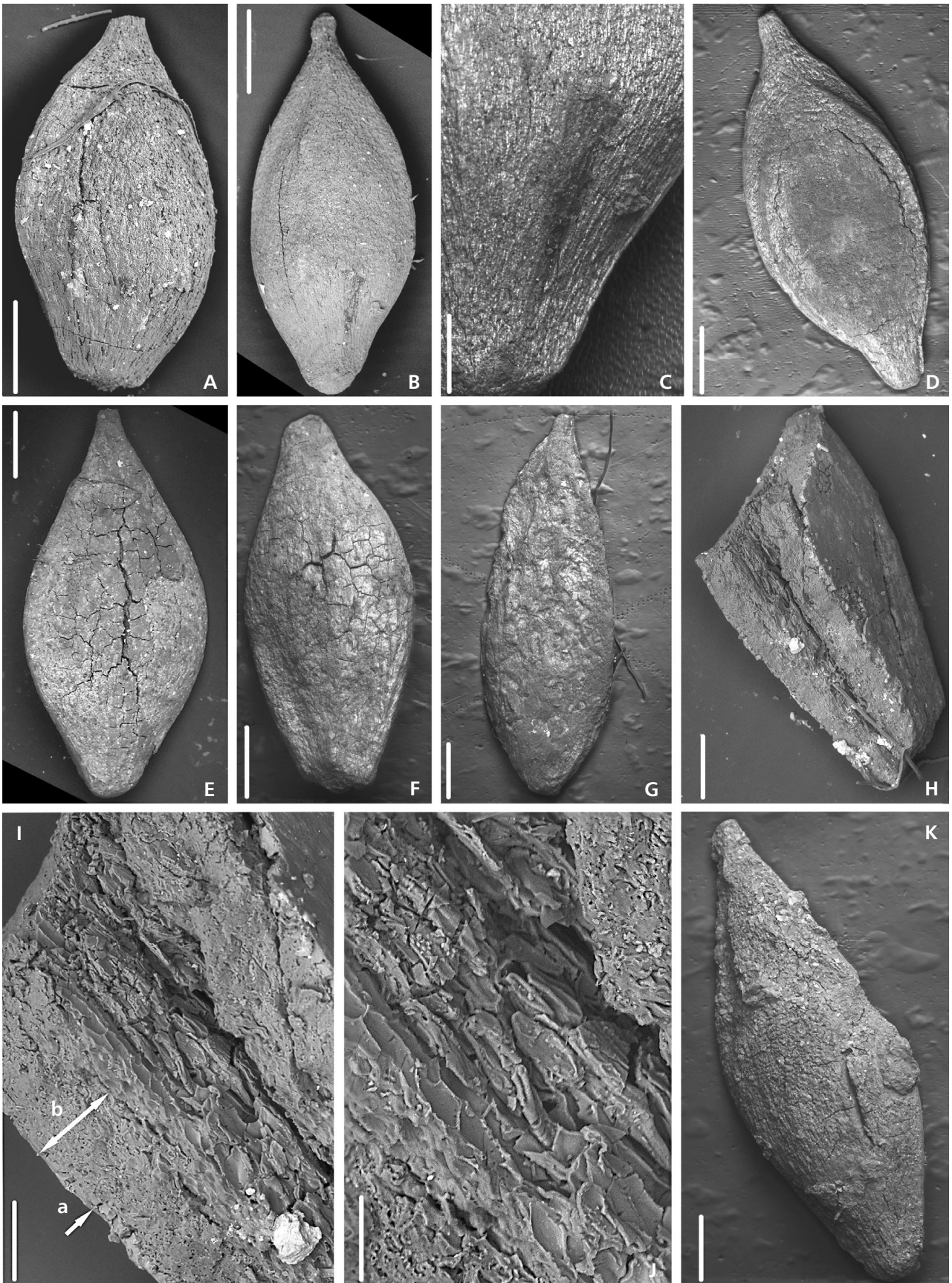
Description. – Leaves linear to narrow elongate to oblong (Fig. 6A–F), 21–80 mm long and 3–16 mm wide, acuminate at apex, abruptly cuneate at base narrowing to a short petiole stout at base (Fig. 6B, F), lamina pinnatifid to pinnatisect, segments (lobes or leaflets) opposite to alternate, entire-margined, more than 14 on either side of the midrib, sessile, obliquely oval to shortly triangular on the leaf base, blunt or rounded and mucronulate at apex, venation craspedodromous to semicraspedodromous, 2–8 secondary veins entering each segment, three of them thicker, stretching to margin, one of them entering the segment apex, the other looping near the margin. Epidermal anatomy fragmentarily preserved (Fig. 6G–H). Adaxial cuticle smooth, showing outlines of cells ca. 20–25 µm in diameter, demarcated by almost straight to wavy anticlinal cell walls, abaxial cuticle thin, hairy, showing glandular trichomes with occasionally attached disc-shaped glandular heads ca. 50 µm in diameter on short simple stalks ca. 12 µm in diameter (Fig. 6H).

Discussion. – The above-described leaf material from the Czech Republic can be assigned to *Comptonia difformis* (Sternberg) Berry on the basis of typical pinnately lobed leaves with entire-margined lobes and conforms in epidermal anatomy with the lower Miocene material from the

type area. It differs from most other European Paleogene records of *Comptonia* foliage (*e.g.*, Andreánszky 1955, Hably 2010, as *Comptonia acutiloba* var. *serrata*; Kvaček & Hably 1991, as *Comptonia dryandroides*), which have usually, but not always (*e.g.*, Kovar 1982), serrate lobes.

