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# Latest Cretaceous leaf floras from southern Poland and western Ukraine

ADAM T. HALAMSKI



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Latest Cretaceous (Campanian to Maastrichtian) leaf fossil assemblages are described from 33 exposures ranging from the southern border of the Holy Cross Mountains (southern Poland) through the Roztocze region (south-eastern Poland) to the vicinity of L'viv (western Ukraine). The fossil assemblage is allochthonous, preserved in marine sediments, yet complete compound leaves strongly argue for the transport having been short. Krasnobród and Potelych (Potylicz) are the richest localities; both are late Campanian. The abundance of angiosperm remains in this period is explained by a marine lowstand resulting in nearby emergent vegetated areas. The flora was composed of ferns (three species), conifers (five species, including the commonest *Geinitzia reichenbachii*), dicotyledons (seventeen taxa; *Debeya paulinae* sp. nov., two other species of *Debeya*, and *Rarytkinia polonica* being the most frequent), and a single presumed monocotyledon. The eudicot clade is formalised as supersubclass Eudicotyledoneae Doyle and Hotton ex Halamski, herein. The approximately equal abundance of serrate/lobate and entire-margined dicots attests to an intermediate character of the flora between more thermophilic and polar vegetation. The material may have come from at least two communities: xeromorphic mixed *Debeya*-conifer forests and platanoid-Lauraceae forests growing in disturbed environments along rivers. The assemblage is most similar to approximately coeval floras from Westphalia and the Netherlands.

**Key words:** Angiospermae, Coniferae, Leptosporangiateae, *Debeya*, palaeobotany, taxonomy, Campanian, Maastrichtian, Cretaceous, Poland, Ukraine.

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## Introduction

Latest Cretaceous (Campanian to Maastrichtian) leaf floras have been reported from several regions worldwide (e.g., Nichols and Johnson 2008 and references therein). In central Europe they are known from over thirty localities scattered on a territory extending from the southern border of the Holy Cross Mountains (central Poland) in the west to the L'viv region (western Ukraine) in the east (Fig. 1). The aim of the present paper is the systematic revision of this flora as a whole, the assessment of its temporal dynamics, and the exploration of its palaeogeographic context.

Latest Cretaceous plants have been collected in Potylicz (now Potelych, western Ukraine) since about 1860 (Lilpop 1957), but the rarity of plant fossils was the reason why their description could be prepared only several years later (Nowak 1907a). Even rarer plant specimens from the southern border of the Holy Cross Mountains were studied together with vertebrate remains by Ciesliński and Milaković (1962). The material from south-eastern Poland was described in a series of papers by Karczmarz and Popiel (Karczmarz and Popiel 1966,

1971; Malicki et al. 1967). The fossil flora of Pidtemne (western Ukraine) was studied by Drygant (1998). All these papers treated single localities or restricted areas separately. This, along with the rarity of the plant fossils, was the reason why poorly preserved, sometimes even unidentifiable material was identified (in a large part erroneously) at species level and in some cases served to introduce new taxa.

The area dealt with in the present study may be treated as a single unit (see Geological setting below). Nearest approximately coeval localities yielding leaf floras are situated either ca. 600 km to the south (Grünbach in Austria; Herman and Kvaček 2009) or about the same distance to the west in central Germany (e.g., Rüffle and Krutzsch 2005).

**Institutional abbreviations.**—BSPG, Bavarian State Collections of Palaeontology and Geology, Munich, Germany; G, open-air Museum “Zagroda Guciów”, Guciów, Poland; GFAP, Geoscience Friends Association “Phacops”, Łódź, Poland; F, Field Museum (herbarium), Chicago, USA; IB, Institute of Botany, Polish Academy of Sciences, Cracow, Poland; IRSNB, Institut royal des Sciences naturelles, Brus-

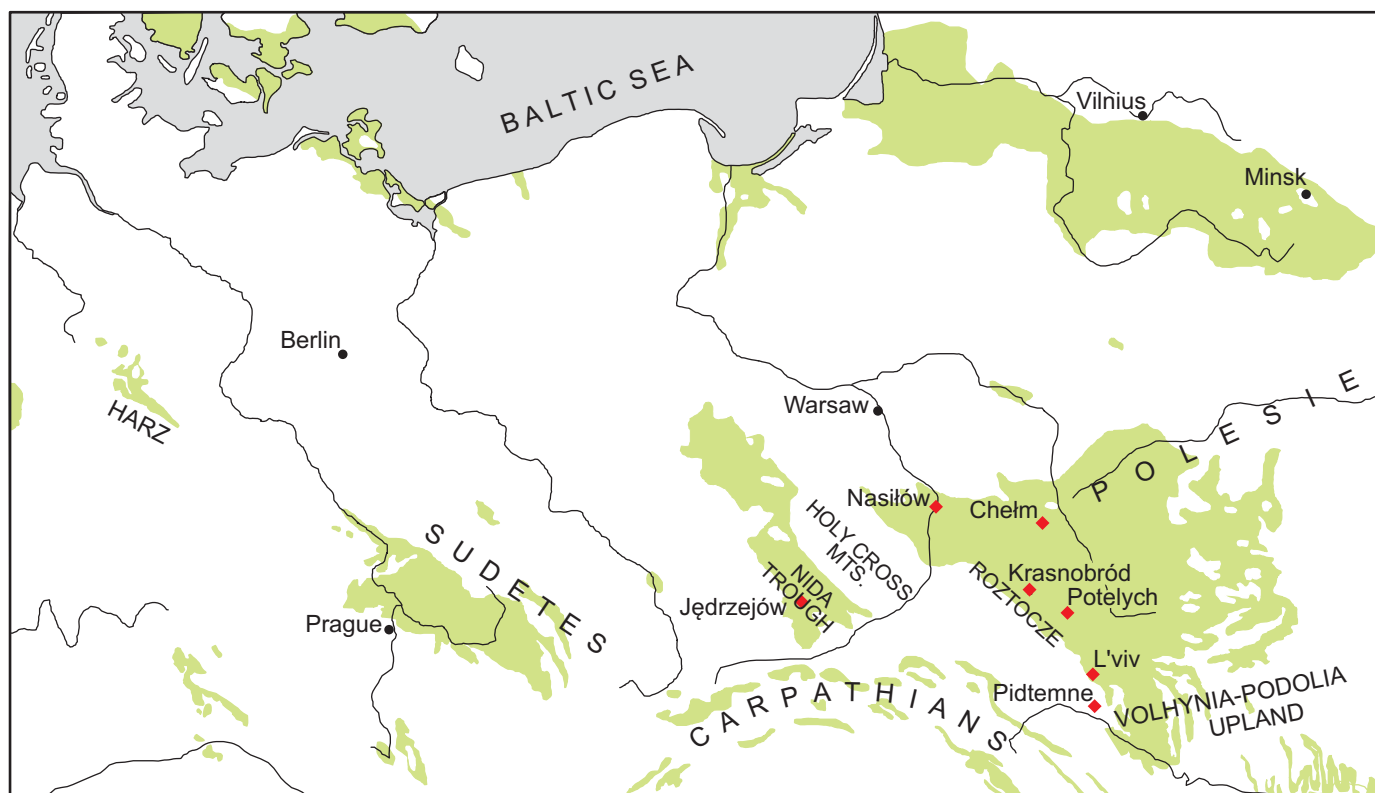


Fig. 1. Map of central Europe showing the extent of upper Cretaceous deposits (both cropping out and under Quaternary cover; simplified after von Gaertner and Walther 1971). Main studied localities are represented by diamonds.

sels, Belgium; JS, Museum of the Zamość Inspectorate of the Home Army (Jan Sitek's collection), Bondyż, Poland; KrM, Museum of Geology and Ceramics affiliated to the Roman Catholic parish, Krasnobród, Poland; KrS, Liceum im. Jana Pawła II (geologic collection), Krasnobród, Poland; L, State Natural History Museum (formerly Dzieduszycki Museum), L'viv, Ukraine (the specimen numbers in L have recently been changed, so specimens are quoted according to both the old and the new systems; the old numbers [referred to in Drygant 1998] are preceded by "formerly"); MB, Museum für Naturkunde, Berlin, Germany; MMG, Senckenberg Naturhistorische Sammlungen Dresden, Germany; MZ, Museum of Earth, Warsaw, Poland; NM, National Museum, Prague, Czech Republic; PIG, Polish Geological Institute, Warsaw, Poland; PBO, Forschungsstelle für Paläobotanik der Westfälischen Wilhelms-Universität Münster, Münster, Germany; RGM, National Museum of Natural History, Leiden, Netherlands; U, Museum of Palaeobotany and Palynology, Utrecht, Netherlands; UJ, Palaeobotanic Museum, Institute of Botany, Jagiellonian University, Cracow, Poland; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

*Other abbreviations.*—auct., *auctorum*, for a taxon of uncertain authorship; LMA, leaf margin analysis; LMAT, mean annual temperature calculated by LMA; P, ratio of entire-margined species in a flora; UDC, Universal Decimal Classification.

## Material and methods

A preliminary survey of known localities was undertaken in autumn 2009 and spring 2010 and resulted in the two most promising outcrops being excavated using heavy machinery in the summer and autumn of 2010. The town quarry in Krasnobród yielded several well preserved plant fossils and allowed detailed taphonomic observations. Contrary to the expectations, very few plant megafossils were found in the quarry in Bliżów.

The material used in the present work encompasses: (i) the collections of previous authors, namely those of Nowak (1907a) and Drygant (1998) stored in L; that of Cieśliński and Milaković (1962) stored in PIG; that of Karczmarz and Popiel (1966) and Malicki et al. (1967) stored partly in MZ and partly in JS (some specimens, however, could not be traced); (ii) unpublished collections from G, IB, JS, KrM, KrS, L, RGM, and UJ; (iii) material collected by the present author and his collaborators during the field seasons 2010 (mostly) and 2011, mainly in Krasnobród (stored in ZPAL for the largest part).

In total, about 160 identifiable specimens of fossil plants, out of which 47 were previously unpublished, were studied. It should be noted that this material represents the results of about 150 years of collecting in strata where plant remains do occur but are rare.

The plant fossils are usually preserved as imprints in rather coarse carbonate rocks admixed with significant amounts of

organogenic silica (known under the regional petrographic name of “opoka”; more seldom calcareous gaizes). In some cases fine venation up to the fifth order is preserved; quite often, however, as few as two venation orders and sometimes only the midvein can be observed. Cuticles are not preserved. The single exception is the material from the Chełm quarry (two specimens of *Cunninghamites squamosus*), preserved in chalk, where an imprint of the cuticle has survived.

Uncoated specimens were photographed, most often under oblique light, using a Canon 350D digital camera either with a Canon EFS 17–85 mm lens or, if required, with a Canon EF 100 mm macro lens. One specimen from Chełm was studied under a Hitachi S3700 N scanning electron microscope with an environmental chamber (National Museum, Prague). Pictorial reconstructions of leaves of the most characteristic angiosperm species have been provided. They have been made by taking preserved parts or details of (two to four) conspecific specimens in order to obtain an idealised image of a complete leaf. Usually the shape of a reconstructed leaf is based on one specimen and venation details on another one.

## Geological setting

At present, the studied outcrops are situated in two major synclinal zones bordering the Mid-Polish Anticlinorium, namely the north-eastern Pomeranian-Warsaw-Lublin-L'viv Synclinorium and the south-western Usedom-Szczecin-Łódź-Miechów Synclinorium (Voigt et al. 2008: 927). In the latest Cretaceous this area formed a single unit, namely the Mid-Polish Trough, a rift or aulacogen situated at a palaeolatitude of ca. 40–45°N that became inverted during a period that began in the Turonian and ended in the Palaeocene (Krzywiec 2006; Leszczyński 2010).

In the terms of the present geography, the studied outcrops are scattered in several regions (Fig. 1). The Roztocze hills (Ukrainian: Roztichchia; 343.2 in the Universal Decimal Classification of geographical regions of Europe) include the richest localities of Potelych (Potylicz) and Krasnobród. Further to the east, two outcrops are situated in the western extremity of the Volhynia-Podolia Upland (851 in the UDC; vicinity of L'viv). A single quarry is located in the Chełm Hills, a part of the Polesie lowland (845 in the UDC). There are several localities in the Middle Vistula Valley (343.11 in the UDC) and in the Nida Trough (342.2 in the UDC).

The age of the outcrops from the Roztocze and from the vicinity of L'viv had been considered to be Maastrichtian in age by all previous authors (and even in earlier communications of the present author: Halamski 2007, 2008); however, they used the traditional Boreal definition based on the first occurrence of the belemnite species *Belemnella lanceolata*. Following the redefinition of the Campanian–Maastrichtian boundary (Odin 1996; Christensen et al. 2000; Odin and Lamaurelle 2001; see also Machalski 2005; Stolarski and Vertino 2007 for regional details) part of the outcrops previously included into the lower Maastrichtian should be now considered as belonging to the

upper Campanian. The Chełm quarry and the Middle Vistula Valley localities are well dated on the basis of macro- and micropalaeontological stratigraphy. In the Nida Trough lower Campanian to lower Maastrichtian outcrops are now destroyed (personal observations 2009), and in most cases detailed stratigraphy cannot be provided.

Detailed descriptions and ages of outcrops are given in the Appendix 1 and follow the Tercis definition of the Campanian–Maastrichtian boundary.

## Taphonomy

This section is based in a large part on field observations made in Krasnobród. The latest Campanian strata crop out in the town quarry. They are marine, with numerous cephalopods and other stenohaline fauna, including foraminifers, scaphopods, bivalves, gastropods, brachiopods, and fish scales. Crustacean (and possibly bivalve) burrows are rather common. There is, however, some evidence for freshwater influx (see Appendix 1 for details). Plant fossils are quite rare (although not so for marine strata) and occur irregularly in all parts of the succession; no particular concentration has been detected. Leaves are preserved either parallel to the stratification or they lie at some angle to it. Occurrences of vertically placed leaflets of *Debeya* spp. in Krasnobród and in Bliżów (Fig. 7F) may be interpreted as remains of crustacean burrows, the walls of which have been strewn with plant material (Krzysztof Dembicz, personal communication 2011).

Noteworthy is the occurrence of subcomplete compound leaves of *Debeya* spp. (Figs. 2B, C, 9E) in several outcrops (Krasnobród, Potelych, Zgubieniec). This suggests that the transport of the plant material must have been relatively short. Although it is very difficult to give a quantitative estimation of the distance to the land, because to date suitable observations and experiments in the marine domain have never been conducted, it was arguably of order of kilometres rather than tens of kilometres. This is a slightly more reserved inference than that of Spicer et al. (2002: 84) who estimated that presence of compound leaves with intact leaflets at their site 11 suggested “minimal transport prior to deposition”.

A single mass accumulation of plant material from Potelych (Fig. 2E) with five species on a single slab not exceeding 40 cm in width is also strongly suggestive of a very short transport, although it can also be imagined that such a concentration has resulted of some eddy process.

A different interpretation might be proposed, namely of a longer transport, by reference to either the Mo clay (Fur Formation, Lower Eocene), a deep sea deposit from Jutland (Denmark) containing numerous plant remains (Bonde 1966, 1979) or to the very delicate *Argonauta* (Nautiloidea) shells that may be transported over several hundred kilometres (from the central Indian Ocean to Madagascar; Mikołaj Zapalski, personal communication 2011). In the present author's opinion, both comparisons are inappropriate. The plant material of the Fur Formation consists of woods, seeds, and leaves (in order of



frequency: the leaves are rare; Kai Raunsgaard Pedersen, personal communication 2010). In the plant material from the studied outcrops, leaves are by far dominant, woods and twigs are subordinate, while only a single seed has been found up to now (*Carpolithes* sp. sensu Nowak 1907a). The case of *Argonauta* is most probably inappropriate as well because the shells, even very delicate, may be conserved nearly indefinitely in marine conditions if they are not broken. This is not the case with leaves that undergo gradual bacterial decay.

The Cerin locality (Late Jurassic of the Jura Mts., France), although animal and plant fossils co-occur in the same strata similarly as in the studied material, cannot provide a model for our material either. The strata exposed in Cerin were deposited in a lagoonal environment, as testified, e.g., by the preservation of soft-bodied animals (Gaillard et al. 2006); this is not the case in Roztocze.

The situation in the Vistula valley (Kazimierz Dolny, Nasiłów) is slightly different. The strata are also marine (with cephalopods, brachiopods, and numerous sponges) but the plant material is composed nearly exclusively of small fragments of *Geinitzia reichenbachii*. Here the transport may have been longer due to higher resistance of conifer tissues imbued with resins (in this Karczmarz and Popiel 1966 have been right) although not necessarily from the same source area. The frequency of the findings, however, precludes a very long distance from the land.

## Systematic palaeontology

The highest systematic units are accepted after either Cavalier-Smith (1998) or Kenrick and Crane (1997) against Chase and Reveal (2009); this means that earlier non-typified names are preferred over later typified names (thus Krassilov 1997a is followed against Cronquist et al. 1966; Recommendation 16B of the ICBN: Greuter et al. 2000). The classification of ferns is after Smith et al. (2006), with some modifications. Arrangement of angiosperm morphotaxa follows Krassilov (1979) and Crabtree (1987).

At the request of the Editors, both fossil and extant plant taxa and higher units of the botanic system are cited with fully spelt authors' names and the year of publication, according to the zoological usage.

