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.


script received September 15, 2016; accepted in revised form March 23, 2017; published online June 23, 2017; issued June 30, 2017.

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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, cor-

rectly suggested this plant fossil to belong to *Comptonia* L’Hérier ex Aiton. Consequently, paleobotanists studying fossil angiosperms reported fossil foliage of the genus *Comptonia* many times. After Sternberg (1821) and Brongni-

art (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 Hemi-

sphere (e.g., Berry 1906, Florin 1920, Bůžek 1971, Rüffle 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 Mioocene 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 refer-

cence 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 con-

cept 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 re-

cords of *Comptonia* is only partially attempted, although some preliminary suggestions express our views on species diversity of fossil *Comptonia* in Eurasia.

DOI 10.3140/bull.geosci.1633 185
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 Doubské 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 re-activation of the basin occurred during the Pliocene, when the basin was enlarged within tectonic activation of the Domažlice-Tachov tectonic structure (Špičáková et al. 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 prolluvial 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. The Bišina Delta on the top of the seam in the Bíliná 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 Libkovice 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 prolluvial 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 (Tatimice), KU (Kundratice, boreholes KU 115, KU 127), BM (Bílina Mine), BS (Břešťany), BZ (Břežánky), JU (Jenišův Újezd, borehole JU 399), HD (Holedeč),
NS (Nesuchyně), CM (Čermníky), DL (Dolany), NC (Nečranice), ZH (Záhoří near Žatec), PK (Přívlaky), NL (Nechvalice); Chab Basin – FL (Františkovy Lázně + borehole BJ 1), LC (Liba u Chebu + boreholes 4393 and 4395), BH (other boreholes HV 11, HV 19a, V 3a, D 7, A 28, A 42, D 2, D 10, V 12, H 13); České středohoří Mts – HH (Hrazený Hill), KZ (Knížecí near Šluknov).
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 elastic 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 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 Vídlštejn 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 Vonsőv 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 Vonsőv 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 be a marginal facial equivalent of the lowermost part of the Cypris Formation. Fossil mammals occurring plentifully in green clays with calcareous oncitle nodules were classified as representing the MNS 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 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 (Bílin 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 changing 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,
Systematic part

Family Myricaceae Richard ex Kunth

Genus Comptonia l'Hérier 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 Libkovicke 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.
but are usually smaller. Details of areolation (Fig. 2I) are similar to those of \textit{C. peregrina} (Chevalier 1901, text-fig. 6; Fig. 9E). Adaxial cuticle (Fig. 3A) reflects polygonal straight-walled cells and a few rounded trichome bases. Dense, simple to paired (orstellate) trichomes 30–60 μm long up to 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 \textit{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), Záhoří u Žatce (Teodoridis 2003, p. 264, pl. 2, figs 11–12, text-fig. 2.15); Břešťany Clay – exploited in former clay pits at Břešťany (formerly Preschen in German) in the Bílina Mine area, Břešťánky (Priesen in German), Jenišův Újezd (Languajděz in German, JÚ 399/36–55 m), the Libkovicke Member of the Most Formation [\textit{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; \textit{Myrica acutiloba} (Brongniart) Schimper 1870–1872, p. 560; Brabenec 1909, p. 95, text-figs 73–74], Čermníky and Dolany, Nechanice (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 narrowly ovate 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). Abrerrant 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 (Figs 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 narrowed 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.

\textbf{Foliage} – population of \textit{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 \textit{Comptonia acutiloba} Brongniart) Františkovy Lázně (core BJ1/73–75 m) and Libá u Chebu (cores 4393/62–68 m)}.
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 anticinal 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 středoohří 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 ob-long (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 pinnafidd 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 anticinal 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 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), serrat 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 Haring in Austria (Ettingshausen 1853, Butzman & Gregor 2002, Erdei & Rákosi 2009) or known from Geiseltal in Germany (Rüffle 1976) and Csordákút 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 Nikolichevan – 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* 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 oehningenensis* A. Br. or *Myricia 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-
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. Rüffle (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” difforis (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.