Foliage of *Comptonia difformis* as described above matches in general both gross morphology and epidermal anatomy of the records from the Miocene of Denmark (Christensen 1975, as *C. acutiloba*) and Weichang (Liang *et al.* 2010, as *C. naumannii*). Different species of *Comptonia* have been distinguished in the European Paleogene and Neogene on account of gross morphology such as *C. dryandrifolia* Brongniart, which is typified from the Oligocene of Armissan (S France) and synonymised with *C. schrankii* (Sternberg) Berry described from the Oligocene of Häring in Austria (Ettingshausen 1853, Butzman & Gregor 2002, Erdei & Rákosi 2009) or known from Geiseltal in Germany (Rüffle 1976) and Csordakút in Hungary (Erdei & Rákosi 2009). Recently *C. dryandrifolia* was transferred into subg. *Avushia* by Zhilin (1980). It differs in very long and narrow leaves dissected in numerous (up to 50) lobes (Zhilin 1980, p. 16). Foliage of the same subgenus described as *C. yakovlevii* (Palibin) Takhtajan (= *Dryandra yakovlevii* Palibin) from the Cenomanian of the Nackichevan – Aush area (Zhilin 1980, p. 18) differs from the previously mentioned *C. schrankii* by teeth on lobes. Another species with serrate leaf segments is known from the Palaeogene of North America as *C. columbiana* Dawson (Wolfe & Wehr 1987, Meyer & Manchester 1997). Some Oligocene records from Kazakhstan were attributed to *C. longirostris* Jarmolenko (Zhilin 1980) due to long narrow leaf segments. Other kind of foliage from the Paleogene of Kazakhstan [*Comptonia carakulensis* (V. Baranov) Zhilin] was assigned to *Dryandra* by Makulbekov (1977). Leaf impressions assigned to *Comptonia oehningensis* A. Br. or *Myrica vindobonensis* (Ettingshausen) Heer (syn. *Dryandra vindobonensis* – Ettingshausen 1851) described from Oehningen in Germany were rarely recorded also in the North Bohemian Miocene (Bůžek *et al.* 1996). The foliage differs in the lamina incompletely dissected into fewer lobes and a long decurrent base. In none of the above mentioned species the epidermal anatomy is known to help confirming the antici-

Figure 7. *Comptonia srodoniowae* Friis, carbonaceous and three-dimensionally preserved fruits from the Cheb Basin, early Miocene. • A, B – almost complete endocarp with typical sharp stalk and distinct suture of dehiscence at the basal part, NM G 8240 (Dolnice, testpit D2, 12,8–13 m). • C – detail of figure B. • D – almost complete endocarp with typical stalked base and acuminate apex (fragment of style), NM G 8241 (Dolnice, testpit D2, 12, 8–13 m). • E – incomplete endocarp NM G8242a (borehole H 13, 25 m, the Cheb Basin). • F – incomplete endocarp with distinct suture of dehiscence, NM G 8242d (borehole H 13, 25 m, the Cheb Basin). • G – incomplete endocarp with rounded base, NM G 8242e (borehole H 13, 25 m, the Cheb Basin). • H – fragment of endocarp showing the anatomical structure, NM G8242c (borehole H 13, 25 m, the Cheb Basin). • I – detail of the figure H showing: “a” layer of very compressed cells resembling mesocarp, “b” several compressed layers of cells building inconspicuous and compact structure of the endocarp’s wall. • J – detail of the figures H and I, showing the inner part of the endocarp covered by oblong and polygonal cells with straight walls. • K – almost complete endocarp with acute apex and stalked base, NM G8242f (borehole H 13, 25 m, the Cheb Basin). Scale bars A, B, D–G, K = 500 µm, C = 200 µm, H 250 µm, J = 50 µm.



pated affinity to *Comptonia*. So far no associated stipules have been observed.

Because of delicate nature of cuticles, the epidermal anatomy of fossil *Comptonia* has been rarely described. Besides the records mentioned above (Christensen 1975, Liang *et al.* 2010) more details are known only from the Eocene of Geiseltal. Ruffle (1976, p. 346, pl. 44, figs 1–12, pl. 63, figs 6–12) described from a leaf, which was not shown among macrofossils, an epidermal pattern recalling that from the Miocene of North Bohemia in straight-walled adaxial epidermis with stellate trichomes but differing in poorly preserved abaxial cuticle with papillae. Wilde & Frankenhäuser (1999) described from Eckfeld as “*Comptonia*” *difformis* (Sternberg 1825) Berry 1906, emend. based on numerous narrow leaves with serrate lobes partly half separated from each other and epidermal anatomy different from our material by four-celled attachment of glandular trichomes.

C. naumannii from the Miocene of China (Liang *et al.* 2010) has a similar epidermal structure with that described in the present paper. However, the European and Chinese Miocene foliage differ in subtle details in gross morphology: lobes of *C. naumannii* are invariably falcate and less regular. Other distinctions given by Liang *et al.* (2010), *e.g.*, incomplete dissection of leaves in *C. difformis*, may not be valid in view of the expanded characteristics of *C. difformis* presented here from the type area. Comparing *C. difformis* and its extant relative, Kotlaba (1961) noticed a larger size of foliage in the fossil population from the Břešňany clay contrary to *C. peregrina*. This preliminary observation requires a more extensive biometrical study, which is beyond the scope of the present paper.

As noted by Christensen (1975), the leaf epidermal structure of the recent *C. peregrina* does not differ much from that of *C. difformis*. We confirm his observations that the size of cells in recent *Comptonia* may in the mean exceed the dimensions of the fossils from Denmark as well as the Bohemian Miocene. In the adaxial cuticle of *C. peregrina* the anticlinal walls tend to be undulate and trichomes are more common (Fig. 9G). Pubescence on the abaxial leaf side varies in the recent as well the Miocene material, but simple and paired trichomes in *C. peregrina* are more robust (Fig. 9H). Stipules of *C. difformis* do not deviate

in form from recent *Comptonia* (see Chevalier 1901, text-fig. 8). Reduced small leaves noted from the Bílina Mine (Fig. 4G–H) may have grown near the base of the leaf shoots or on aborting branches before winter season, as it happens in recent *Comptonia peregrina* (see Macdonald 1981; Fig. 8E). Further records of *C. difformis* are known from the European Oligocene, *e.g.*, Hrazený, previously Pirskenberg (Knobloch 1961, Kvaček *et al.* 2015, this paper) and Kleinsaubernitz (Walther 1999).