Infrakingdom Cormophyta Endlicher, 1836  
(= Embryophyta Engler, 1892)

Division Tracheophyta Sinnott ex Cavalier-Smith, 1998

Subdivision Euphyllophytina auct.

Infradivision Moniliformopses Kenrick and Crane, 1997

Class Leptosporangiateae von Goebel, 1881  
(= Pteridopsida Ritgen, 1828)

Order Gleicheniales Frank in Leunig, 1877

Family Matoniaceae Presl, 1847

Genus *Matonidium* Schenk, 1871

Type: *Matonidium goepperti* Schenk, 1871; Germany, Wealden.

*Matonidium* sp.

Figs. 2E, 3C, E, G.

1907 *Gleichenia* (?) *Zippei* Heer; Nowak 1907a: 45–46, pl. 1: 6.

1907 *Gleichenia longipennis* Heer; Nowak 1907a: 46, pl. 2: 22.

**Material.**—Fragmentary sterile leaves L PB-K.10 (formerly 7672), L PB-K.20[.1] (formerly 7652), both from Potelych; fragmentary fertile leaf ZPAL PI 4/5/1, Szozdy.

**Description.**—The single fertile specimen ZPAL PI 4/5/1 (Fig. 3E) is a fragment about 11 mm long with six quite closely spaced pinnules ca. 5 mm wide, at least two of which possess recognisable sporangia. The sporangia are very small, disposed in a two single rows parallel to the midvein; there are 1–2 sporangia per mm. The rachis is ca. 0.5 mm wide.

The sterile specimen L PB-K20[.1] (Fig. 3C) has similar shape and dimensions of the pinnules and the rachis, so it is assumed to belong to the same species. The fronds are probably palmate, composed of at least five pinnae (maximal preserved length 31 mm), although organic connection is not preserved. The pinnules are alternating, quite closely spaced, subtriangular with rounded tips, although sometimes their margins are subparallel; they measure up to 50 mm in length and up to 30 (exceptionally 35) mm in width at the base.

**Remarks.**—The specimen L PB-K.10 (Fig. 3G) described by Nowak (1907a) as a separate species “*Gleichenia longipennis*” (as opposed to the more complete specimen L PB-K.20.1 identified as “*Gleichenia zippei*”) differs in having more rounded pinnules. It may represent the same species under different conditions of fossilisation (pinnule margin may be curved down because of desiccation).

Order and family unknown

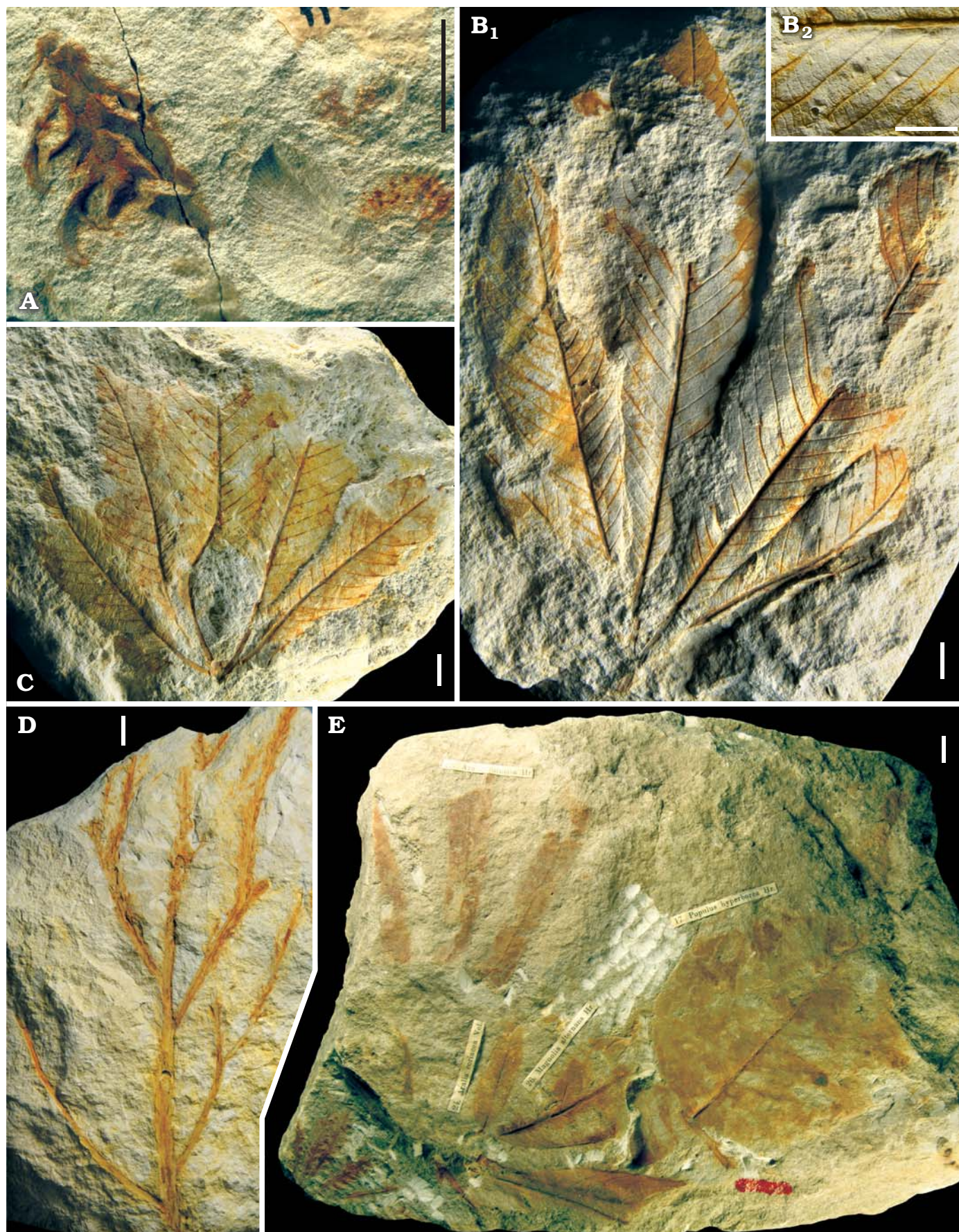
Genus *Microphylopteris* Arber, 1917 sensu Cantrill and Nagalingum, 2005

Type: *Microphylopteris pectinata* Arber, 1917; Triassic, New Zealand.

**Remarks.**—Following Cantrill and Nagalingum (2005), the genus *Microphylopteris* Arber, 1917 is used here for ferns

Fig. 2. Taphonomy. **A.** Co-occurrence of *Geinitzia reichenbachii* (Geinitz, 1842) Hollick and Jeffrey, 1909 with a scaphitid ammonite, L PB-K.24; Potelych, upper Campanian. **B, C.** (Sub)complete leaves of *Debeya paulinae* sp. nov.; Krasnobród, upper Campanian. **B.** Holotype JS 3. General view (B<sub>1</sub>), venation detail (B<sub>2</sub>). **C.** Paratype KrS 1 (see enlargement in Fig. 7F). **D.** A ramified branch of *Geinitzia reichenbachii*, JS 7; Krasnobród, upper Campanian. **E.** A mass accumulation of leaves of *Araliopsoides*? cf. *minor* (Berry, 1925) comb. nov., *Rarytkinia polonica* (Karczmarz and Popiel in Malicki et al., 1967) comb. nov., *Matonidium* sp., and *Dicotylophyllum* cf. *proteoides* (Unger, 1867) Herman and Kvaček, 2010 (see enlargements in Figs. 3C, 6D, 12E, J). Specimen L PB-K.20; Potelych, upper Campanian. Scale bars 10 mm.







that possess some characters of the Gleicheniaceae but cannot be assigned conclusively to any family.

### *Microphyllopteris* sp.

Fig. 3B, D.

1971 *Didymosorus comptoniifolius* Debey et Ettingsh.; Karczmarz and Popiel 1971: 644–645, pl. 1: 1–2.

1998 *Gleichenia zippei* (Corda) Heer; Drygant 1998: 143, pl. 1: 1–2.

**Material.**—Fragmentary leaves L PB-K.21 (formerly 37921), Pidtemne; L PB-K.60, L'viv; ZPAL Pl 4/1/6, Krasnoblód.

**Description.**—The subparallel position of the fragmentarily preserved last order pinnae is suggestive of a pinnate arrangement (Fig. 3D). Pinnae fragments up to ca. 20 mm long, rachis very slender, up to 0.2 mm wide; pinnulae either (sub)opposite or alternating, obliquely inserted, subtriangular, with either both margins straight or basisopic one convex and acroscopic one concave, with acute tip, up to 3 mm long and 1.5 mm wide. Pinnules coalescent up to one third of their length.

**Remarks.**—*Microphyllopteris* sp. differs from *Matonidium* sp. (see above) in possessing subopposite, acuminate pinnules and a finer rachis. Although organic connections of the pinnae are not preserved, their preservation suggests that the arrangement was pinnate in the former taxon and palmate in the latter. Either forking (diagnostic of the Gleicheniaceae) or fertile structures could not be observed, wherefore the assignment to any family is not possible.

### Genus *Cladophlebis* Brongniart, 1849

**Type:** *Neuropteris albertsii* Dunker, 1846; Cretaceous, Wealden; northern Germany.

### *Cladophlebis* sp.

Fig. 3A.

1962 *Cladophlebis arctica* (Heer) Kryštof.; Cieřliński and Milaković 1962: 174, pl. 1: 1.

**Material.**—Fragment of a leaf PIG 60 III 1, Ignacówka near Pińców, upper Campanian or lower Maastrichtian.

**Description.**—The single specimen is a fragment of a last order pinna about 45 mm in length with about thirteen variously preserved pinnules. The rachis is slightly wider than 1 mm. The pinnules are alternating, obliquely inserted, and densely spaced: each one covers a fragment of the adjacent basisopic pinnule. The pinnules are elliptic in shape, integrimarginate, quite large and short (up to 10 mm long and 7–8 mm wide), asymmetric (the catadromous side is about one fourth wider than the acrodromous one). The main vein is straight, departing from the rachis at an angle of about 45–55°; the angles between the main vein and the secondary veins are about 30°.

The secondary veins are sometimes forking dichotomously just after leaving the main vein.

**Remarks.**—A large part of representatives of the form genus *Cladophlebis* belong to the Osmundaceae and some of them to other families (e.g., Dicksoniaceae). The available characters do not permit the assignment of *Cladophlebis* sp. described here to any family.

Infradivision Radiatopses Kenrick and Crane, 1997

Subinfradivision Gymnospermae auct.

Class Coniferae (Jussieu, 1789) Engler, 1892

(= Pinopsida Burnett, 1835)

Family Cupressaceae Richard ex Bartling, 1830

Genus *Cunninghamites* Presl in Sternberg, 1838

**Type:** *Cunninghamites oxycedrus* Presl in Sternberg, 1838; Cretaceous, Cenomanian; Niederschöna, Saxony, Germany.

### *Cunninghamites squamosus* Heer, 1871

Figs. 4, 5A–C.

1871 *Cunninghamites squamosus* m.; Heer 1871: 9–10, pl. 1: 5–7.

1907 *Cunninghamia elegans* (Corda) Endl.; Nowak 1907a: 47, pl. 1: 11.

1962 *Cunninghamia elegans* (Corda) Endl.; Cieřliński and Milaković 1962: 253, pl. 1: 3.

1967 *Cunninghamia elegans* Corda; Malicki et al. 1967: 226–227, fig. 17.

1967 *Cunninghamia stenophylla* Velen.; Malicki et al. 1967: 227, figs. 18–19.

1975 *Cunninghamia stenophylla* Velen.; Kohlman-Adamska 1975: 163, 164, pl. 1: 6.

2009 *Cunninghamites squamosus* Heer 1871; Bosma et al. 2009: 486–487, figs. 3A, 4C–F, 5.

2012 *Cunninghamites squamosus* Heer; Bosma et al. 2012: 24–25, pls. 1: 5, 6; 2: 4, 7 [ubi syn.].

**Type material:** lectotype, fragmentary twig BSPG coll. Univ. Würzburg no. 6166 (ex coll. Schenk), designated by Bosma et al. (2012: 24); see Bosma et al. (2012: 24) for the list of epitypes.

**Type locality:** “Altenburg” near Quedlinburg, Saxony-Anhalt, Germany.

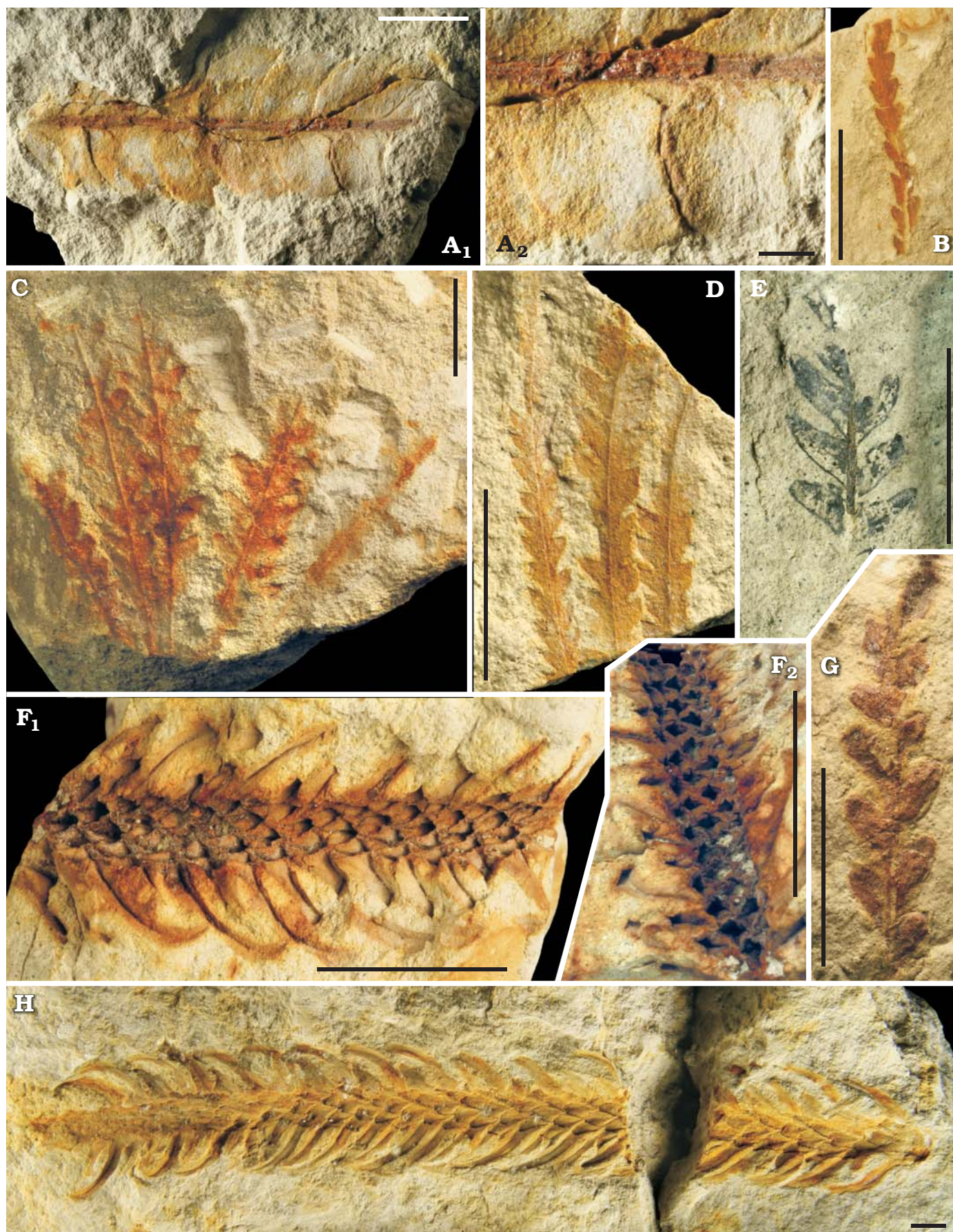
**Type horizon:** Heidelberg Formation, upper Santonian.

**Material.**—Fragmentary leafy twigs: two from Chełm, MZ VII/32/13 (investigated under the SEM) and MZ VII/33/1; single specimen from Jasionna, PIG 60 III 3 and from Potelych, L PB-K.16 (formerly 7678); two from Krasnoblód, MZ VII/32/11 and JS 6.

**Description.**—The preserved part of shoots up to 10 cm long; leaf scars rhomboid, ca. 3 mm wide and 3.5–5 mm long. Leaves spirally arranged, either straight or slightly adaxially incurved, linear (Chełm) or lanceolate (other local-

Fig. 3. Campanian and Maastrichtian ferns and conifers. **A.** *Cladophlebis* sp., sterile specimen PIG 60 III 1; Ignacówka near Pińców, lower Maastrichtian? → General view (A<sub>1</sub>), enlargement of a single pinnule (A<sub>2</sub>). **C, E, G.** *Matonidium* sp. **C.** Sterile specimen L PB-K.20[.1]; Potelych, upper Campanian. **E.** Fertile specimen ZPAL Pl 4/5/1; Szozdy, Campanian. **G.** Sterile specimen L PB-K.10; Potelych, upper Campanian. **B, D.** *Microphyllopteris* sp. **B.** Sterile specimen L PB-K.60; L'viv, Maastrichtian? **D.** Sterile specimen L PB-K.21; Pidtemne, upper? Maastrichtian. **F, H.** *Geintzia reichenbachii* (Geinitz, 1842) Hollick and Jeffrey, 1909. **F.** Specimen L PB-K.25, holotype of *Araucarites cryptomeriefolius* Drygant, 1998; Pidtemne, upper? Maastrichtian. Lateral (F<sub>1</sub>) and axial (F<sub>2</sub>) views. **H.** Specimen MZ VII/32/9; Krasnoblód, upper Campanian. Scale bars 10 mm, except A<sub>2</sub>, for which it is 2.5 mm.