Comptonia 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. difforis, may not be valid in view of the expanded characteristics of C. difforis presented here from the type area. Comparing C. difforis and its extant relative, Kotlaba (1961) noticed a larger size of foliage from the fossil population from the Břešťany 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. difforis. 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. difforis do not deviate in form from recent Comptonia (see Chevalier 1901, text-fig. 8). Reduced small leaves noted from the Bilina 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. difforis 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 (nutslets)
Figures 7, 8A–I

1974 Comptonia longistyra (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 29.6–9.8 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 Libkovice 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 longistyra (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
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 diachronic 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 (Fris 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...
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 Wedehouse’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, Labraferoidae pollenites and Alabraferoidae pollenites, and emphasized their botanical affinity to Myricaceae and Juglandaceae (Table 2). In agreement with the description of the genus Myricipites by Wedehouse (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 porous 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 stenopalous genera 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. Aporotracheal 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 “thrive 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
makes difficult its recognition in fossil record. Kruse (1954) described a wood from the lower Eocene of Wyoming as *Myrica scalariformis*. Müller-Stoll & Mädel (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 & Mädel. 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.

# Paleoeology

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. *aspleniiifolia* (Linnaeus) Fernald. It is presently restricted to North America ranging from New Mexico to British Columbia and eastern Canada.

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

<table>
<thead>
<tr>
<th>Reference</th>
<th>Stratigraphy and location</th>
<th>Morphology of endocarps</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Length [mm]</td>
</tr>
<tr>
<td>Nikitin (1976)</td>
<td>early Miocene (Russia, E Siberia)</td>
<td>19–25</td>
</tr>
<tr>
<td>Dorofeev in Budantsev et al. (1994)</td>
<td>late Eocene (Russia, E Siberia)</td>
<td>21–25</td>
</tr>
<tr>
<td>Dorofeev (1966), Dorofeev in Budantsev et al. (1994)</td>
<td>early Pliocene (Belarus)</td>
<td>40–50</td>
</tr>
<tr>
<td>Dorofeev (1966), Dorofeev in Budantsev et al. (1994)</td>
<td>Miocene (Russia, E Siberia)</td>
<td>38–51</td>
</tr>
<tr>
<td>Nikitin (1976)</td>
<td>early Miocene (Russia, W Siberia), middle Miocene (Russia, E Siberia)</td>
<td>15–20</td>
</tr>
<tr>
<td>Mai (1997), Mai &amp; Walther (1978, 1991)</td>
<td>late Oligocene to Early Miocene (Germany)</td>
<td>30–55</td>
</tr>
<tr>
<td>Dorofeev (1966), Dorofeev in Budantsev et al. (1994)</td>
<td>Oligocene (Russia, W Siberia)</td>
<td>32–67</td>
</tr>
<tr>
<td>Dorofeev in Budantsev et al. (1994)</td>
<td>Oligocene (Russia, E Siberia)</td>
<td>22–39</td>
</tr>
<tr>
<td>Dorofeev (1969), Dorofeev in Budantsev et al. (1994)</td>
<td>early Miocene (Russia, E Siberia)</td>
<td>31–42</td>
</tr>
<tr>
<td>Dorofeev in Budantsev et al. (1994)</td>
<td>Miocene (Russia, W Siberia)</td>
<td>25–33</td>
</tr>
<tr>
<td>Dorofeev in Budantsev et al. (1994)</td>
<td>Miocene (Russia, E Siberia)</td>
<td>20–27</td>
</tr>
<tr>
<td>Dorofeev in Budantsev et al. (1994)</td>
<td>early Miocene (Lithuania)</td>
<td>24–27</td>
</tr>
<tr>
<td>Dorofeev (1966), Dorofeev in Budantsev et al. (1994)</td>
<td>Oligocene (Russia, W Siberia) to Miocene (E Siberia)</td>
<td>14–33</td>
</tr>
<tr>
<td>Mai &amp; Walther (1991), Mai (1997)</td>
<td>late Oligocene to Early Miocene (Germany)</td>
<td>14–23</td>
</tr>
<tr>
<td>Dorofeev in Budantsev et al. (1994)</td>
<td>Miocene (Russia, E Siberia)</td>
<td>25–44</td>
</tr>
<tr>
<td>Friis (1974, 1979)</td>
<td>Middle Miocene (Denmark)</td>
<td>20–44</td>
</tr>
<tr>
<td>Bůžek et al. (1996), Teodoridis &amp; Kvaček (2006)</td>
<td>early Miocene (Czech Republic)</td>
<td>18–40</td>
</tr>
<tr>
<td>Dorofeev in Budantsev et al. (1994)</td>
<td>Oligocene (Russia, W Siberia)</td>
<td>24–41</td>
</tr>
<tr>
<td>Dorofeev (1966), Dorofeev in Budantsev et al. (1994)</td>
<td>early Miocene (Russia, W Siberia)</td>
<td>18–32</td>
</tr>
<tr>
<td>Dorofeev (1966), Dorofeev in Budantsev et al. (1994)</td>
<td>Oligocene (Russia, W Siberia)</td>
<td>21–50</td>
</tr>
<tr>
<td>Liang et al. (2010)</td>
<td>early Miocene (China)</td>
<td>31–58</td>
</tr>
<tr>
<td>Friis (1979), FNAEC (1997), personal observation</td>
<td>recent (USA, Canada)</td>
<td>31–52</td>
</tr>
</tbody>
</table>
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. *asplenifolia* 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).