Comptonia srodoniowae Friis (nutlets)

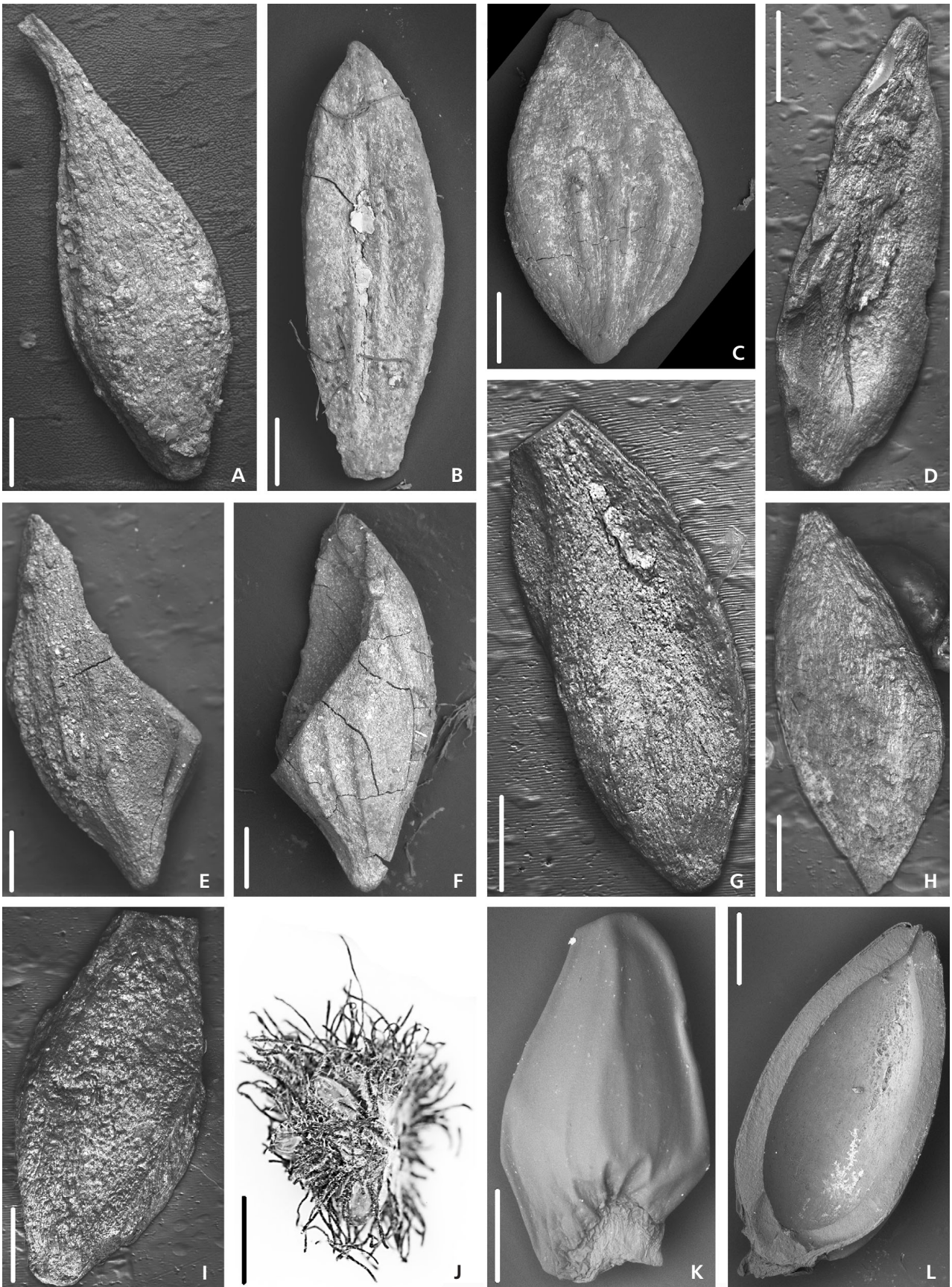
Figures 7, 8A–I

- 1974 *Comptonia longistyla* (Nikitin) Dorofeev; Friis, p. 264, fig. 1g–i.
- 1979 *Comptonia srodoniowae* Friis, p. 124, fig. 6a–l.
- 1985 *Comptonia srodoniowae* Friis, p. 37.

Material. – The Cheb Basin (the Lower Clay and Sand, the Main Lignite Seam and the Cypris Formation, drill core D 2/9.6–9.8 m, 12.8–13.5, 13–13.5 m, D 10/98–98.2 m depth, V 12/90.8–91 m depth, H 13/25 m depth as *Comptonia srodoniowae* and *C. cf. srodoniowae* in Bůžek *et al.* 1996, p. 16, pl. 5, figs 7–10); the Most Basin (the Libkovic Member of the Most Formation – Kundratice KU 127/70–71 m, 64–66 m, 68–69 m depth, KU 115/98.5–98.6 m depth, partly as *Comptonia goniocarpa* Mai and *Comptonia longistyla* (Nikitin) Dorofeev in Teodoridis & Kvaček 2006, p. 94, fig. 2k–l).

Description. – Endocarp one-loculed, two-valved with dehiscence along a marginal suture, elongate to ovoid in outline, often secondarily flattened, 1.8–(2.9)–4.0 mm long and 0.8–(1.2)–1.9 mm wide, apex acute or often acuminate into style, style fragmentary and often curved (Fig. 8A), up to 0.78 mm long, base widely cuneate to rounded, rarely narrowed in a sharp stalk (Fig. 7B, D), suture of dehiscence distinct from the keeled edge to the style (Fig. 7B–C); external surface poorly preserved, 2–6 poorly distinct relatively short longitudinal ribs extending from the basal scar into the medial rarely to apical part of the endocarp (Fig. 8B–C, E–F). Locule oval to obovate in longitudinal section. The wall (Fig. 7H–I) is constructed by

Figure 8. *Comptonia srodoniowae* Friis, carbonaceous and three-dimensionally preserved fruits from the Cheb and Most basins, early Miocene. • A – almost complete endocarp with acuminate and curved style, NM G 8243 (borehole V 3, 61–62 m, Cheb Basin). • B – elliptic endocarp with conspicuous longitudinal ribs and acute apex. NM G 8484 (drill core KU 127). • C – almost complete ovate endocarp with widely cuneate base and conspicuous ribs, NM G 8485 (drill core KU 115). • D – incomplete ovate endocarp with inconspicuous ribs, NM G 9999c (drill core KU 127). • E, F – incomplete one-loculed, elliptic endocarp with conspicuous ribs and cuneate base, NM G 9999b (drill core KU 127). • G – incomplete ovate endocarp with inconspicuous ribs, NM G 9999f (drill core KU 127). • H – almost complete elliptic endocarp with inconspicuous ribs and cuneate base, NM G 9999e (drill core KU 127). • I – incomplete endocarp with inconspicuous ribs and cuneate widely base NM G 9999a (drill core KU 127). *Comptonia peregrina* (Linnaeus) J.M. Coulter, KRAM–P, Nova Scotia, Halifax. • J – round bur-like cluster of fruit. • K – complete nutlet with conspicuous longitudinal ribs and distinct stalk at base. • L – one-locule ovate nutlet. Scale bars A–I = 500 µm, J = 5 mm, K–L = 1 mm.



a relatively distinct outer part probably consisting of two or three layers of very compressed cells (0.85 µm thick) that may represent fragments of mesocarp (Fig. 7I arrow “a”), an inner part with several compressed layers of cells showing inconspicuous and compact structure 200 µm thick (Fig. 7I arrow “b”), cells oblong and polygonal, 38 to 68 µm long, 4 to 8 µm wide, cell walls straight (Fig. 7J).