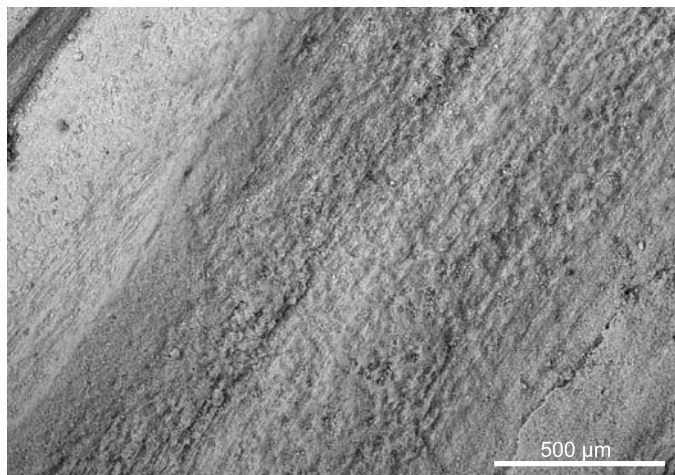


Fig. 4. Conifer *Cunninghamhamites squamosus* Heer, 1873. Single leaf from the specimen MZ VII/32/13, Chelm, Maastrichtian, SEM view.

ities), up to at least 40 mm long and 2 mm wide; the greatest width is in the basal part.

Leaves of the Chelm specimens ca. 1.2 mm wide (Fig. 4). Two parallel stomatal bands ca. 350 μm wide separated by an intercostal zone ca. 300 μm wide; intercostal cells elongate, ca. 20 μm wide.

**Remarks.**—The cuticular features of the specimen MZ VII/32/13 from Chelm, although poorly preserved, allow to refer the described material to *Cunninghamhamites squamosus* Heer, 1871, initially described from the Santonian of Quedlinburg, characterised by absence of microscopic marginal serration (Bosma et al. 2009). *C. lignitum* from the Cenomanian of Bohemia has serrate leaves (Kvaček 1999).

The material from Chelm is rather different in overall aspect when compared to specimens from other localities, the leaves being narrower and linear. This feature is tentatively interpreted as reflecting intraspecific variability and preservation artifacts (chalk versus “opoka”) rather than taxonomically important characters.

**Stratigraphic and geographic range.**—North America and Europe, Santonian to Maastrichtian (Bosma et al. 2012).

*Cunninghamhamites ubaghsii* Debey ex Ubaghs, 1885 emend. van der Ham, van Konijnenburg-van Cittert, and Nieuwenhuis, 2004

Figs. 5J, 6B.

1885 *Cunninghamhamites Ubaghsi*; Ubaghs 1885: 28.

2004 *Cunninghamhamites ubaghsii* Debey ex Ubaghs, 1885; van der Ham et al. 2004: 89–94, figs. 3–6 [ubi syn.].

2012 *Cunninghamhamites ubaghsii* Debey ex Ubaghs; Bosma et al. 2012: 25; pl. 2: 1.

**Type material:** holotype, subcomplete twig IRSNB-Paleobot. b4318 (van der Ham et al. 2004: fig. 3).

**Type locality:** Kunrade, Limburg, the Netherlands.

**Type horizon:** Maastricht Formation, upper Maastrichtian.

**Material.**—Fragmentary leafy twigs MZ VII/33/36 from Krasnobród and ZPAL PI 4/9/1 from Wola Pawłowska.

**Description.**—Axis fragment unbranched, ca. 10 cm long. Leaf base cushions poorly preserved. Leaves decurrent, their free portions spreading in all directions at an angle not exceeding 30°, dorsiventrally flattened, linear, up to at least 9 cm long (apices not observed) and 2–4 mm wide. Margin entire. Blade with a distinct median keel or vein, sometimes also with finer longitudinal striations.

**Remarks.**—Two relatively large bark impressions devoid of leaves (therefore specifically unidentifiable) from Krasnobród (KrM Pb 2/1, 2) are referred here as *Cunninghamhamites* sp. (Fig. 5I). Leaf cushions are obovoid-rhomboid, spirally arranged, 8–10 mm long and 5–7 mm wide.

**Stratigraphic and geographic range.**—Limburg (Kunrade and vicinity of Maastricht), upper Maastrichtian (van der Ham et al. 2004); Roztocze (Krasnobród and Wola Pawłowska), uppermost Campanian.

## Family unknown

### Genus *Geinitzia* Endlicher, 1847 sensu Harris, 1979

**Type:** *Geinitzia cretacea* Endlicher, 1847, nomen dubium; Cretaceous; Bohemia and Saxony (Endlicher 1847: 281).

**Remarks.**—The generic name *Geinitzia* was used in several different ways (Zijlstra et al. 2010). A recent proposal of typification with *G. formosa* Heer, 1871 as the type of a natural genus (Zijlstra et al. 2010) has been rejected (Herendeen 2011). *Geinitzia* is therefore used here as a rather wide form genus, as emended by Harris (1979).

### *Geinitzia reichenbachii* (Geinitz, 1842) Hollick and Jeffrey, 1909

Figs. 2C, D, 3F, H, 5D–F, K.

1907 *Geinitzia formosa* Heer; Nowak 1907a: 48, pl. 1: 4, 14.

1907 *Sequoia pectinata* Heer (?); Nowak 1907a: 47–48, pl. 2: 18.

1967 *Sequoia reichenbachii* Heer; Malicki et al. 1967: 223–224, figs. 4–7.

1967 *Sequoia pectinata* Heer; Malicki et al. 1967: 224, fig. 8.

part 1967 *Geinitzia cretacea* Unger; Malicki et al. 1967: 225, figs. 11, 12, non figs. 9, 10.

part 1967 *Cunninghamia elegans* Corda; Malicki et al. 1967: 226–227, non fig. 10.

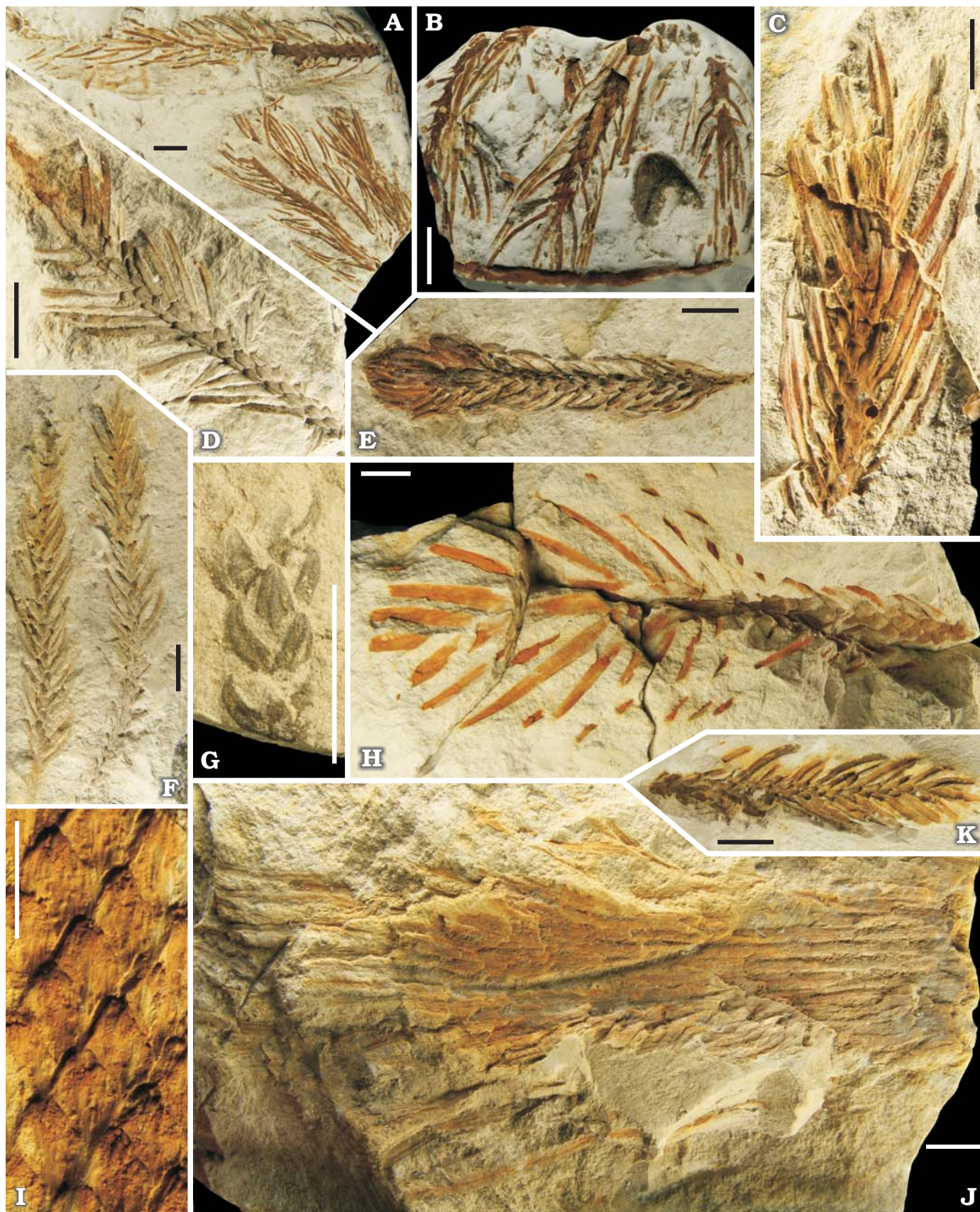
1998 *Araucarites cryptomeriefolius* Drygant, sp. nov.; Drygant 1998: 144; pl. 1: 5.

2006 *Araucarites cryptomeriefolius* Drygant 1998; Mamčur 2006: 41, pl. 1: 1–2.

2010 *Geinitzia reichenbachii* (Geinitz, 1842) Hollick and Jeffrey, 1909; Kunzmann 2010: 126–134, text-figs. 3–4, pls. 1–4 [ubi syn.].

Fig. 5. Campanian and Maastrichtian conifers. **A–C.** *Cunninghamhamites squamosus* Heer, 1871. **A.** Specimen MZ VII/33/1; Chelm, Maastrichtian. **B.** Specimen MZ VII/32/13, Chelm; Maastrichtian. **C.** Twig PIG 60 III 3; Jasionna, upper Campanian or lower Maastrichtian. **D–F, K.** *Geinitzia reichenbachii* (Geinitz, 1842) Hollick and Jeffrey, 1909; Kazimierz Dolny, upper Maastrichtian. **D.** Twig MZ VII/32/11. **E.** Twig MZ VII/32/4. **F.** Two twigs MZ VII/33/10. **K.** Twig MZ VII/33/21. **G.** *Pagiophyllum* sp. Fragment of a twig L PB-K.90; Nemyriv, Campanian. **H.** *Cunninghamhamites* sp., twig ZPAL PI 4/7/1; →





Nasiłów, upper Campanian. **I.** *Cunninghamites* sp., bark impression KrM Pb 2/1; Krasnobród, upper Campanian. **J.** *Cunninghamites ubaghsii* Debey ex Ubaghs, 1885 emend. van der Ham et al., 2004, twig MZ VII/33/36; Krasnobród, upper Campanian. Scale bars 10 mm.



*Type material*: neotype, fragmentary twig MMG PB CsK 220 selected and illustrated by Kunzmann (2010: pls. 1, 4: 3A).

*Type locality*: Hudcov/Hundorf, Bohemia.

*Type horizon*: Teplice Formation, upper Turonian.

*Material*.—A single ramified branch system, JS 7, from Krasnobród and several twig fragments from Krasnobród (MZ VII/32/9, ZPAL PI 4/1/1), Kazimierz Dolny (MZ VII/32/4bis, 7, 10–11, 14–16, 18, 20–28, 30–35, MZ VII/33/13–15, 17–19, 21–22, 26, 40, 47, 53), Piotrawin (MZ VII/33/4), Rachodoszcze (MZ VII/32/1–2), Pidtemne (L PB-K.25), Potelych (L PB-K.3, 7, 14 formerly 7665, 7669, 7676), Tarnawatka (L PB-K.60), Zashkiv (ZPAL PI 4/4/1).

*Description*.—Branches departing at an angle of 30–50° from a main branch up to 7 mm wide (Fig. 2D). Twig fragments up to ca. 13 cm in length; leaf scars 2 mm wide and 3–4 mm long. Leaves densely packed, spirally arranged, falcate, basally not contracted, spreading from the axis at a variable angle (30–70°), rhomboid in cross-section (two keels, one adaxial and one abaxial), up to 17 mm long; apices acute (often they are not preserved, so an appearance of rounded apex results).

*Remarks*.—The described specimens belong to the genus *Geinitzia* on account of their quadrangular subdecurent leaves. Among the species of this genus they are most similar to *G. reichenbachii* in form and size of the leaves. Those of *G. formosa* are smaller than in the studied material. The leaves are falcate through straight to S-shaped in the fossil conifer termed “*G. cretacea* Unger, 1852” by Němejc and Kvaček (1975), from the Senonian of Bohemia, and nearly straight in *G. rigida* (Phillips, 1875) Harris, 1979, from the Jurassic of Yorkshire (Kunzmann 2010). However, lack of cuticular characters and considerable stratigraphic interval between the analysed sample (Campanian to Maastrichtian) and the type level of *G. reichenbachii* (late Turonian) indicate that our identification should be treated with some caution. Detailed comparison with coeval conifers from Limburg (van der Ham et al. 2001) is also precluded by lack of cuticles; nonetheless, macromorphological differences between those taxa and the described material can also be shown: *Cryptomeriopsis eluvialis* van der Ham, 2001 has broadly decurrent leaves (subdecurent in our material), whereas *Elatidopsis cryptomerioides* (Miquel, 1853) van der Ham, 2001 has flattened needles (quadrangular in our material).

*Stratigraphic and geographic range*.—Bohemia, Turonian; Swalmen, Netherlands, Santonian; Roztocze and Volhynia-Podolia Upland, Campanian to Maastrichtian (outside the studied area after Kunzmann 2010).

## Genus *Elatocladus* Halle, 1913

*Type*: *Elatocladus heterophylla* Halle, 1913; Jurassic; Hope Bay, Antarctica.

### *Elatocladus*? sp.

Fig. 5H.

*Material*.—A single fragmentary shoot from Nasiłów, ZPAL PI 4/7/1.

*Description*.—The preserved part of the single shoot is ca. 13 cm long; leaf scars rhomboid, ca. 5 mm wide and 6 mm long. Leaves spirally arranged, either straight or slightly adaxially incurved, elliptic in cross section (about twice as wide as thick; no keel), with a distinct midvein, up to at least 4 cm long and 5 mm wide; the greatest width is at ca. one fifth of the length. The tip is probably acuminate.

*Remarks*.—This twig is quite different from the rest of the material described here in its much wider needles (5 mm compared to 2 mm in *Cunninghamites squamosus* for leaves of the same length of ca. 4 cm). There is also a distinct midrib (absent in *C. squamosus*, present in *C. ubaghsii* the leaves of which have, however, a very different form). This specimen is tentatively accommodated within *Elatocladus* Halle, 1913, a very wide form genus, the species of which may belong to Taxodiaceae, Cephalotaxaceae, Podocarpaceae, Araucariaceae, Pinaceae, Taxaceae, or Cupressaceae (Miller and Hickey 2010).

## Genus *Pagiophyllum* Heer, 1881

*Type*: *Pagiophyllum circinicum* Heer, 1881; Jurassic, Portugal.

### *Pagiophyllum* sp.

Fig. 5G.