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 Krušně Hory Ms, 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), *Symlocos* (E3–2), *Toddalia* (E2), *Mastixia* (E3–2), *Leguminosites* (E3–2), *Lauros 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 interfingers 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 *senso* Boulter et al. (1993).

Similarly, the *Comptonia* records are well known from other sites of the Holešíce 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, Čermničy, Dolany, Nechvalice, Holec, Žáhoři near Žatec, Nesaný – 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 *senso* 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 Františkove Lázěně and Cheb (drill cores 4393, 4395 and BJ 1) containing a mixture of azonal and

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**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).

<table>
<thead>
<tr>
<th>Morphotaxon</th>
<th>Botanical affinity</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Labraferoidaepollenites aborigen</em> (Gladkova 1965) Kedves 1992</td>
<td>–</td>
</tr>
<tr>
<td><em>Triatriopollenites clementia</em> (Gladkova 1965) Kedves 1992</td>
<td>–</td>
</tr>
<tr>
<td><em>Alabroidaepollenites compacta</em> (Gladkova 1965) Kedves 1992</td>
<td>–</td>
</tr>
<tr>
<td><em>Triatriopollenites grandi</em> (Gladkova 1965) Kedves 1974</td>
<td>Myricaceae vel Juglandaceae (Kedves 1974)</td>
</tr>
<tr>
<td><em>Triatriopollenites imperfectus</em> (Gladkova 1965) Kedves 1992</td>
<td>–</td>
</tr>
<tr>
<td><em>Labraferoidaepollenites insolitus</em> (Gladkova 1965) Kedves 1992</td>
<td>–</td>
</tr>
<tr>
<td><em>Triatriopollenites podagriarius</em> (Gladkova 1965) Kedves 1974</td>
<td>Myricaceae (Kedves 1974)</td>
</tr>
<tr>
<td><em>Triatriopollenites sauerae</em> (Gladkova 1965) Kedves 1974</td>
<td>Myricaceae (Kedves 1974, 1992)</td>
</tr>
<tr>
<td><em>Triatriopollenites sibiricus</em> (Gladkova 1965) Kedves 1974</td>
<td>Myricaceae (Kedves 1974)</td>
</tr>
<tr>
<td><em>Triatriopollenites subtriangulius</em> (Stanley 1965) Frederiksen 1979</td>
<td>?<em>Comptonia, Myricaceae</em> (Gladkova 1965)</td>
</tr>
</tbody>
</table>
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 Holesíce Member and of the lowermost part of the Libkovice 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 Lusatia are Mockrehna near Eilenburg and Witznitz near Borna belonging to the Thierbach layers (Mai & Walther 1991), and Brandis (Mai & Walther 1991), Aldtobern, Spremberg, Jahnem, Welzow (Mai 1997). Generally, these plant assemblages are well comparable to those from the Most Basin but the carpollonal records particularly of Mastixiaceae and Syplocaceae 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. srodonio-wae*. 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/srodo-nio-wae* 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.

### Acknowledgments

We are thankful to Katy Chayka from Minnesota Wildflowers, who kindly allowed us to freely use a photo of *C. peregrina* displaying foliage with permanent stipules. Greatly appreciated are also the suggestions and notes made on the first version of the manuscript by Steven R. Machester, Johanna Eder and Boglarka Erdei. This research was supported by grants GA14-23108S, PRVOUK 15 and 44, Progress Q17 and Q45 of the Charles University.
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