Discussion. – The above-described endocarps/nutlets morphologically correspond to the genus *Comptonia* based on their typical shape and unilocular condition. As we mentioned above, the genus includes only one extant species of *C. peregrina* that shows almost identical morphological and anatomical character, but the endocarps are bigger than the studied fossils, i.e., 3.3–(4.3)–5.2 mm long and 2.0–(2.5)–2.8 mm wide (see Table 1, Figs 8J–K, 9A–B).

Generally, the fruits are round bur-like clusters (9–20 mm in diameter) containing 8–15 ovoid nutlets nestled among the bur-like bracts (see Fig. 8J). However, this kind of bracteate cluster of *Comptonia* fruits is not known in fossil record. The nutlets of *Comptonia* are known only from the lower Miocene of the Cheb and Most basins and were originally described as *Comptonia srodoniowae* Friis, *C. cf. srodoniowae* Friis (Bůžek *et al.* 1996), *C. goniocarpa* Mai and *C. longistyla* (Nikitin) Dorofeev (Teodoridis & Kvaček 2006). The size, shape and character of the upper surface, mainly the number and character of the longitudinal ribs, are the most important diacritic morphological features to determinate the *Comptonia* nutlets at the specific level (Table 1).

The Bohemian material is mostly incomplete, but seems to be coherent in size (Table 1) and shape of the endocarps. However, the material suffers from relatively poor preservation of the upper surface, mainly in the case of the record from micaceous facies that often does not allow determining the number and character of the longitudinal ribs. Friis (1979) defined her new species of *C. srodoniowae* based on 100 endocarps from the middle Miocene flora of Damgaard and included there the previous finds from FASTERHOLT assigned to *C. longistyla* (Friis 1985). The main differences between both species are in a large variation in size and shape and in having generally shorter and higher ribs in *C. srodoniowae* (Friis 1979, p. 127).

Dorofeev (1966, 1969), Dorofeev in Budantsev (1994) and Nikitin (1976) described 17 different species of *Comptonia* from the Paleogene and Neogene of Belarus, Lithuania and Russia (for summary see Table 1). Focusing on morphological character of these fruits/endocarps from the former Soviet Union and the material described from the European Paleogene and Neogene (i.e., *C. longistyla*, *C. srodoniowae* and *C. goniocarpa* Mai) presented in Table 1, *C. longistyla* (Dorofeev 1966, Mai & Walther 1991, Dorofeev in Budantsev 1994, Mai 1997) and *C. srodoniowae* show the closest morphological affinity to our studied material.

Bůžek *et al.* (1992) excluded the affinity of the endocarps from the Cheb Basin to *C. longistyla* due to the absence of the keeled edge on the outer dehiscence suture and the presence of the higher number of very long ribs on the endocarps. These important features are characteristic of endocarps of *C. srodoniowae*, however they are not mentioned in the species diagnosis by E.M. Friis even if they are clearly visible and figured there (e.g., Friis 1979, Fig. 7D–G). The endocarps of G8240a and G8043 showing relatively long attenuate and curved fragments of the style may correspond with *C. longistyla* (Figs 7E, 8A); however, the number and shape of the ribs and the character of the dehiscence suture match better to *C. srodoniowae*. Also, an incomplete endocarp (G8485 – Fig. 8C), originally described as *C. goniocarpa* by Teodoridis & Kvaček (2006), is of that form.