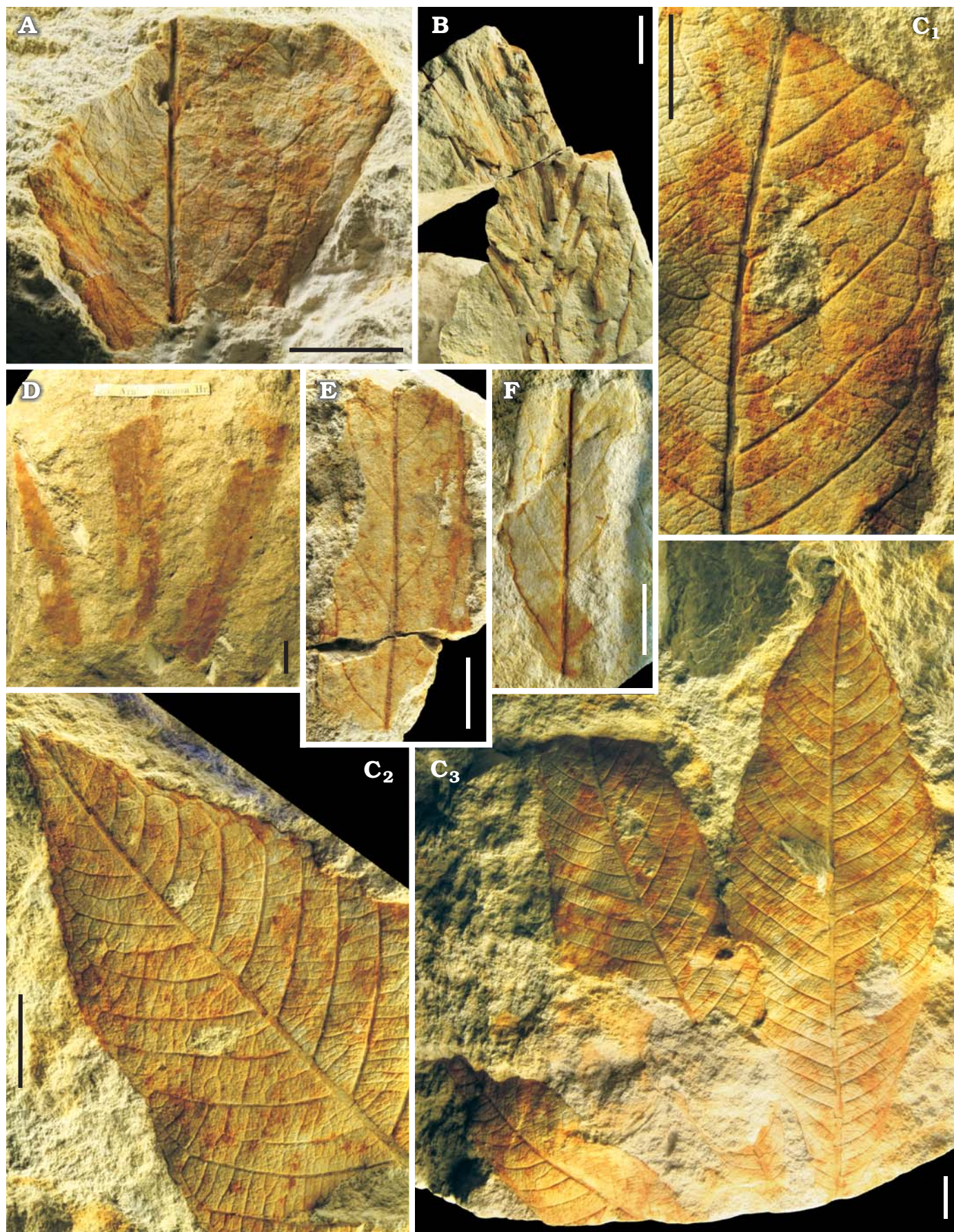
*Material*.—A single fragmentary twig L PB-K.90 from Nemyriv borehole, depth 58 m; (upper?) Campanian.

*Description*.—The twig fragment is unbranched, 15 mm long and 5 mm wide. Leaves persistent, spirally arranged. Free leaf portions spreading under angles about 30–45°, 3.5–5 mm long and up to 2.5 mm wide. Three distinct keels present on abaxial surfaces, one median and two near the margins; adaxial side concave, curving towards the axis.

*Remarks*.—The described fragment is quite similar to *Pagiophyllum* sp. represented by the single specimen RGM 21188 from the Vaals Formation (lower Campanian) of Vaalsbroek (Limburg, Netherlands) described by van der Ham and van Konijnenburg-van Cittert (2004: fig. 12) in the spiral arrangement and form of leaves (permitting to infer a probable taxodiaceous affinity) as well as the presence of keels on their

Fig. 6. Campanian conifers and angiosperms. **A.** *Dicotylophyllum* sp. 3, fragmentary leaf ZPAL PI 4/1/5; Krasnobród, upper Campanian. **B.** *Cunninghamites ubaghsii* Debey ex Ubaghs, 1885 emend. van der Ham et al., 2004, fragmentary twig ZPAL PI 4/9/1; Wola Pawłowska, Campanian. **C.** *Debeya paulinae* sp. nov., fragmentary compound leaf G PbK 1 (paratype); Krasnobród, upper Campanian. General view (C<sub>3</sub>), enlargement of the apical region of the median leaflet showing venation and serration of the margin (C<sub>2</sub>), enlargement of a fragment of the medio-lateral leaflet showing venation and serration of the margin (C<sub>1</sub>). **D.** *Araliopsoides*? cf. *minor* (Berry, 1925) comb. nov., fragmentary specimen L PB-K.20[.2]; Potelych, upper Campanian. **E.** Cf. *Eucalyptolaurus* sp., fragmentary leaf MZ VII/33/28; Krasnobród, upper Campanian. **F.** *Dicotylophyllum* sp. 2, fragmentary leaf MZ VII/33/27; Krasnobród, upper Campanian. Scale bars 10 mm.







lower surfaces. The specimens differ in the density of leaves which is lower in the one described here.

Subinfradivision Angiospermae Brown and Doell ex Doell, 1857 (= Magnoliophytina Cronquist, Takhtajan, and Zimmermann, 1966)

Class Dicotyledoneae de Candolle, 1819  
(= Magnoliopsida Brongniart, 1843)

*Remarks.*—As discussed elsewhere (Halamski 2010), the heterogeneous class Dicotyledoneae may be maintained for practical reasons. Although no unequivocal attribution to a natural taxon can be given for any of the studied leaves, some of them are tentatively arranged according to the natural system after proposed affinities. Remaining leaves are arranged according to an artificial (morphographic) system (Krassilov 1979; Crabtree 1987) and those too poorly preserved or otherwise unclassifiable are referred to *Dicotylophyllum* auct. (for the reasons why *Dicotylophyllum* de Saporta, 1894 may not be used for that effect, see below). Leaf descriptions are standardised after Ellis et al. (2009) with following minor additions and corrections: pedate leaves are considered an organisation type separate from palmate ones; the hyphodromous venation (Hickey 1973: 26; Dilcher 1974: 32) is considered a separate organisation model; the description of blade characters follows the ontogenetic pattern (therefore “increasing distally” and not “decreasing proximally”); moreover, the term “quinternary” has been replaced by a linguistically more correct “quinquenary” (Latin *quinquenarius*, fivefold).

Subclass Magnoliidae Novák ex Takhtajan, 1967 emend.

Order Laurales Perleb, 1826

Family Lauraceae Jussieu, 1789 nom. cons.

Genus unknown, aff. *Eucalyptolaurus* Coiffard, Gomez, Thiébaud, Kvaček, Thévenard, and Néraudeau, 2009

aff. *Eucalyptolaurus* sp.

Fig. 6E.

part 1967 *Laurus affinis* Velen.; Malicki et al. 1967: 229–230; pl. 8: 25, non pl. 8: 24.

*Material.*—A single fragmentary leaf MZ VII/33/28 from Krasnohrod.

*Description.*—The preserved part is about 5 cm long and 2.2 cm wide; the total length cannot be estimated. Shape probably oblong, margin entire, primary venation pinnate with one basal vein and alternating eucamptodromous secondaries, their spacing possibly increasing apically. Poorly preserved intercostal tertiary veins percurrent, rarely spaced. A possible fragment of an intramarginal vein present.

*Remarks.*—This fragmentary leaf is compared to *Eucalyptolaurus depreii* Coiffard Gomez, Thiébaud, and Kvaček, 2009 from the uppermost Albian–lowermost Cenomanian of

Charente-Maritime (western France; Coiffard et al. 2009) on account of an elongate shape, pinnate venation and presence of an intramarginal vein (it should be noted that this may also be a subadjacent secondary asymptotically approaching the margin). Differences in our taxon include greater width to length ratio and gradual incurving of the secondary veins (*E. depreii* has very elongate leaves and relatively short secondaries reaching the intramarginal vein). A somewhat speculative accommodation within Lauraceae may be suggested.

The second leaf included within the same taxon by Malicki et al. (1967) has straight, subopposite secondaries and no intramarginal vein. It is referred to here as *Dicotylophyllum* sp. 2 (see below).

Supersubclass Eudicotyledoneae Doyle and Hotton ex Halamski, herein.

*Diagnosis.*—Angiospermae pollinis granis tricolpatis vel formas a tricolpatis procedentes habentibus, nec tamen trichotomosulcatis (sensu Doyle et Endress 2000); foliis simplicibus vel pinnatis, palmatis, pedatis, aliterve compositis.

Angiosperms with tricolpate pollen or tricolpate-derived pollen forms, trichotomosulcate pollen (sensu Doyle and Endress 2000) being excluded. Leaves either simple or pinnately, palmately, pedately, or otherwise compound.

*Remarks.*—The term “tricolpates” was introduced by Donoghue and Doyle (1989: 29) and its more widely used synonym “eudicots” by Doyle and Hotton (1991: 184). The concept of a monophyletic group defined by tricolpate or tricolpate-derived pollen has gained general acceptance (Magallón et al. 1999; Judd and Olmstead 2004 and references therein; Judd et al. 2008; Endress 2010; Soltis et al. 2010, 2011; Friis et al. 2011; see also Kubitzki 2007: 13, for a discussion of palynologic characters in a phylogenetic context). It has been formalised under the provisions of the PhyloCode (Cantino et al. 2007) but never according to the ICBN rules. As a result this taxon is absent from recently published classification systems (Thorne and Reveal 2007; Takhtajan 2009), a major discrepancy with molecular-based results (Halamski 2010). This situation is amended herein through formalisation of the supersubclass Eudicotyledoneae.

The diagnosis consists of two parts. The first one refers to palynologic characters and is taken without change from Doyle and Hotton (1991). The second one refers to foliar characters (for a discussion of leaf characters in a phylogenetic context see Hickey and Wolfe 1975; Doyle 2007). The analysis of angiosperm leaf architecture shows that the leaves of non-eudicot dicotyledons (ANITA group, Chloranthales, Ceratophyllaceae, and magnoliids; i.e., subclasses Chloranthidae Wu, 2002 and Magnoliidae Novák ex Takhtajan, 1967 sensu Thorne and Reveal 2007) are nearly always simple (*Illigera* of Hernandiaceae is the only exception, with trifoliolate, seldom pentafoliolate leaves; Kubitzki 1993; Li et al. 2008). Compound leaves are also relatively rare in monocots (Gunawardena and Dengler 2006). Pinnate, palmate, pedate, and other compound leaves are common in

several groups of the Eudicotyledoneae. This character is therefore of some diagnostic value especially when dealing with fossil material. Earliest angiosperm compound leaves are known from the middle Albian (Hickey 1974).

A supersubclass is considered a rank intermediate between a class and a subclass (Art. 4.3 of the ICBN).

### Subclass, order, and family incertae sedis

#### Informal group *Debeya* sensu Krassilov, Lewy, Nevo, and Silantieva, 2005

*Genera included:* *Debeya* Miquel, 1853; *Eudebeya* Krassilov, 2005; *Platydebeya* Krassilov, 2005; *Retrodewalquea* Krassilov, 2005.

*Species excluded from the Debeya group:* *Debeya pentaphylla* (Velenovský, 1884) Knobloch, 1964; *Debeya coriacea* (Velenovský, 1884) Knobloch, 1964.

*Remarks.*—The genus *Debeya* s.l. is probably heterogenous (Krassilov 1979; Kvaček et al. 2001; Krassilov et al. 2005). A eudicotyledonous affinity of the *Debeya* group (with *Debeya* as restricted here) is inferred on account of compound architecture of the leaves.

The Cenomanian species *Dewalquea pentaphylla* Velenovský, 1884 and *Aralia coriacea* Velenovský, 1889 (both transferred to *Debeya* by Knobloch 1964) differ from the true *Debeya* (incl. *Dewalquea*) in having “leaflets” of equal size, often inflated “petiolules” and in frequent occurrence of single “leaflets” (Velenovský 1889; this is rather rare in the entire material described here). Probably they do not belong to the *Debeya* group.

#### Genus *Debeya* Miquel, 1853

*Type:* *Debeya serrata* Miquel, 1853; Maastrichtian, Kunrade, Limburg, Netherlands.

*Remarks.*—The subdivision of the genus *Debeya* into two subgenera, *Debeya* and *Dewalquea* based on the number of leaflets (three in the former, five in the latter; Herman and Kvaček 2010) might not seem to be the best solution given great variability that may be observed in living plants (e.g., *Clematis x jackmannii* Moore, 1863 having tri- and penta-foliolate leaves with both free and coalescent leaflets; this argument was given by Rüffle 1995: fig. 2). Nonetheless, as a matter of fact, intermediate forms (with pair numbers of leaflets) are rare and penta-foliolate leaves occur very seldom (if ever) in trifoliolate species and vice versa; similar observations are given by Krassilov et al. (2005). The type of *Debeya serrata* (U 444, illustrated by Miquel 1853: pl. 1: 1) is trifoliolate and the material from the type region contains five trifoliolate specimens, two tri- or tetra-foliolate and one hexa- or hepta-foliolate (Raymond van der Ham, personal communication 2010). In the case of the material described here, none of the specimens is undoubtedly trifoliolate (MZ VII/33/40 is most probably incomplete). The extraordinary variation of *Clematis x jackmannii* is explained by its hybrid character. Within *Helleborus*, a Recent genus containing species with pedate organisation of leaves, there are no intermediates between trifoliolate and pedate conditions (Tamura 1995).

All this suggests that the trifoliolate versus pedate character of leaves is a valid systematic criterion (although probably not to be used alone).

According to Knobloch (1964: 150) the serrate versus entire character of the margin is an important systematic criterion. This point of view seems to be problematic (as it was already for Berry 1916) for the following reasons: (i) serrate and (apparently) integrimarginate leaves (otherwise identical) are present in the same levels; (ii) variation between serrate and integrimarginate leaves has been documented in a contemporary species of similar leaf architecture, namely *Helleborus lividus* Aiton, 1789 (the type is serrate, while *H. lividus* var. *integrifolius* de Candolle, 1805 has no teeth; Saporta and Marion 1873); (iii) the serrate margin may roll down into the rock, wherefore the leaves appear as entire: such a situation has been described, e.g., for *Rhamnus salicifolius* Lesquereux in Hayden, 1868 from the Maastrichtian of North Dakota (Peppe et al. 2007). On the other hand, it is not excluded that species may be predominantly serrate or predominantly integrimarginate; or else that some species may be indistinctly serrate and integrimarginate and other exclusively either serrate or integrimarginate. This character may be of some systematic value but, once more, should not have to be used alone.

#### Subgenus *Debeya* (*Dewalquea*) (de Saporta and Marion, 1873) stat. nov.

*Type:* *Dewalquea haldemiana* Debey ex de Saporta and Marion, 1873; Late Cretaceous, Haldem, Westphalia.

*Species included:* *Dewalquea haldemiana* Debey ex de Saporta and Marion, 1873; *Dewalquea aquisgranensis* de Saporta and Marion, 1873; *Dewalquea insignis* Hosius and von der Marck, 1880; *Dewalquea smithii* Berry, 1910; *Dewalquea lusitanica* Teixeira, 1950; *Debeya bohémica* Knobloch, 1964.

*Species excluded:* *Dewalquea gelindenensis* de Saporta and Marion, 1873 (*Platanus*; see Kvaček et al. 2001).

#### *Debeya paulinae* sp. nov.

Figs. 2B, C, 6C, 7E, F, 8, 9B, 10A.

1907 *Dryophyllum aquamarum* Ward; Nowak 1907a: 50, pl. 1: 9.

1907 *Dewalquea pentaphylla* Vel.; Nowak 1907a: 54, pl. 2: 20.

1966 *Dewalquea pentaphylla* Velen.; Karczmarz and Popiel 1966: 274–275.

1967 *Dewalquea pentaphylla* Velen.; Malicki et al. 1967: 230, pl. 9: 27.

1967 *Dryophyllum aquamarum* Ward; Malicki et al. 1967: 228, pl. 7: 21.

1975 *Dewalquea pentaphylla* Velen.; Kohlman-Adamska 1975: 164, pl. 1: 4.

*Etymology:* In honour of my spouse Paulina.

*Type material:* Holotype: a subcomplete leaf JS 3, figured herein in Fig. 2B. Paratypes: three subcomplete leaves MZ VII/32/36, IB sub *Dewalquea pentaphylla* (part and counterpart), JS 3, KrS 1, all from Krasnobród; fragmentary leaves KrM Pb 1/1, 3, 6, G Pb-K1, IB 721, MZ VII/33/42 from Krasnobród, L PB-K.1 (formerly 7663) from Potelych; fragments of leaves L PB-K9 (formerly 7671) from Potelych, L PB-K.67 (formerly 30743) from the vicinity of Rava-Rus'ka, ZPAL 4/1/8, KrM Pb 1/2, 4, 5, 7, MZ VII/33/25, 34, 36, 45, 47, 49 from Krasnobród, ZPAL Pl 4/2/1 from Blizów.

*Type locality:* Krasnobród, town quarry.