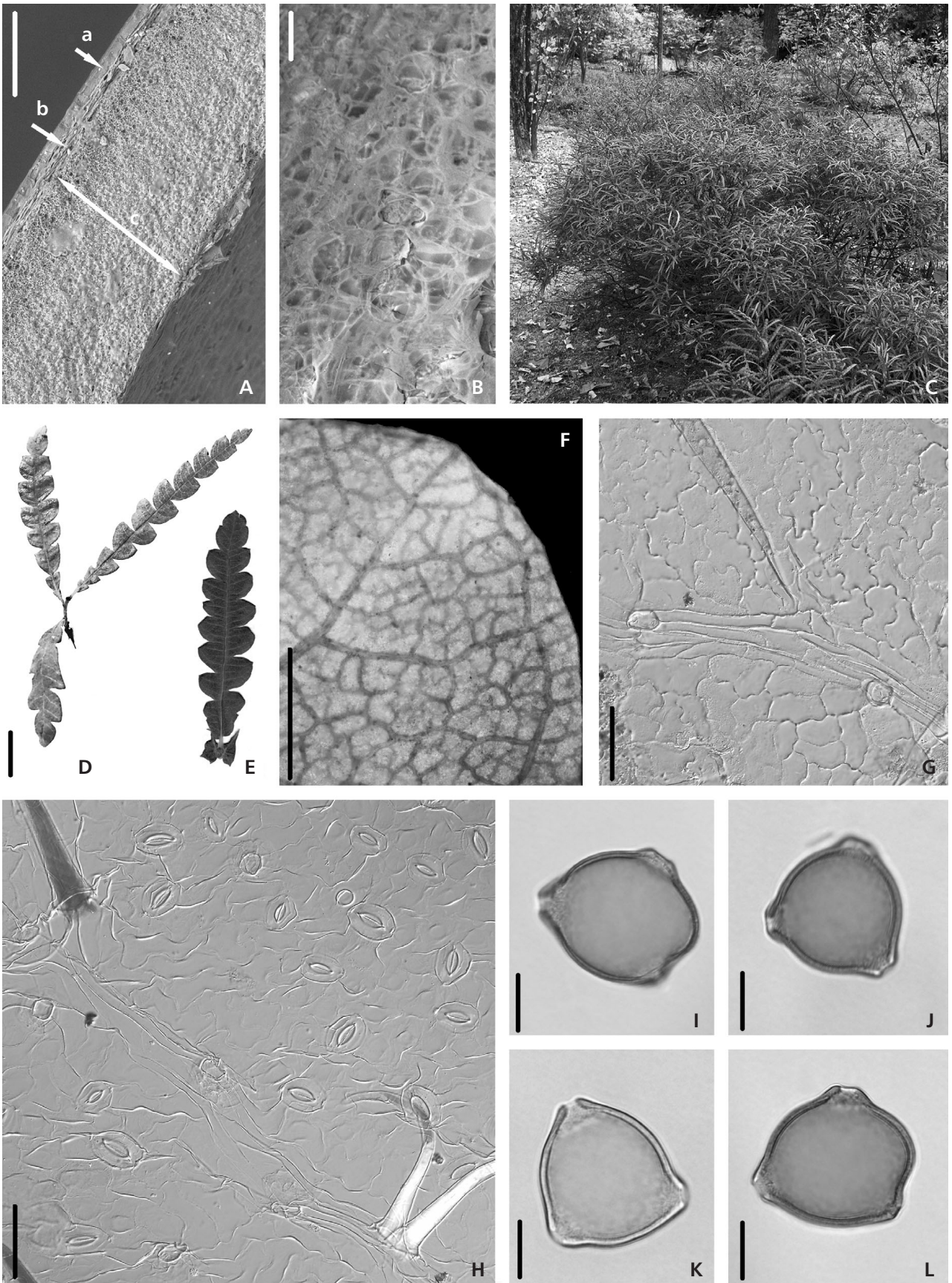
The endocarps of *C. longistyla* investigated from the upper Oligocene to lower Miocene of Germany by Mai (Mai 1997; Mai & Walther 1978, 1991) are morphologically very close to our material and most probably belong to *C. srodoniowae*. Recently, Liang *et al.* (2010) described slightly larger fruits from the lower Miocene of Weichang that are very similar to those of *C. tymensis* Dorofeev from the Oligocene of Western Siberia.

Discussion

Comments on *Comptonia* pollen

According to Wodehouse (1935), the pollen grains of *Comptonia* are more or less flattened, about 27 µm in

Figure 9. *Comptonia peregrina* (Linnaeus) J.M. Coulter, KRAM-P, Nova Scotia, Halifax. • A – detail of figure 8L showing cross-section of nutlet wall with anatomical structure: “a” pericarp consisting of compact cells layers, “b” mesocarp built by several layers of cells, “c” endocarp showing inconspicuous and compact structure of several compressed layers of cells. • B – detail of figure 8L showing inner part of endocarp covered by oblong and polygonal cells. • C – a deciduous shrub growing in the Arboretum of Kostelec upon Černými Lesy. • D – a branch of leaves with typically pinnatifid to pinnatisect leaf lamina. • E – persisted leaf shoots on leaf resembling the fossil stipules (source Minnesota Wildflowers website). • F – detail of well-developed leaf areolation. • G – adaxial cuticle with undulate anticlinal walls and simple trichome base. • H – abaxial cuticle showing uniseriate trichome on simple base and anomocytic stoma. • I–L – triporate pollen grains with protruding pores and visible atrium. Scale bars A = 150 µm, B = 50 µm, D–E = 10 mm, F = 1 mm, G, H = 20 µm, I–L = 10 µm.



diameter, having 3 very often 4 or rarely 6 pores – circular apertures (3.5 µm in diameter), which are slightly more protruding than in those of *Corylus* and *Betula*. Pores are very often irregularly arranged (in contrast to *Myrica*) and they can be placed into one hemisphere. The linear thickenings – arci – are not present (in contrast to *Alnus*). In spite of the Wodehouse's (1935) observations, the pollen grains of modern *Comptonia* pollen that we studied are predominantly 3-porate, rarely 4-porate and only some of them have pores irregularly arranged (Fig. 9I–L). Pores are slightly protruding, having atrium, which is also developed in *Myrica* and *Carpinus*.

Eleven species of *Comptonia* were distinguished by Gladkova (1965) based on palynological studies from Western Siberia. Kedves (1974, 1992) redefined all species of Gladkova to three morphogenera: *Triatriopollenites*, *Labraferoidaepollenites* and *Alabroidaepollenites*, and emphasized their botanical affinity to Myricaceae and Juglandaceae (Table 2). In agreement with the description of the genus *Myricipites* by Wodehouse (1935) Grabowska et Wazynska (in Stuchlik et al. 2009) re-classified one of the Gladkova's species as *Myricipites peregriniformis* (Gladkova) Grabowska & Wazynska. The authors mentioned the similarity to living *Comptonia peregrina*. *M. peregriniformis* is characterized as Arcto-Tertiary (warm-temperate) element, very sporadically found from the early Oligocene to middle Miocene in central and south-western Poland (Stuchlik et al. 2009). Frederiksen (1979) discussed the similarity of *Triatriopollenites subtriangulus* (Stanley) Frederiksen and modern *Comptonia* pollen, e.g., character of polar areas, rounder outline of the grain, but also mentioned that all Gladkova's species have a thicker exine. Later Frederiksen (1980) mentioned that he could not see many differences between recent pollen of *Gale palustris* (i.e., *Myrica gale*) and *Comptonia peregrina* and he grouped similar specimens from the Eocene of the Jackson Group to *Triatriopollenites propirus* (Frederiksen) Frederiksen. Pollen of *Myrica* can be distinguished from that of *Betula* and *Corylus* types by comparing the porus structure (Erdtman 1943, Blackmore et al. 2003) and the scabrae of *Betula* and *Corylus*, as in other Betulaceae, are arranged on short ridges. Sundberg (1985) also characterised Myricaceae as stenopalynous family with pollen similar to those of Betulaceae. He claims that the pollen of the *Comptonia* type may be identified with certainty, however, no details on its characteristics are given.

Myricaceae are widespread in the Neogene of the Czech Republic, but the pollen of *Comptonia* has not been detected or determined there as such so far. However, Konzalová (1976, p. 17, pl. 3, figs 5, 8–12) described pollen from the Coal Seam Formation (Holešice Member of the Most Formation in Chomutov and Žatec area), which may correspond to *Comptonia*. The pollen

measures 30–35 µm in diameter, and has an irregular number of pores with one often in subequatorial position. A summary of the occurrences and distribution of Myricaceae pollen in the Bohemian Cenozoic is shown in Table 3.

Comments on *Comptonia* wood

The wood anatomy of modern *Comptonia* was partly presented by Chevalier (1901) and Youngken (1919) in their general monographic works on Myricaceae. Muhammad (1984) mentioned it also in a paper dealing with a special type of “scalaroid” perforation plates.

The most comprehensive overview of wood anatomy of the Myricaceae including *Comptonia* was done by Carlquist (2002). The wood of *Comptonia* is described there as follows (Carlquist 2002, p. 25): “Vessels narrow, scattered among tracheids. Vessel elements short. Perforation plates mostly simple, mean number of bars very low. Tracheid length intermediate. Tracheid wall thickness varies with position in growth rings. Apotracheal diffuse, diffuse-in-aggregates, occasionally scanty vasicentric; strands composed of about four long cells, none subdivided into cuboidal cells. Multiseriate rays few, short, lacking sheath cells, Heterogeneous Type IIB. Uniseriate rays more common than multiseriate rays. Crystals absent.” According to present day's accepted terminology, the above mentioned “tracheids”, which represent all imperforate tracheary elements in Myricaceae with the exception of two species of *Myrica* Linné (Carlquist 2002), must be called “fibres with distinctly bordered pits” (see IAWA Committee 1989, feature 62); and “heterogeneous rays type IIB” roughly corresponds to the “body ray cells procumbent with mostly 2–4 rows of upright and/or square marginal cells” (see IAWA Committee 1989, feature 107). The wood of *Comptonia* is unique within Myricaceae in having narrowest and most densely spaced vessels, which are also short with mostly simple perforation plates or only very rarely scalariform with 1 to 3 bars (Carlquist 2002, Table 1). Moreover, *Comptonia* has no crystals and shows a higher proportion of rather short uniseriate rays. This uniqueness, especially the elevated vessel density, may be related to its habitats, which are probably among the driest for Myricaceae as *Comptonia* “thrives in dry sterile soil” (Youngken 1919, p. 393) and the higher number of small vessels would better resist embolism in times of drought (Carlquist 2002).

The fossil record reveals several woods related to the Myricaceae, especially to the genus *Myrica*, but not any wood connected to *Comptonia* (see in Gregory et al. 2009, Inside Wood 2004–onwards). This can be explained by its shrubby character, but also by the fact the *Comptonia* wood shows a rather unspecific combination of characters, which

Table 1. Fruit characters of fossil and extant *Comptonia*.

Reference	Stratigraphy and location	Morphology of endocarps		
		Length [mm]	Width [mm]	Shape and character of upper surface
Dorofeev (1966, 1969)	Miocene (Russia, E Siberia)	28–46	13–26	elliptic, ribs 3–7 conspicuous
Nikitin (1976)	early Miocene (Russia, E Siberia)	19–25	11–14	elliptic, ribs conspicuous
Dorofeev in Budantsev et al. (1994)	late Eocene (Russia, E Siberia)	21–25	13–16	elliptic, ribs thin with spicules
Dorofeev (1966), Dorofeev in Budantsev et al. (1994)	early Pliocene (Belarus)	40–50	22–30	ovate, 3–9 ribs conspicuous
Dorofeev (1966), Dorofeev in Budantsev et al. (1994)	Miocene (Russia, E Siberia)	38–51	23–32	elliptic to ovate, no ribs or 1–3 low ribs
Nikitin (1976)	early Miocene (Russia, W Siberia), middle Miocene (Russia, E Siberia)	15–20	8–10	fusiform or guttiform, no ribs
Mai (1997), Mai & Walther (1978, 1991)	late Oligocene to Early Miocene (Germany)	30–55	20–40	ovate to fusiform, inconspicuous ribs
Dorofeev (1966), Dorofeev in Budantsev et al. (1994)	Oligocene (Russia, W Siberia)	32–67	18–38	elliptic to cylindrical, 5–12 ribs
Dorofeev in Budantsev et al. (1994)	Oligocene (Russia, E Siberia)	22–39	13–25	elliptic, 3–5 conspicuous ribs
Dorofeev (1969), Dorofeev in Budantsev et al. (1994)	early Miocene (Russia, E Siberia)	31–42	19–26	ovate to elliptic, 2–3 inconspicuous ribs
Dorofeev in Budantsev et al. (1994)	Miocene (Russia, W Siberia)	25–33	13–15	fusiform, 5 conspicuous ribs
Dorofeev in Budantsev et al. (1994)	Miocene (Russia, E Siberia)	20–27	9–17	fusiform to ovate, elliptic, 3–5 conspicuous ribs
Dorofeev in Budantsev et al. (1994)	early Miocene (Lithuania)	24–27	15–18	ovate to elliptic, 1–3 short ribs
Dorofeev (1966), Dorofeev in Budantsev et al. (1994)	Oligocene (Russia, W Siberia) to Miocene (E Siberia)	14–33	8–30	fusiform or guttiform, 3–5 conspicuous ribs
Mai & Walther (1991), Mai (1997)	late Oligocene to Early Miocene (Germany)	14–23	8–19	fusiform or guttiform, 3–7 conspicuous ribs
Dorofeev in Budantsev et al. (1994)	Miocene (Russia, E Siberia)	25–44	14–24	ovate to elliptic, inconspicuous ribs
Friis (1974, 1979)	Middle Miocene (Denmark)	20–44	8–21	guttiform to fusiform, conspicuous ribs, often high
Bůžek et al. (1996), Teodoridis & Kvaček (2006)	early Miocene (Czech Republic)	18–40	8–19	elongate to ovoid, 2–6 short ribs
Dorofeev in Budantsev et al. (1994)	Oligocene (Russia, W Siberia)	24–41	16–25	ovate to elliptic, 5–7 conspicuous ribs
Dorofeev (1966), Dorofeev in Budantsev et al. (1994)	early Miocene (Russia, W Siberia)	18–32	13–17	elliptic to ovate, thin 1–6 ribs
Dorofeev (1966), Dorofeev in Budantsev et al. (1994)	Oligocene (Russia, W Siberia)	21–50	14–25	widely ovate, 3–5 conspicuous ribs
Liang et al. (2010)	early Miocene (China)	31–58	18–29	ovate, 4–6 conspicuous ribs
Friis (1979), FNAEC (1997), personal observation	recent (USA, Canada)	31–52	21–33	ovate, conspicuous ribs