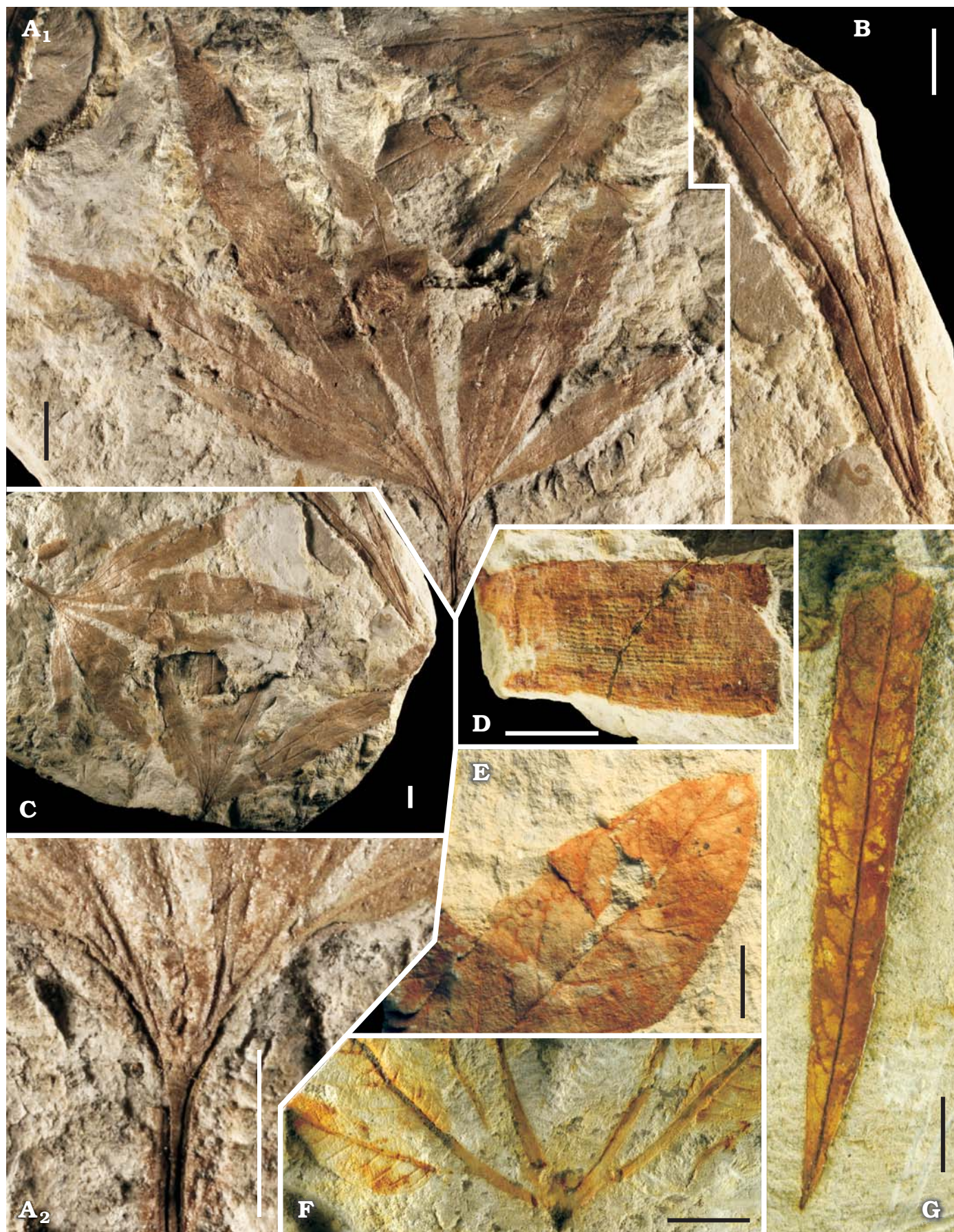




Table 1. Comparison of species of *Debeya* present in the studied material.

Species	<i>Debeya paulinae</i> sp. nov.	<i>Debeya insignis</i> (Hosius and von der Marck, 1880) Knobloch, 1964	<i>Debeya haldemiana</i> (Debey ex de Saporta and Marion, 1873) Knobloch, 1964
Type locality	Krasnoblód	Haldem	Haldem
Number of leaflets	(4–) 5 (–6)	5–7	5–7
Leaflet length to width ratio	2.5–3.5	5.5–7	12.5–16
Margin	most often serrate, seldom entire?	serrate?	entire
Geographic distribution	Roztocze, Nida Trough?	Westphalia, Nida Trough, Roztocze	Westphalia, Nida Trough, Roztocze, Volhynia-Podolia Upland

Type horizon: upper Campanian.

**Diagnosis.**—Pentafoiolate *Debeya* with broad leaflets (width to length ratio 2.5–3.5).

**Description.**—Leaf compound, pedate, petiolate, of four to six (most commonly five) petiolulate leaflets. Petiole up to 2.7 cm, longitudinally striate, proximally inflate; petiolules up to at least 2 cm. Blade attachment marginal. Leaflet blades notophyll to mesophyll, up to ca. 16 cm in length, symmetric, oblong, length to width ratio from 2.5:1 to 3.5:1. The median leaflet is usually the widest, but more seldom all leaflets are subequal in size. Base cuneate, apex weakly acuminate (possibly to rounded; Fig. 7E). Margin unlobed, most often serrate, seldom (apparently?) untoothed (Fig. 7E). Teeth small (ca. 1 mm wide and <0.5 mm high), rounded, either with both flanks convex or proximal flank convex and distal one concave (Fig. 6C<sub>1</sub>).

Primary venation pinnate with a single strong, straight primary vein. Major secondaries festooned semicraspedodromous, their spacing regular, 1.5–2 per cm, attachment excurrent, angle to midvein uniform, ca. 60°. Intersecondary proximal course parallel to major secondaries, their length <50% of the subjacent secondary, distal course tending and joining the subjacent secondary; frequency less than one per intercostal area. Intercostal tertiary veins percurrent, most often straight, sometimes sinuous or alternate. Quaternary and quinquenary venation regular reticulate. Principal vein terminates at tooth apex.

**Remarks.**—*Debeya paulinae* sp. nov. is nearest to *D. smithii* (Berry, 1910) Knobloch, 1964 from the Tuscaloosa and Black Creek Formations (Coniacian?) of Alabama and South Carolina in having pentafoiolate pedate leaves with relatively wide, ovate, petiolulate leaflets. They are distinguished by the form of the median lateral leaflets, symmetric in the former and asymmetric in the latter (Berry 1919: 86). *Debeya aquisgranensis* (Saporta and Marion, 1873) Knobloch, 1964 from

the Santonian of Aachen has external leaflets always, or often, coalescent with median lateral ones (de Saporta and Marion 1873: 61). Neither condition is ever seen in our material. The comparison of *D. paulinae* with other representatives of the genus *Debeya* present in the studied material is given in Table 1 and in Fig. 8.

**Stratigraphic and geographic range.**—Roztocze (south-east Poland), late Campanian to early Maastrichtian.

*Debeya insignis* (Hosius and von der Marck, 1880) Knobloch, 1964

Figs. 7A, C, 8, 9A, F.

1880 *Dewalquea insignis* Hos. & v. d. Marck; Hosius and von der Marck 1880: 172–173, pls. 32: 111–113, 33: 109, 34: 110.

1962 *Dewalquea coriacea* Vel.; Cieřliński and Milaković 1962: 253–254, pl. 2: 2.

non 2010 *Debeya insignis* (Hosius and Marck) Knobloch, 1964; Herman and Kvaček 2010: 68–69, text-fig. 29, pl. 24: 1–3.

**Type material:** Lectotype (selected herein), leaf PBO 1021-1 figured by Hosius and von der Marck (1880: pl. 33: 109) and refigured herein in Fig. 7A, C. Paralectotype, leaf PBO 1021-2 figured by Hosius and von der Marck (1880: pl. 33: 109) and refigured in Fig. 7C. Other para-

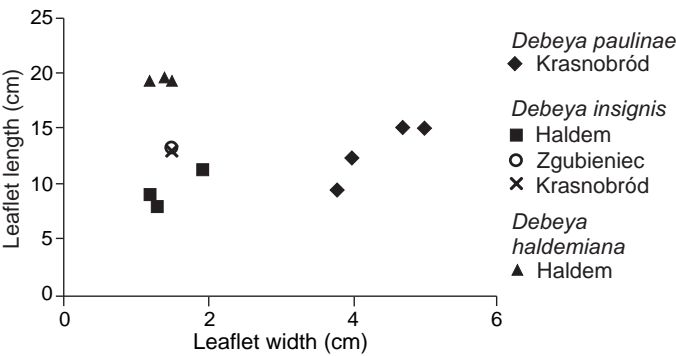


Fig. 8. Biometric characteristics of species of *Debeya* present in the studied material: length to width scatter diagram of leaflet shapes.

← Fig. 7. A, C. Eudicot *Debeya insignis* (Hosius and von der Marck, 1880) Knobloch, 1964. A. Lectotype PBO 1021[-1]; Haldem, Stewweder Berg, upper Campanian. General view (A<sub>1</sub>), enlargement of the petiolule branching (A<sub>2</sub>). C. General view of the slab PBO 1021 showing the lectotype (shown in A) and a paralectotype (PBO 1021[-2]) of *Debeya insignis* as well as two leaflets of *Debeya haldemiana* (shown in B); Haldem, Stewweder Berg, upper Campanian. B, G. *Debeya haldemiana* de Saporta and Marion, 1873. B. Fragmentary leaf PBO 1021[-3]; Haldem, Stewweder Berg, upper Campanian. G. Isolated leaflet ZPAL 4/2/2; Bliźów, lower Maastrichtian. D. *Eolirion* sp., fragmentary leaf ZPAL Pl 4/1/9; Krasnoblód, upper Campanian. E. *Debeya paulinae* sp. nov., fragmentary leaf KrM Pb 1/6 (paratype); Krasnoblód, upper Campanian. F. *Debeya paulinae* sp. nov., paratype KrS 1, enlargement of the petiolule branching (see general view in Fig. 2C). Scale bars 10 mm.



lectotypes, leaves figured by Hosius and von der Marck (1880: pl. 32: 111–113, 34: 110), repository not traced.

*Type locality:* Haldem, Westphalia, Germany.

*Type horizon:* upper Campanian.

*Material.*—A subcomplete leaf PIG 60.III.7 from Zgubieniec; two more fragmentary leaves, JS 4 and JS 5 from Krasnobród.

*Description.*—Leaf compound, pedate, petiolate, of six to seven? petiolulate leaflets. Petiole up to 3.5 cm, longitudinally striate, proximally inflate; petiolules <1 cm. Blade attachment marginal. Leaflet blades microphyll, up to at least 9 cm in length, symmetric, oblong, length to width ratio about 6:1. Base cuneate, apex probably weakly acuminate. Margin unlobed, untoothed.

Primary venation pinnate with a single strong, straight primary vein. Major secondaries festooned semicraspedodromous, their spacing regular, ca. 2 per cm, attachment excurrent, angle to midvein uniform, 50–60°. Intersecondaries absent. Intercostal tertiary veins percurrent.

*Remarks.*—The comparison of *Debeya insignis* with other representatives of the genus *Debeya* present in the studied material is given in Table 1 and in Fig. 8.

The type material was interpreted as having serrate leaves (Hosius and von der Marck 1880: fig. 109). In the present author's opinion, the presence of serration cannot be considered proven (Fig. 7A, C). The leaves in the studied Polish material are entire-margined.

*Stratigraphic and geographic range.*—Westphalia, Nida Trough, Roztocze; “Senonian”.

### *Debeya haldemiana* (Debey ex de Saporta and Marion, 1873) Knobloch, 1964

Figs. 7B, G, 8, 9C, D, E, 10C.

1873 *Dewalquea haldemiana* (*Araliophyllum haldemianum* Deb. Ms.); Saporta and Marion 1873: 60–61, pl. 7: 1–2.

1880 *Dewalquea haldemiana* Sap. & Mar. var. *latifolia*; Hosius and von der Marck 1880: 173, pls. 35: 114, 34: 115.

1880 *Dewalquea haldemiana* Sap. & Mar. var. *angustifolia*; Hosius and von der Marck 1880: 173, pls. 33: 116–117, 34: 118–121.

1907 *Dewalquea haldemiana* Sap. et Mar.; Nowak 1907a: 53, pl. 1: 7, 13.

1998 *Podocarpus mucronatus* Velenovsky et Viniklar; Drygant 1998: 144, pl. 1: 6a, b.

*Type material:* syntypes, leaves figured by de Saporta and Marion (1873: pl. 7: 1, 2); repository not traced (“Krantz collection” according to the protologue). For topotypic material see Remarks, below.

*Type locality:* Haldem, Westphalia, Germany.

*Type horizon:* Upper Campanian.

*Material.*—Subcomplete leaves L PB-K.17 (formerly 156) from Potylicz and L PB-K.26 (formerly 37926A) from Pidtemne; isolated leaflets ZPAL Pl 4/6/1 from Lubycza Królewska and 4/2/2 from Blizów; fragmentary and doubtful specimens from Krasnobród, IB 296.

*Description.*—Leaf compound, pedate; petiole not preserved; bifurcations of the rachis concentrated within a small interval (< 1 cm). Petiolules ca. 1 mm wide and up to 30 mm long. Leaflets linear, up to 10 mm wide, linear, total length of the blade unknown, exceeding 14 cm; margins parallel in the median region, entire. Base shape decurrent, apex not preserved.

A very strong midvein is straight and keeps the same width as the petiolule all along the leaflet. It is depressed in respect to the two parts of the blade on both sides, each half being U-shaped and convex in cross-section. Venation pinnate, eu-camptodromous. Secondaries subopposite, excurrent, departing at an angle of 30–50°, first straight, then curving; the straight part of the secondaries is longer in the distal part of the leaflet.

*Remarks.*—As the types are apparently lost, it may be of interest to note the existence of types of *Dewalquea haldemiana* var. *angustifolia* Hosius and von der Marck, 1880, a taxonomically insignificant variant from the same locality: lectotype, fragmentary leaf MB Pb 2002/388 (designated herein), figured by Hosius and von der Marck (1880: fig. 116) and re-figured herein (Fig. 9D); paralectotype MB Pb 2002/387 figured by Hosius and von der Marck (1880: fig. 117); other paralectotypes (figured by Hosius and von der Marck 1880: figs 118–121) not traced. The types of *D. haldemiana* var. *latifolia* Hosius and von der Marck, 1880 could not be traced either.

*Debeya haldemiana* (along with *Debeya aquisgranensis*) was described from the Cretaceous (Campanian) of Haldem in Westphalia in a paper devoted to the Palaeocene (Thanetian) flora of Gelinden in Belgium (de Saporta and Marion 1873). This resulted in some confusion and both the above-mentioned species were mistakenly listed among Palaeocene taxa by Mai (1995: 347).

*Stratigraphic and geographic range.*—Westphalia (Haldem), Senonian. Roztocze (Lubycza Królewska, Krasnobród?), probably upper Campanian. Volhynia-Podolia Upland (Pidtemne), upper? Maastrichtian.

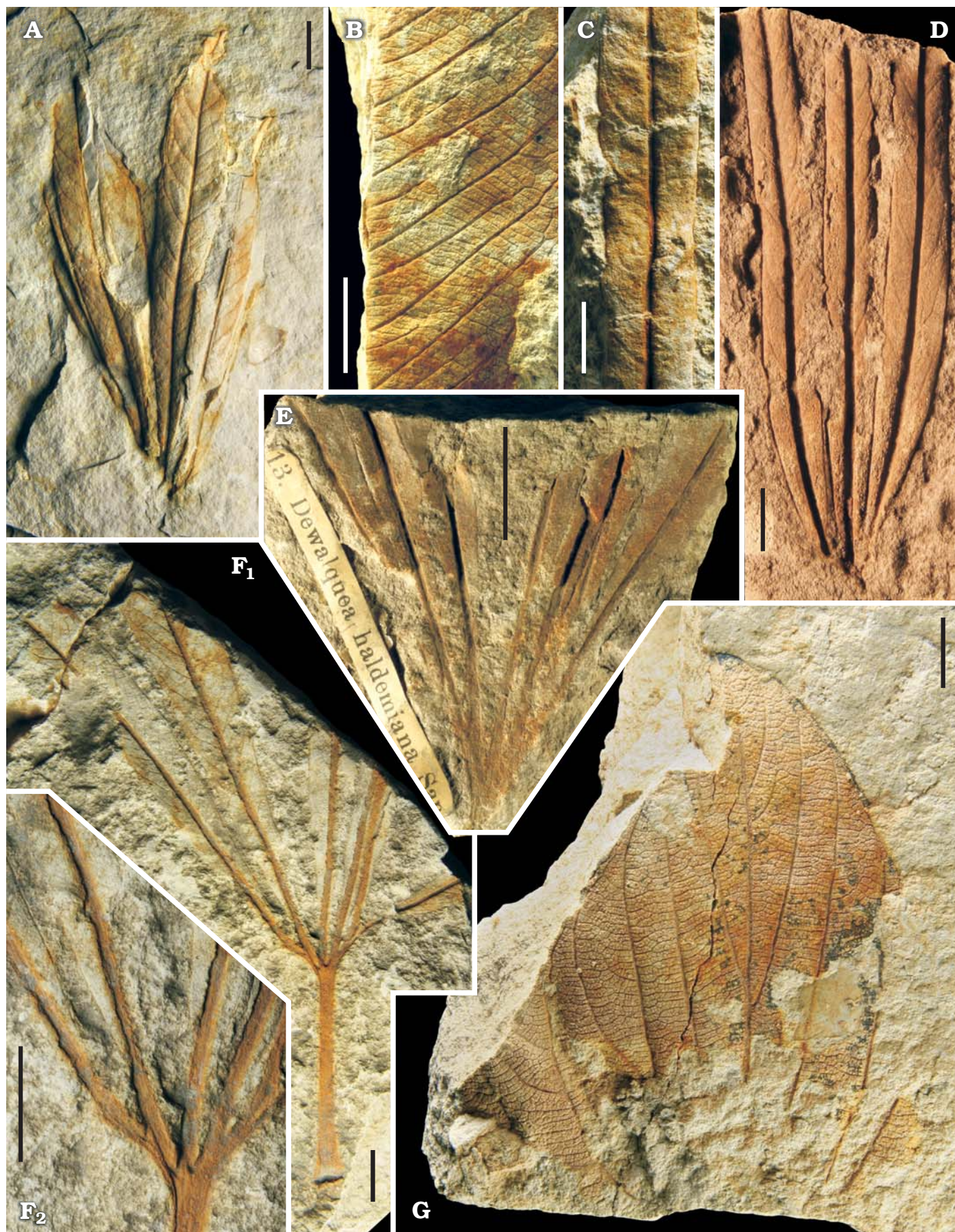
Supersubclass, subclass, order, and family incertae sedis

Form group Platanofolia Krassilov, 1979

Genus *Ettingshausenia* Stiehler, 1857

Fig. 9. Campanian (and Maastrichtian?) angiosperms. **A, F.** *Debeya insignis* (Hosius and von der Marck, 1880) Knobloch, 1964. **A.** Fragmentary leaf JS4; Krasnobród, upper Campanian. **F.** Subcomplete leaf PIG 60.III.7; Zgubieniec, upper Campanian or lower Maastrichtian. General view (F<sub>1</sub>), enlargement of the petiolule branching (F<sub>2</sub>). **C–E.** *Debeya haldemiana* (Debey ex de Saporta and Marion, 1873) Knobloch, 1964. **C.** Isolated leaflet ZPAL Pl 4/6/1 showing venation; Lubycza Królewska, Campanian? **D.** Fragmentary leaf MB Pb 2002/388, lectotype of *D. haldemiana* var. *angustifolia* Hosius and von der Marck, 1880. Haldem, upper Senonian. **E.** Subcomplete leaf L PB-K.17; Potelych, upper Campanian. **B.** *Debeya paulinae* sp. nov., paratype, fragmentary (median?) leaflet showing venation, KrM Pb 1/5; Krasnobród, upper Campanian. **G.** *Cinnamomoides*? sp. nov., fragmentary leaf GFAP JW/Fel-1; Jędrzejów, upper Campanian. Scale bars 10 mm. →







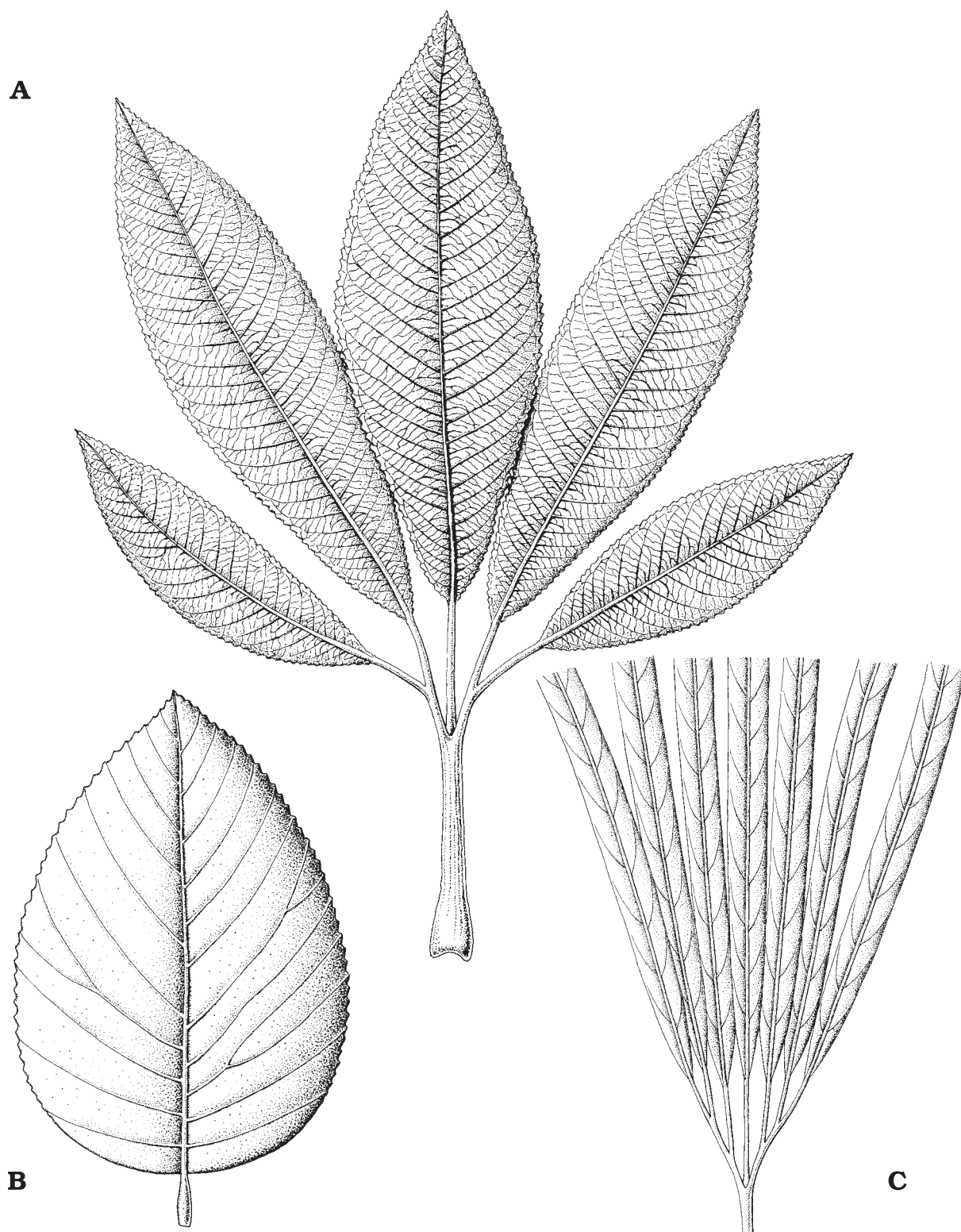


Fig. 10. Reconstructions of leaves of the most characteristic taxa of the late Campanian flora of the studied area (not to scale). **A.** Eudicot *Debeya paulinae* sp. nov. **B.** Dicot *Rarytkinia polonica* (Karczmarz and Popiel in Malicki et al. 1967) comb. nov. **C.** Eudicot *Debeya haldemiana* (Debey ex de Saporta and Marion, 1873) Knobloch, 1964. Drawings by B. Waksmundzki.

*Type:* *Credneria cuneifolia* Bronn, 1835–37; Upper Cretaceous, Cenomanian, Niederschöna, Saxony, Germany.

*Remarks.*—The genus *Ettingshausenia* is accepted here as a

morphogenus (Maslova et al. 2005; Kvaček and Váchová 2006; Maslova and Shilin 2011; against Tschan et al. 2008). Its representatives are often thought related to the Platanaceae

although in some cases a relationship to other families (e.g., Menispermaceae) can be postulated (Rüffle 1995, Kvaček and Váchová 2006).

*Ettingshausenia? lublinensis* (Karczmarz and Popiel, 1971) comb. nov.

Figs. 11C, E.

1907 *Platanus affinis* (?) Lesqx.; Nowak 1907a: 51, pl. 1: 1.

1971 *Platanus lublinensis*; Karczmarz and Popiel 1971: 647–648, pl. 3: 9, 4: 10, ?11.

*Basionym*: *Platanus lublinensis* Karczmarz and Popiel, 1971.

*Type material*: Holotype JS1, large part of a leaf figured by Karczmarz and Popiel (1971: pl. 3: 9) and re-figured herein (Fig. 7C); paratype, a fragmentary leaf figured by Karczmarz and Popiel (1971: pl. 4: 10) (collection number 163, specimen not traced). The second paratype figured by Karczmarz and Popiel (1971: pl. 4: 11) is a loose bark impression and therefore unrecognisable.

*Material*.—Holotype and a single fragmentary leaf L PB-K.2 from Potelych.

*Description*.—Leaf and blade attachment not preserved. Laminar size mesophyll (length of the preserved part 23 cm, estimated total length ca. 30 cm), laminar length to width ratio about 1.25:1, laminar shape obovate, shallowly palmately trilobed (the unlobed part represents about 80% of the total leaf length); margin slightly undulating but mostly entire. Apex of the lateral lobe flattened, that of the median lobe not preserved. Base not preserved.

Primary veins three, basal actinodromous. Secondary veins craspedodromous, their spacing decreasing distally, departing at about 20° (thus parallel to leaf margins); the angle of departure is rather constant throughout the entire leaf, while the secondaries bend inwards in the distal parts of the leaf. Interior secondaries probably absent. Intercostal tertiary vein fabric alternate percurrent; epimedial tertiaries percurrent; exterior tertiaries looped. Quaternary vein fabric irregularly reticulate; quinquenary vein fabric poorly preserved, probably similar to the precedent.

*Remarks*.—The discussed species is tentatively placed within the form genus *Ettingshausenia* Stiehler, 1857 on account of pronounced lobes and probable absence of suprabasal veins (Kvaček and Váchová 2006). As a matter of fact, the base of the leaf is not preserved but the relatively narrow surface of the blade between the leaf margin and the lateral primary vein is rather suggestive of a leaf organisation without suprabasal veins. Cenomanian *Ettingshausenia bohémica* (Velenovský, 1882) Kvaček and Váchová, 2006 is the nearest species, differing, however, from *Ettingshausenia? lublinensis* in much wider blade, more marked serration, and more pronounced lobes (Knobloch 1997; Kvaček and Váchová 2006). *Ettingshausenia senoniana* (Knobloch, 1964) Kvaček and Váchová 2006 from the Senonian of Bohemia and *E. gruenbachiana* Herman and Kvaček, 2010 from the lower Campanian of Grünbach in Austria (Herman and Kvaček 2010) both have more acute lobes.

Genus *Grewiopsis* de Saporta, 1865

*Type*: *Grewiopsis tiliacea* de Saporta, 1865; lower Eocene, Sézanne, Marne, France.

*Grewiopsis* sp.

Fig. 11A.

*Material*.—A single fragmentary leaf (part and counterpart) from Krasnobród, ZPAL Pl 4/1/7.

*Description*.—Leaf attachment petiolate, marginal blade attachment. Laminar size notophyll (width probably slightly exceeding 60 mm; length unknown, well over 50 mm). Laminar shape probably rounded, asymmetric; base probably asymmetric, apex not preserved; base angle obtuse. Margin entire in basal part, otherwise not preserved.

The single primary vein, 2 mm wide along all its length, is curved at about 10° (difference between directions at base and at the extremity of the preserved part). Major secondary veins probably semicraspedodromous, their attachment excurrent, spacing gradually decreasing distally, angle decreasing distally from ca. 50° to ca. 20° on the convex side of the midvein and from ca. 30° to ca. 20° on the concave side. The basal two secondaries are notably thinner than those closer to the apex. Minor secondaries departing from the first secondary at an angle of <10°, from the second one at ca. 20°, from the third at ca. 50°, all curving inwards. Higher order venation not preserved.

*Remarks*.—The described leaf is similar to *Grewiopsis credneriaeformis* de Saporta, 1868 and to *G. tiliacea* de Saporta, 1868, both from the Eocene of Sézanne (de Saporta 1868: pls. 12: 7, 11: 9) in having a pair of weak first secondaries, a finely serrate margin, a slightly asymmetric base and a curved midvein (last two characters in the former species). The affinities of the form genus *Grewiopsis* are unknown. Cretaceous species referred to this genus were described from the mid-Late Cretaceous of the Vilui Basin of Yakutia (Budantsev 1968; age after Spicer 2003) and from the Santonian of Kamchatka (Herman and Lebedev 1991). Out of them, *G. styracifolia* Budantsev, 1968 and *G. akhmetjevii* Vachrameev and Herman, 1991 are similar to the Polish species in shape, overall venation pattern and fine serration of the margin; the former differs in symmetric base and straight midvein and the latter has a finer midvein and a different teeth form.

*Dicotylophyllum varienerve* (Drygant, 1998) comb. nov. from Pidtemne (see below) has a midvein incurved similarly to that of *Grewiopsis* sp. The secondaries, however, are more rarely spaced and depart at a higher and more constant angle.

Genus *Araliopsoides* Berry, 1916

*Type*: *Sassafras cretaceum* Newberry, 1868; Dakota Group, Cenomanian, Blackbird Hill, Nebraska and Fort Hartker, Kansas, USA.

*Remarks*.—The name *Araliopsoides* Berry, 1916 was introduced (Berry 1916: 878) as a replacement for the form genus *Araliopsis* Berry, 1911, a junior homonym of *Araliopsis* Engler, 1896 (Recent Rutaceae; synonym of *Vepris* Commerson ex Jussieu, 1825 according to Kubitzki et al. 2011).



Both *Araliopsis* Lesquereux, 1874 and *Araliopsis* Lesquereux ex de Saporta and Marion, 1878 lacked generic diagnosis or description (Lesquereux 1874; de Saporta and Marion 1873) and thus were not validly published (Art. 32 of the ICBN). The type of the genus is therefore the same as that of *Araliopsis* Berry, 1911, namely *Sassafras cretaceum* Newberry, 1868, a widely distributed late Albian and Cenomanian species (Berry 1911a; Crabtree 1987: 717 and references therein), not *Araliopsis breviloba* Berry, 1911, as indicated erroneously by Andrews (1970).

*Araliopsoides?* cf. *minor* (Berry, 1925) comb. nov.

Figs. 2E, 6D.

1907 *Aralia formosa* Heer; Nowak 1907a: 54, pl. 2: 23.

cf. 1925 *Aralia wellingtoniana minor* Berry, n. var.; Berry 1925: 82–83, pls. 19:4, 5, 23: 4, 5.

non 1962 *Aralia formosa* Heer; Cieśliński and Milaković 1962: pl. 2: 4.

*Basionym*: *Aralia wellingtoniana minor* Berry, 1925.

*Material*.—A single fragmentary specimen from Potelych, L PB-K.20[.2] (formerly 7652).

*Description*.—Three presumed parts of a leaf (the organic connection is not preserved) are disposed to suggest a palmate arrangement. They are probably linear (width 9–15 mm, maximal preserved length ca. 80 mm; the margins are subparallel in the three preserved leaflets), diverging at an angle of 35°. The margins are slightly sinuous; this feature might in part correspond to the original serration (left leaflet; Fig. 6D) with very small (ca. 1 mm) teeth. A strong midvein is present all along the leaf; secondary venation not preserved.

*Remarks*.—This specimen has been compared by Nowak (1907a) to “*Aralia*” *formosa* Heer, 1869 from the lower Upper Cretaceous of Starý Maletín (Moletín) in Moravia (Velenovský 1881: 21–22, pls. 5: 2, 6: 7, 7: 2–4; see also Frič and Bayer 1902: fig. 116). Although neither specific identification is possible for such a poorly preserved material nor is conspecificity between the lower upper Cretaceous and the latest Campanian plants plausible, the proximity of both forms is very probable. The same may be said about *Araliophyllum elongatum* Němejc, 1961 from the Senonian of Klikov in Bohemia (Němejc 1961) and about “*Aralia*” *parvidentata* Hollick, 1930 from the lower Upper Cretaceous of the Yukon valley (Alaska; Hollick 1930). *Crassidenticulum trilobum* Dilcher and Wang, 2006 (Laurales) from the Dakota Formation (Albian) of Kansas (USA) might also perhaps be a related form (Wang and Dilcher 2006). The material described as *Debeya insignis* by Herman and Kvaček (2010) from the Campanian of Grünbach is also quite similar to the specimen from Potelych. All these leaves have serrate margins.

Similar entire-margined forms were described under the generic name *Sassafras* (Recent Lauraceae) (e.g., “*Sassa-*

*fras*” *angustilobum* Hollick, 1906 from the lowermost Campanian of Martha’s Vineyard, Massachusetts; Hollick 1906: 77, pl. 29: 1–3; age after Tiffney 1977). However, these forms may belong not only to the Lauraceae but also to the Platanaceae (Doyle and Hickey 1976: 173, 175; Crane 1989: 177–178; Friis et al. 2011: 236–237). Fritel (1914), Berry (1916, 1925), and Imkhanitzkaya (1968) interpreted some of them (e.g., representatives of the form genus *Sachalinella* Imkhanitzkaya, 1968) as ancestors or members of the Araliaceae. The relationships between lobate leaves with entire and serrate margins (more or less pentalobophylls and platano-phylls sensu Crabtree 1987, respectively) are unclear.

*Araliopsoides?* *minor* (Berry, 1925) comb. nov. from the Ripley Formation (Maastrichtian) of Tennessee (Berry 1925) is the most similar to the described specimen in general form and serrate margins but has a higher divergence angle of the lobes (ca. 50–60° in all the three figured specimens). This form is provisionally accommodated within the form genus *Araliopsoides* Berry, 1916, although dentate leaves (moreover, with very long lobes) should probably be segregated into another taxon.