makes difficult its recognition in fossil record. Kruse (1954) described a wood from the lower Eocene of Wyoming as *Myrica scalariformis*. Müller-Stoll & Mädler (1962) erected a new fossil genus *Myricoxylon* with the type species *M. hungaricum* from the Miocene of Hungary. They also proposed a new combination *Myricoxylon scalariforme* (Kruse) Müller-Stoll & Mädler. Wheeler et al. (1978) described *Myrica absarokensis* from the middle Eocene of the Yellowstone National Park. Myricaceae can be also noted as one of several families to which Page's (1980) fossil wood of "CASG 60133" could belong. Gottwald (1997) defined *Myricoxylon zonatum* from the lower Miocene of Bavarian "Ostmolasse" in Germany.

Finally, fossil woods called simply, *Myrica*, were mentioned both by Melchior (1998) from the Paleocene of South Carolina and by Figueiral et al. (1999) from the Miocene Lower Rhine Basin in Germany.

Paleoecology

Today, *Comptonia* is a monotypic genus. *C. peregrina* (sweetfern) has, besides the typical variety, two more varieties *C. peregrina* var. *tomentosa* A. Chevalier and *C. peregrina* var. *aspleniifolia* (Linnaeus) Fernald. It is presently restricted to North America ranging from New

Table 2. Botanical affinity of species formerly associated with genus *Comptonia* by Gladkova (1965) redefined by Kedves (1974, 1992) and Grabowska & Wazynska (in Stuchlik *et al.* 2009).

Morphotaxon	Botanical affinity
<i>Labraferoidapollenites aboriginus</i> (Gladkova 1965) Kedves 1992	–
<i>Triatriopollenites clementia</i> (Gladkova 1965) Kedves 1992	–
<i>Alabroidapollenites compactus</i> (Gladkova 1965) Kedves 1992	–
<i>Triatriopollenites grandis</i> (Gladkova 1965) Kedves 1974	Myricaceae vel Juglandaceae (Kedves 1974)
<i>Triatriopollenites imperfectus</i> (Gladkova 1965) Kedves 1992	–
<i>Labraferoidapollenites insolitus</i> (Gladkova 1965) Kedves 1992	–
<i>Triatriopollenites minimus</i> (Gladkova 1965) Kedves 1974	Juglandaceae, <i>Engelhardtia</i> (Kedves 1974, 1992)
<i>Myricipites peregriniformis</i> (Gladkova 1965) Grabowska & Wazynska 2009 in Stuchlik <i>et al.</i> 2009	<i>Comptonia</i> (Grabowska & Wazynska in Stuchlik <i>et al.</i> 2009)
<i>Triatriopollenites podagrarius</i> (Gladkova 1965) Kedves 1974	Myricaceae (Kedves 1974)
<i>Triatriopollenites saueriae</i> (Gladkova 1965) Kedves 1974	Myricaceae (Kedves 1974, 1992)
<i>Triatriopollenites sibiricus</i> (Gladkova 1965) Kedves 1974	Myricaceae (Kedves 1974)
<i>Triatriopollenites subtriangulus</i> (Stanley 1965) Frederiksen 1979	? <i>Comptonia</i> , Myricaceae (Gladkova 1965)

Brunswick south through the New England states to the northern tip of Georgia and west through northern Illinois, Indiana, and the Great Lakes states to eastern Saskatchewan and North Dakota (Elias & Dykeman 1983, Wilbur 1994, FNAEC 1997). *Comptonia peregrina* var. *tomentosa* is confined to upland areas while var. *asplesifolia* occurs in coastal plains from Long Island, New York, south to Virginia (Hall *et al.* 1976). Sweetfern is a low (up to 1.5 m), deciduous, monoecious or dioecious shrub with pinnately lobed leaves (Fig. 8C–E). It grows in openings in coniferous forests in well-drained, dry, acid, sandy or gravelly soils (Del Tredici 1977, Hayward 1991, FNAEC 1997). Because it fixes nitrogen, it does well on disturbed sites or sites with sterile soil, such as abandoned fields and pine-lands or northern pine-barrens (FNAEC 1997, Christensen 1999). *C. peregrina* is usually associated with *Gaylussacia baccata*, *G. frondosa*, *Kalmia latifolia*, *Ilex glabra*, *Clethra alnifolia*, *Quercus ilicifolia*, *Q. prinoides* and *Pinus rigida* and *P. echinata* (Christensen 1999).

The above-described autecological conditions of *C. peregrina* correspond to those predicted for the fossil plant *Comptonia difformis*/*C. srodoniowae*, which is also known from sandy and micaceous facies of the Libkovice Member of the Most Formation in the Most Basin. The most typical forest vegetation is the evergreen broad-leaved forest passing into pine stands in uplands. This association occupied crystalline rock elevations of the Krušné Hory Mts. with mesophytic vegetation and biotopes on acid soils covered by monotonous *Pinus* stands (E3) in combination of Lauraceae (*Laurophyllum*, *Daphnogene* – E3–2), Theaceae (*Eurya* – E3–2), *Comptonia* (E2), *Myrica* (E2), *Symplocos* (E3–2), *Toddalia* (E2), *Mastixia* (E3–2), *Leguminosites* (E3–2), *Laurus abchasica* (E3), *Gordonia hradekensis* (E3–2), *Quercus kubinyii* (E3), *Lygodium* (E1), *Cedrelospermum* (E2) and *Platanus*

neptuni (E4). This assemblage with characteristic elements defined as the above named *Comptonia–Pinus oviformis* association (Kvaček and Bůžek 1982) occurs also in lacustrine sediments beneath the Lom Seam and it intertongues towards the centre of the basin with swamp and riparian forests of *Pinus–Laurophyllum pseudo-princeps* and *Quercus kubinyii–Myrica lignitum* associations (Kvaček & Bůžek 1982) or the colline forest *sensu* Boulter *et al.* (1993).