Form group *Viburnifolia* Krassilov, 1979

Genus *Rarytkinia* Vassilevskaya and Golovneva in Golovneva and Abramova, 1990

*Type*: *Rarytkinia terechovae* Vassilevskaya and Golovneva, 1990; Rarytkin Formation, upper Maastrichtian–Danian, Koryak Upland, northeastern Russia.

*Rarytkinia polonica* (Karczmarz and Popiel in Malicki et al., 1967) comb. nov.

Figs. 2E, 10B, 11B, D, 12J.

1907 *Populus hyperborea* Heer; Nowak 1907a: 50–51, pl. 2: 17.

part 1967 *Ficus polonica* Kar. et Pop., n. sp.; Malicki et al. 1967: 228–229, pls. 7: 22, 8: 23.

1975 *Ficus polonica* Kar. et Pop.; Kohlman-Adamska 1975: 164, 166, pl. 1: 3.

*Basionym*: *Ficus polonica* Karczmarz and Popiel in Malicki et al., 1967.

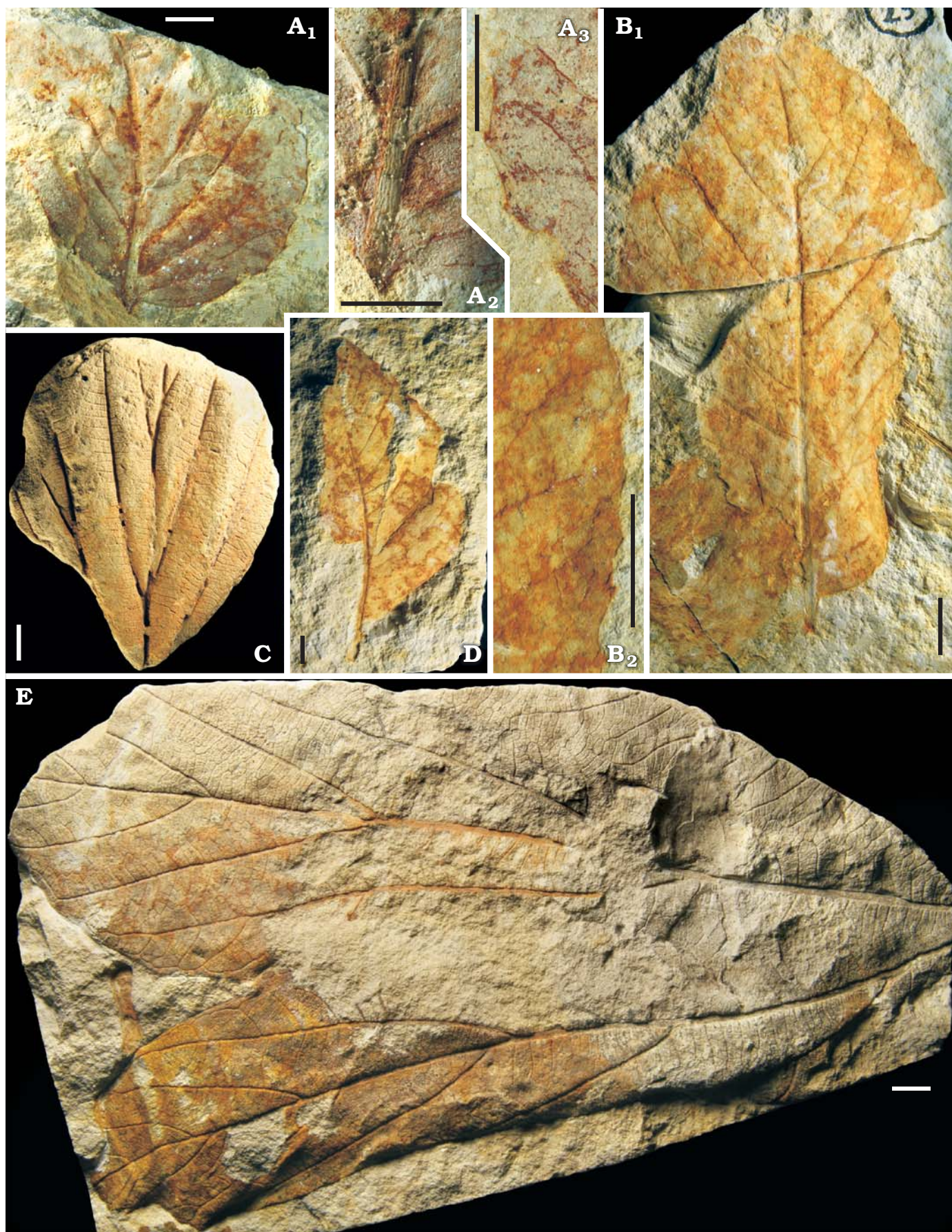
*Type material*: Holotype MZ VII/33/32, an incomplete leaf from Krasnobród; paratype from Kosobudy (Malicki et al. 1967: pl. 8: 23; MZ VII/33/30) is unidentifiable.

*Material*.—Four incomplete leaves: L PB-K.20 from Potylicz, JS 3, ZPAL Pl 4/1/2, 4 from Krasnobród.

*Description*.—Blade attachment marginal, laminar size mesophyll (length up to at least 10 cm), laminar length to width ratio 1.8:1, laminar shape elliptic, blade medially symmetric, basal width asymmetric, margin unlobed with dentate and serrate teeth. Apex not preserved, base angle obtuse, base shape convex.

Fig. 11. Campanian angiosperms. **A**. *Grewiopsis* sp., incomplete leaf ZPAL Pl 4/1/7; Krasnobród, upper Campanian. General view (A<sub>1</sub>), enlargement of the midvein (A<sub>2</sub>), enlargement of the serrate margin (A<sub>3</sub>). **B**, **D**. *Rarytkinia polonica* (Karczmarz and Popiel in Malicki et al., 1967) comb. nov.; Krasnobród, upper Campanian. **B**. Holotype, incomplete leaf MZ VII/33/32. General view (B<sub>1</sub>), enlargement of the serrate margin (B<sub>2</sub>). **D**. Incomplete leaf JS2. **C**, **E**. *Ettingshausenia? lublinensis* (Karczmarz and Popiel, 1971) comb. nov. **C**. Fragmentary leaf L PB-K.2; Potelych, upper Campanian. **E**. Holotype, subcomplete leaf JS1; Krasnobród, upper Campanian. Scale bars 10 mm. →







Primary venation pinnate craspedodromous. The first two pairs of secondaries depart under an angle of 70–90°, whereas all the following ones keep a uniform angle of 50–60°. Spacing of secondaries slightly decreasing distally, attachment excurrent. Secondaries sometimes bifurcate; no intersecondaries. Tertiaries poorly preserved.

Tooth spacing irregular with one order of teeth and two to three teeth per cm. Teeth low, sinus shallow. Teeth either perpendicular to the leaf margin or directed distally. Sinus shape mostly rounded, tooth shape biconcave.

*Remarks.*—The discussed poorly preserved leaves are included in *Rarytkinia* on account of their shape, serration, and venation. In particular, the lowest veins depart from the midvein at a much higher angle, wherefore they are shorter than the following ones, a character shared with the *R. terechovae*, the type of the genus. The differences between *R. polonica* and *R. terechovae* are difficult to define given the great variability of both species (Golovneva and Abramova 1990) and the poor preservation of our material. However, the serration of our taxon seems much finer.

The affinities of this form genus are unknown. It is known from the Maastrichtian to Danian of the Koryak Mountains, Russian Far East: *R. terechovae* and *R. amaamensis* Moiseeva, 2008 (Golovneva and Abramova 1990; Moiseeva 2008) and from the Palaeocene of Alaska (*Rarytkinia* sp., Early Sagwon flora; Herman et al. 2009). *R. quercifolia* Golovneva, 2000 from Greenland is excluded following Kvaček (2010). *R. polonica* is therefore the oldest and the southernmost known species of an otherwise northern genus.

*Stratigraphic and geographic range.*—Krasnobród, Potelych, late Campanian.

### Form group Cinnamomophylls Crabtree, 1987

*Remarks.*—The original description of cinnamomophylls (Crabtree 1987: 727) included leaves only with brochidodromous venation pattern. However, transitions between camptodromous and brochidodromous patterns occur within a single species (e.g., *Alangium densiflorum*, see below, Remarks on *Cinnamomoides*? sp. nov.). The diagnosis should therefore be emended accordingly.

### Genus *Cinnamomoides* Seward, 1925

*Type:* *Cinnamomoides newberryi* sensu Seward, 1925; Cretaceous?; Atanikerdluk, Greenland.

*Remarks.*—The systematic position and the stratigraphy of the type of the form genus *Cinnamomoides* are rather unclear. First, it is not assured that *Cinnamomoides newberryi* sensu Seward (1925) be synonymous with either “*Cinnamomum*” *newberryi* Berry, 1911 from the Cenomanian Raritan Formation of New Jersey (Berry 1911b) or with *Daphnogene sezannensis* (Watelet, 1866) de Saporta, 1868 from the Eocene of Sézanne (France) (the latter was the opinion of Heer [1882] who first described Cretaceous leaves from Greenland). Then, the material from the locality Atanikerdluk (Atanikerdluk) in the Nuussuaq (Nûgssuaq, Nugssuak) Peninsula in western

Greenland is a mixture of Cretaceous and Paleocene plants (Lower and Upper Atanikerdluk floras, respectively; Graham 1999: 152; Dam et al. 2009).

### *Cinnamomoides*? sp. nov.

Fig. 9G.

*Material.*—A single fragmentary leaf GFAP JW/Fe1-1, 2 (part and counterpart) from Jędrzejów.

*Description.*—Blade attachment unknown. Laminar size notophyll (length of the preserved part 70 mm, width of the preserved part 57 mm; estimated total length >90 mm), shape probably elliptic, medially asymmetric, base not preserved. Margin entire with obtuse apex angle, apex rounded. Primary venation pinnate. Major secondaries (four on the right side of the leaf, three on the left) eucamptodromous, their spacing increasing distally, attachment excurrent, angle of attachment constant, ca. 20°. Minor secondaries attached to the first two pairs of secondaries, probably camptodromous. Two intersecondaries present on one side of the midvein between the third and the fourth pair of the main secondaries and parallel to them, one on the other side; one and zero, respectively, between the fourth pair of the secondaries and the apex. Intersecondaries short. A secondary marginal vein or thickening present (interpretation uncertain); this structure is not connected with the secondaries. Tertiaries mixed percurrent, their attachment angle constant, perpendicular. Quaternary venation percurrent, quinquenary venation reticulate.

*Remarks.*—As the proximal part of the leaf is lacking, a doubt subsists whether the general venation pattern is pinnate or acrodromous. The first interpretation is favoured and the leaf is included within the form group of cinnamomophylls (acrodromous venation is characteristic for rhamnophylls; Crabtree 1987: 727) and the form genus *Cinnamomoides* Seward, 1925. The cinnamomophylls include both Laurales and forms of uncertain relationships (Crabtree 1987: 716). “*Ficus*” *ovata* Newberry, 1895 from the Magothy Formation (Coniacian to Santonian; Newberry 1895: 70, pl. 24: 1–3) may serve as an example of the latter.

The natural affinities of *Cinnamomoides*? sp. nov. are probably within the Magnoliidae, either Piperaceae or Lauraceae, although more distant analogues may be found within the Cornaceae s.l. and the form group of rhamnophylls sensu Crabtree (1987). The venation patterns of the Recent *Piper bredemeyeri* Jacquin, 1815 (Piperaceae) (Burger 1971: fig. 11) and of the Eocene *Laurophyllum conspicuum* Hill, 1986 (Lauraceae; cuticles studied) (Hill 1986: fig. 2B) are very similar to that of the described form. The marginal vein or marginal thickening is present in some representatives of both Lauraceae (e.g., Recent species of *Cryptocarya* and *Pleurothyrium*; de Moraes 2007: 12; van der Werff 1991: 386) and Piperaceae (e.g., at least in the distal region of the lamina of *Piper reticulatum* Linnaeus, 1753; specimen F 1769884). Pronounced median asymmetry is uncommon in the Lauraceae (*Cinnamomum parthenoxylon* [Jack, 1820] Meissner in de Candolle, 1864, figured by Koorders and

Valeton 1913–1918: fig. 209; *Neolitsea levinei* Merrill, 1918, figured by Yu and Chen 1991: pl. 18: 12], while it is rather common in the Piperaceae (e.g., *Piper carpinteranum* de Candolle, 1897; *P. biauratum* de Candolle, 1897; and several other species; Burger 1971: figs. 10, 12), a character arguably related to the distichous phyllotaxy diagnostic for the Piperales (as opposed to spiral or opposite in the Laurales; Doyle and Endress 2000; Soltis et al. 2005). The Piperaceae are characterised by strong variability of leaf form both among and within taxa (Miquel 1844; Tebbs 1993). Recent *Alangium densiflorum* (Koorders and Valeton, 1899) Wangerin, 1910 (Alangiaceae or Cornaceae s.l.) has asymmetric leaves with primary, secondary, and tertiary venation pattern very similar to *Cinnamomoides?* sp. nov. (a typical morphotype, Koorders and Valeton 1913–18: fig. 188; a brochidodromous morphotype, Wangerin 1910: fig. 4); it differs in the presence of a drip tip. Cretaceous “*Zizyphus*” *areolatus* Bell, 1957 (a rhamnophyll) from the Late Cretaceous Nanaimo Group of British Columbia has a similar primary and secondary venation pattern but the leaf is symmetrical and the tertiary venation is areolate (Bell 1957).

*Piperites tuscaloosensis* Berry, 1919 from the Tuscaloosa Formation of Alabama (Coniacian?; Berry 1919) is similar to *Cinnamomoides?* sp. nov. in camptodromous venation and median asymmetry. It differs in its acute apex. Neither in this case can the piperaceous affinity be proven. The type of the form genus *Piperites* Goeppert, 1854, namely *Piperites miquelianus* Goeppert, 1854 from the Tertiary of Java (Goeppert 1854: figs. 48, 49), is rather different, medially symmetric, with brochidodromous venation and no minor secondaries. *Piperophyllum* Kahlert, Rüffle, and Gregor, 2009, proposed as another form genus of the Piperaceae, is a nomen dubium given the uncertainty concerning the conspecificity between the neotype of *Piperophyllum fibrillosum* from the Santonian of Quedlinburg (Germany) and *Ceanothus fibrillosus* Lesquereux, 1873 from the Palaeocene of Alabama. The epidermis of the former (Kahlert et al. 2009: pl. 1: 5) is apparently consistent with its piperaceous affinities, whereas fine and dense tertiary venation (Brown 1962: pl. 50: 5, 6, 10, 11) of the latter might rather suggest an affinity with the Rhamnaceae (see Jones and Dilcher 1980).

To sum up, *Cinnamomoides?* sp. nov. is probably a new species characterised by pronounced median asymmetry and a eucamptodromous venation pattern with numerous minor secondaries. It is left in open nomenclature due to incomplete preservation. Owing to the absence of diagnostic cuticular characters its natural affinities, perhaps piperaceous or lauraceous, cannot be considered as certain.

## Form group unknown

### Genus *Protohedycarya* Rüffle, 1965

Type: *Proteoides ilicoides* Heer, 1871 sensu Rüffle, 1965; Upper Cretaceous, lower “Senonian”, Quedlinburg, Germany.

### *Protohedycarya?* sp.

Fig. 12B.

1907 *Quercus castanoides* Newb.; Nowak 1907a: 49, pl. 1: 5, 2: 19.

1907 *Myrica acuminata* Ung.; Nowak 1907a: 51, pl. 1: 8.

1962 *Quercus castaneoides* Newb.; Cieśliński and Milaković 1962: 254, pl. 2: 3.

?1962 *Dryophyllum* sp.; Cieśliński and Milaković 1962: 254, pl. 1: 3.

**Material.**—Three incomplete leaves L PB-K.4 (formerly 143) and L PB-K.19, 19A (formerly 158; part and counterpart), both from Potelych, and PIG 60 III 9 (part and counterpart) from Raków.

**Description.**—Blade attachment marginal, laminar size notophyll (length of the preserved part 6.6 cm), length to width ratio possibly about or over 3:1, blade medially symmetric, margin unlobed with serrate teeth. Apex not preserved. Base angle acute, shape decurrent (or cuneate?).

A single thick basal vein is present. Secondary veins are preserved in the specimen from Raków: they depart from the midvein at an angle of 60–80° and at first straight; then they are difficult to observe, at least some of them, however, are curving, suggesting a brochidodromous arrangement.

Teeth spacing irregular (distances between four preserved teeth are 7, 8, and 11 mm). Sinus shape rounded. Tooth shape: proximal flank straight, distal flank concave.

**Remarks.**—The described leaves are quite similar in the form of the leaf base and of the serration to the material described by Rüffle (1965) from the Senonian of Germany (see in particular Rüffle 1965: pl. 1: 2). Despite nomenclatural problems (the type material of the genus is quite poorly preserved) and the rather problematic assignment to Monimiaceae (even if accepted by Friis et al. 1997), the genus *Protohedycarya* seems the best place for the described specimens. *Dryophyllum* Debey ex de Saporta, 1868 has an asymmetric base (Jones et al. 1988) and cannot be used for our material. The second specimen of *Quercus castanoides* sensu Nowak (1907a: pl. 1: 5) could not be traced. The poorly preserved fragmentary leaf PIG 60 III 6 from Zgubieniec (*Dryophyllum* sp. sensu Cieśliński and Milaković 1962) has a different leaf form but a similar serration; given the variability described by Rüffle (1965), it might represent the same species.