Similarly, the *Comptonia* records are well known from other sites of the Holešice and Libkovice members of the Most Formation in the Pětipsy area and the Bílina Delta and Žatec alluvial system (*e.g.*, the Břešťany Clay in the Bílina Mine area, Čermníky, Dolany, Nechvalice, Holedeč, Záhoří near Žatec, Nesuchyně – Bůžek 1971; Kvaček & Hurník 2000; Teodoridis 2002, 2003, 2006), where they are connected to the lacustrine clay and fluvial/delta sediments. *Comptonia* shrubs are usually interpreted here as upland elements of the mesophytic vegetation, which are fixed on dry and low-nutrient biotopes with lower water table on hill side (slopes) under humid conditions (*e.g.*, Bůžek 1971, Teodoridis 2006).

The *Comptonia* leaves were described also from the typically riparian vegetation of Nesuchyně (the Hlavačov gravel and sand – Teodoridis 2002) and from the Bílina Delta (fossiliferous horizons Nos – 1, 2, 4, 5, 33, 36, 41, 65, 66, 71 *sensu* Bůžek *et al.* 1992) and from the Břešťany Clay (Ettingshausen 1866, 1868, 1869; Teodoridis & Kvaček 2006). However, *Comptonia* is also interpreted here as an allochthonous accessory element growing on hill side (slopes) along rivers or the basin.

The occurrence of *Comptonia* in the Cheb Basin is known from the sediments closely underlying the Main Coal Seam at Františkovy Lázně and Cheb (drill cores 4393, 4395 and BJ 1) containing a mixture of azonal and

Table 3. Distribution of Myricaceae pollen in the Paleogene and Neogene sediments of the Czech Republic. Symbols: x – rare, xx – regularly in profiles, but not abundant, xxx – abundant, + – no record of quantity given.

Locality	Stratigraphy	Abundance	Reference
Most Basin/Holešice Member, roof of the main coal seam	Miocene	x	Konzalová (1976), Dašková (2000)
Pilsen area relicts	Oligocene/Miocene	xxx	Mazancová (1960), Konzalová (1973)
relicts (Železný Brod)	middle Miocene	+	Konzalová (1973)
relicts (Jehnědno u Písku)	Miocene/Pliocene	+	Bořková (1959), Březinová <i>et al.</i> (1965)
Sokolov Basin, Staré Sedlo Formation	Pliocene	+	Gabrielová <i>et al.</i> (1970)
Cheb Basin	Eocene/Oligocene	xx	Pačtová & Žert (1961), Konzalová (1972)
Cheb Basin/Main Coal Seam formation, basement of coal seam	late Oligocene	+	Pačtová & Žert (1958, 1959)
Cheb Basin/Main Coal Seam formation, coal seam	early Miocene	xxx	Pačtová & Ganguli (1969), Konzalová (1972, 1981), Bůžek <i>et al.</i> (1982)
Cheb Basin/Main Coal Seam formation, roof of coal seam	early Miocene	xx	Pačtová & Žert (1958, 1959), Pačtová & Ganguli (1969), Konzalová (1972, 1981), Bůžek <i>et al.</i> (1982)
Cheb Basin/Vildštejn Formation	Pliocene	xx	Stuchlík (1982)
Žitava Basin	Oligocene	+	Konzalová & Ziemińska-Tworzydło (1999)
South Bohemian Basin	Miocene/Pliocene	xxx	Pačtová (1960), Pačtová (1963)

zonal elements of early Miocene character, such as *Taxodium dubium*, *Pinus rigios*, *Liquidambar*, *Myrica*, *Laurophyllum pseudoprinceps*, *Platanus neptuni* etc. (Bůžek *et al.* 1982). The vegetation recalls those of the Holešice Member and of the lowermost part of the Libkovic Member in the Most Basin. The most abundant occurrence of leaves and fruits of *Comptonia* in the Cheb Basin is in the claystone deposits of the Cypris Formation containing predominantly *Pinus*, *Glyptostrobus*, *Myrica*, *Alnus*, *Platanus neptuni*, and *Laurophyllum rugatum* in combination with other thermophilous elements (Bůžek *et al.* 1996).

Stratigraphically comparable late Oligocene to early Miocene floras in Saxony and Lausitz are Mockrehna near Eilenburg and Witznitz near Borna belonging to the Thierbach layers (Mai & Walther 1991), and Brandis (Mai & Walther 1991), Altdöbern, Spremberg, Jahmen, Welzow (Mai 1997). Generally, these plant assemblages are well comparable to those from the Most Basin but the carpological records particularly of Mastixiaceae and Symplocaceae are more frequent there. An ecological interpretation of *Comptonia* from the middle Eocene and early Oligocene sites of Europe corresponds also to upland element growing in the transitional zonal vegetation type of mixed mesophytic forest and broad-leaved deciduous forest *sensu* Teodoridis *et al.* (2011) at Hrazený (Kvaček *et al.* 2015) or specific intermediate mesophytic forest type between the notophyllous and the quasi-paratropical forest at Messel (Kvaček 2010), which may correspond to the modern broad leaved evergreen forest of Nara in Japan (Teodoridis *et al.* 2012).

According to Knor *et al.* (2015, p. 52, table 2) leaves of *Comptonia difformis* from North Bohemia are damaged only slightly by insects and show signs of the activity of

only one functional feeding group (FFG), *i.e.*, margin feeding (MF) *sensu* Labandeira *et al.* (2007).

Conclusion

A more holistic understanding of the *Comptonia difformis* plant from North Bohemia, which is the type area of this fossil species, is introduced here. We presented a detailed description of its peculiar pinnately lobed leaves including epidermal structure and the first reference to its stipules, together with the co-occurring fruit fossils of *C. srodoniowae*. Other organs of *Comptonia* as wood or pollen were sought, but remain unconfirmed or not clearly evidenced from the North Bohemian Cenozoic and they are only generally discussed here relative to the fossil record. In addition to the morphological and anatomical descriptions, there is also a circumstantial account of the paleoecology of fossil *Comptonia* and its nearest living relative *C. peregrina*. As a result, the fossil *Comptonia difformis/srodoniowae* plant from the early Oligocene to Early Miocene of Central Europe is presented in a more comprehensive way, with emphasis on multiple organs and a whole-plant approach, also with attention to its ecological role.

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