### Genus *Dicotylophyllum* auct.

Type: See Remarks below.

**Remarks.**—Poorly known dicotyledonous leaves have usually been referred to the genus *Dicotylophyllum*. The author of this name is de Saporta (1894) who described four species (*D. cerciforme*, *D. hederaceum*, *D. corrugatum*, and *D. lacerum*) under the above-mentioned generic name without proposing a type. Several authors mistakenly credited the authorship of the genus to Bandulska (1923). Andrews (1970) proposed *D. cerciforme* as the type of the genus. However, Sender et al. (2010) interpreted *Dicotylophyllum cerciforme* de Saporta, 1894 from the Albian of Portugal as a probable nymphaealean leaf and chose it as the type of *Ploufolia* Sender, Gomez, Diez, Coiffard, Martín-Closas, Villanueva-Amadoz, and Ferrer, 2010. If *D. cerciforme* be indeed the type of *Dicotylophyllum*, then *Ploufolia* is super-



fluous and *Dicotylophyllum* includes only probable nymphaealeans. Such a situation would cause far-reaching nomenclatorial changes and seems thus undesirable. The way to amend such a situation is by no way obvious given that, contrary to the standard requirements, an unrecognisable type is needed to preserve the usual understanding of the genus. The first possibility is to supersede Andrews's (1970) choice by virtue of Art. 10.5.b of the Code (Greuter et al. 2000); in effect, in several cases (this one included) Andrews (1970) selected the first described species of a genus, using thus "a largely mechanical method of selection". *Dicotylophyllum hederaceum* de Saporta, 1894, a minute palmately veined leaf with serrate (lobate?) margin, might be designated. However, the material described by de Saporta (1894) is relatively homogenous and it is not excluded that his four species represent in fact a single biological entity (see also Teixeira 1950). This would result in *Dicotylophyllum* becoming again a form genus of nymphaealeans. A second possibility is to conserve *Dicotylophyllum* Bandulska, 1923 against *Dicotylophyllum* de Saporta, 1894 by virtue of Art. 14 of the Code (Greuter et al. 2000). Pending a decision on this matter, the name of the discussed genus is given here without any author.

*Dicotylophyllum zubaense* (Drygant, 1998) comb. nov.

Fig. 12A.

1998 *Celastrus zubaensis*; Drygant 1998: 149, text-fig. 2, pl. 3: 4a, b.  
2006 *Celastrus zubaensis* Drygant 1998; Mamčur 2006: 42, pl. 1: 4, 5.

*Basionym*: *Celastrus zubaensis* Drygant, 1998.

*Type (and only) material*: Holotype, slightly incomplete leaf L PB-K.35, 35a (formerly 37935, 37935A; part and counterpart).

*Description*.—Blade attachment marginal, laminar size microphyll (leaf ca. 4.8 cm long), laminar length to width ratio 2.7:1, laminar shape oblong, blade medially symmetric, basal insertion probably asymmetric, margin unlobed with serrate teeth. Apex not preserved, base angle probably obtuse, base shape convex.

Primary venation pinnate with probably (see Remarks) one basal vein and probably no agrophic veins. Major secondaries semicraspedodromous with possible intersecondaries. Major secondary spacing smoothly decreasing distally, their attachment decurrent. Higher order venation not preserved.

Tooth spacing regular with one order of teeth and about six teeth per cm. Sinus shape rounded, tooth shape biconcave. Principal vein is present and terminates at the tooth apex.

*Remarks*.—Preservation of the described material is unusual, with major and selected minor veins underlined by such

heavy ferric oxide deposits so as to conceal probable original differences of their width, other veins having disappeared.

The shape and gross venation pattern of this enigmatic taxon are somewhat similar to those of some representatives of the Recent genus *Casearia* von Jacquin, 1760 (Salicaceae or Flacourtiaceae), especially *C. guianensis* (Aublet, 1775) Urban, 1902 or *C. ilicifolia* Ventenat, 1803. As finer venation and cuticular characters are unknown and, moreover, teeth form is different, the Pidtemne specimen should probably be accommodated within a new form genus which cannot, however, be proposed at present for lack of sufficient material. *Dicotylophyllum zubaense* differs from all other taxa described herein under the generic name *Dicotylophyllum* in vein endings situated in teeth.

*Dicotylophyllum varienerve* (Drygant, 1998) comb. nov.

Fig. 12I.

1998 *Platanus pseudoguillelmae* Krasser var. *varieneris* Drygant, var. nov.; Drygant 1998: 147, text-fig. 1, pl. 3: 3.

2006 *Platanus pseudoguillelmae* Krasser var. *varieneris* Drygant, 1998; Mamčur 2006: 41, pl. 1: 3.

*Basionym*: *Platanus pseudoguillelmae* Krasser, 1896 var. *varieneris* Drygant, 1998.

*Type (and only) material*: Holotype, incomplete leaf L PB-K.34 (formerly 37934). Pidtemne, Maastrichtian.

*Description*.—Blade attachment marginal, laminar size notophyll (length ca. 10 cm), length to width ratio <1.3:1. Laminar shape probably elliptic with medial asymmetry and base asymmetry. Base shape convex, base angle acute; apex not preserved. Margin serrate (distally) with small closely spaced (each ca. 4 mm) teeth, possibly entire proximally.

Primary venation suprabasal actinodromous, primaries incurved. Secondaries probably craspedodromous, nearly straight, their attachment excurrent, angle increasing distally. Tertiaries not preserved.

*Remarks*.—*Dicotylophyllum varienerve* from all other taxa described herein under the generic name *Dicotylophyllum* in much larger size. Its relationship to platanoids is unconfirmed.

*Dicotylophyllum* cf. *proteoides* (Unger, 1867) Herman and Kvaček, 2010

Figs. 2E, 12E–G.

cf. 1867 *Phyllites proteoides*; Unger 1867: 652, pl. 2: 11.

1907 *Aralia coriacea* Vel.; Nowak 1907a: 55, pl. 2: 24.

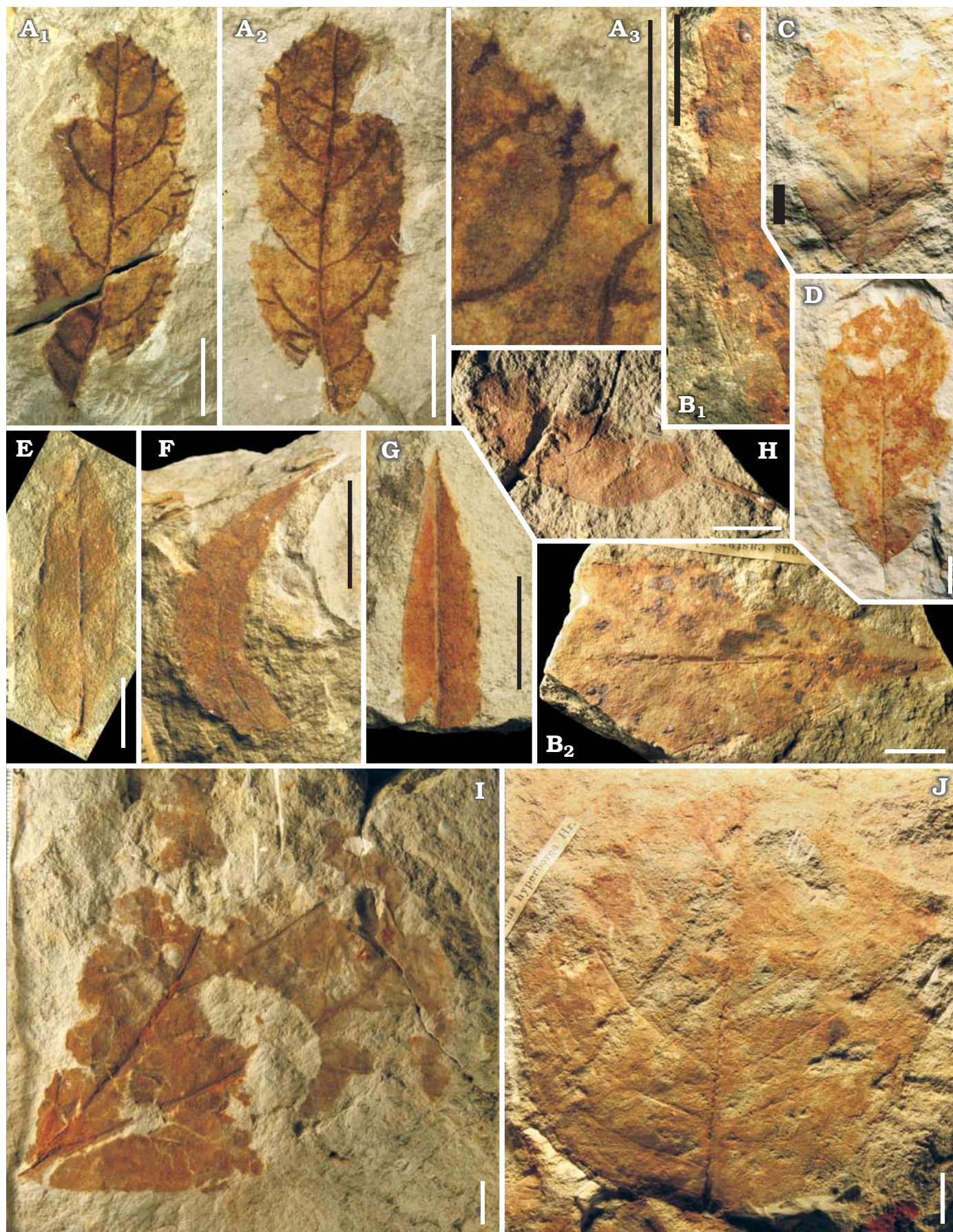
1907 *Eucalyptus haldemiana* Deb.; Nowak 1907a: 52, pl. 1: 16.

1907 *Pimelea delicatula* Lesqx.; Nowak 1907a: 52, pl. 1: 3.

1907 *Aralia* (*Panax*) *dentifera* (?) Vel.; Nowak 1907a: 54, pl. 2: 21.

Fig. 12. Campanian and Maastrichtian angiosperms. **A.** *Dicotylophyllum zubaense* (Drygant, 1998) comb. nov., holotype, subcomplete leaf L PB-K.35; Pidtemne, Maastrichtian. Part (A<sub>1</sub>), counterpart (A<sub>2</sub>), enlargement of the serrate margin (A<sub>3</sub>). **B.** *Protohedycarya*? sp., incomplete leaf L PB K-4; Potelych, upper Campanian. **C.** *Dicotylophyllum* sp. 5, leaf JS9; Krasnobród, upper Campanian. **D.** *Dicotylophyllum* sp. 4. **D.** Leaf JS;. Krasnobród, upper Campanian. **H.** Leaf L PB-K.15; Potelych, upper Campanian. **E–G.** *Dicotylophyllum* cf. *proteoides* (Unger, 1867) Herman and Kvaček, 2010; Potelych, upper Campanian. **E.** Leaf L PB-K.20[.3]. **F.** Leaf L PB-K.8. **G.** Leaf L PB-K.38. **I.** *Dicotylophyllum varienerve* (Drygant, 1998) comb. nov., holotype, fragmentary leaf L PB K-34; Pidtemne, Maastrichtian. **J.** *Rarytkinia polonica* (Karczmarsz and Popiel in Malicki et al., 1967) comb. nov., incomplete leaf L PB-K.20[.4]; Potelych, upper Campanian. Scale bars 10 mm.







1998 "*Cassia*" *antiquorum* Heer; Drygant 1998: 147–149, pl. 3: 6a, b. cf. 2010 *Dicotylophyllum proteoides* (Unger) Herman and Kvaček, comb. nov.; Herman and Kvaček 2010: 95–96; text-figs. 45, 46; pls. 28: 1–15, 29: 1–7, 36: 8 [ubi syn.].

**Material.**—L PB-K.5 (formerly 144), 6 (formerly 145), 8 (formerly 147) from Potelych, L PB-K.38 (formerly 3262) from Pidtemne, ZPAL Pl 4/8/1 from Majdan Nepryski, RGM 234271 from Piotrawin.

**Description.**—Blade attachment marginal, laminar size nanophyll to microphyll, length to width ratio between 3:1 and 7.6:1 (possibly more). Laminar shape elliptic to linear with both medial and base symmetry. Apex shape straight to acuminate (without drip tip), base shape cuneate to convex. The margin is entire.

There is a single straight primary vein; lower order venation not preserved.

**Remarks.**—This taxon corresponds well to *Dicotylophyllum proteoides* (Unger, 1867) Herman and Kvaček, 2010 from the lower Campanian of Grünbach (Austria) in overall shape and variability including both short and lanceolate as well as long linear leaves (e.g., monospecific accumulation illustrated by Herman and Kvaček 2010: pl. 29: 1). However, diagnostic lower order venation (Herman and Kvaček 2010: pl. 28: 10) is never preserved in our material, suggesting the possibility that the leaves were hyphodromous. That is why these specimens have been left in open nomenclature.

*Dicotylophyllum proteoides* might be of lauraceous affinity; however, in absence of cuticles an unequivocal assignment is not possible (Herman and Kvaček 2010).

### *Dicotylophyllum* sp. 1

1967 *Myricophyllum glandulosum* Velen.; Malicki et al. 1967: 227–228, pl. 7: 20.

**Material.**—A single fragmentary leaf, MZ VII/32/41, from Kosobudy.

**Description.**—Blade attachment marginal, laminar size microphyll, length to width ratio  $>3:1$ . Blade shape oblong, medially dissymmetric, basal width symmetric, base shape slightly convex, apex not preserved. Margin entire. Venation pinnate, primary vein slightly curved. Secondaries eucamptodromous, alternating, their angle of divergence ca.  $20\text{--}30^\circ$ .

**Remarks.**—*Dicotylophyllum* sp. 1 is quite similar to the leaf described above as aff. *Eucalyptolaurus* sp. in its slight asymmetry and eucamptodromous secondaries. Differences include lower angle of secondaries ( $20\text{--}30^\circ$  compared to  $40\text{--}50^\circ$ ) and lack of any structure that could be interpreted as an intramarginal vein. *Dicotylophyllum* sp. 2 is symmetric and has subopposite and denser secondaries. Nonetheless, given the poor preservation of all the three specimens, it is not excluded they represent a single biological species. *Dicotylophyllum* sp. 4 and *D.* sp. 5 are more transverse.

### *Dicotylophyllum* sp. 2

Fig. 6F.

part 1967 *Laurus affinis* Velen.; Malicki et al. 1967: 229–230; pl. 8: 24, non pl. 8: 25.

**Material.**—A single fragmentary leaf, MZ VII/33/27, from Krasnobród.

**Description.**—Fragmentarily preserved microphyll, oblong, integrimarginate leaf. Length to width ratio  $>2:1$ . Margin entire. Venation pinnate, primary vein straight; secondaries eucamptodromous, subopposite, their attachment excurrent, spacing slightly decreasing distally.

**Remarks.**—The discussion of similarities and differences between this taxon, aff. *Eucalyptolaurus* sp., and *Dicotylophyllum* spp. has been given above.

### *Dicotylophyllum* sp. 3

Fig. 6A.

**Material.**—A single fragmentary leaf, ZPAL Pl 4/1/5, from Krasnobród.

**Description.**—A fragment of leaf ca. 25 mm in length and ca. 30 mm in width (estimated) might suggest an elliptic shape. Blade possibly medially asymmetric. The irregular course of the margin suggests an original serration but this is inconclusive due to poor preservation.

There is a relatively thick straight primary vein. Major secondaries probably eucamptodromous or cladodromous. Secondary attachment decurrent, angle inconsistent, spacing possibly decreasing distally. Tertiaries sometimes difficult to distinguish from secondaries, irregularly reticulate.

**Remarks.**—This taxon is very different from all the others described here in its low rank venation (except maybe *Protophedycarya*? sp. but only its midvein is preserved in our material). Fragmentary preservation precludes any precise identification.

### *Dicotylophyllum* sp. 4

Fig. 12D, H.

1907 *Diospyros rotundifolia* Lesqx.; Nowak 1907a: 55, pl. 1: 10, 15.

**Material.**—L PB-K.15 (formerly 7677) from Potelych, JS 9 from Krasnobród.

**Description.**—Blade attachment marginal, laminar size nanophyll (L PB-K.15: length of the blade ca. 34 mm) to microphyll (JS 9: length of the blade ca. 7 cm), length to width ratio 1.75 to 1.9, laminar shape elliptic, with median symmetry and basal symmetry. Margin is entire with base shape straight (L PB-K.15) to cuneate (JS 9) and base angle ca.  $70\text{--}80^\circ$ ; apex probably rounded. There is a single straight primary vein; lower order veins poorly preserved.

**Remarks.**—These two poorly preserved leaves are described under a single entry because of their mutual likeness in blade form, despite differences of size and base shape. *Dicotylophyllum* sp. 2 is more elongate and *Dicotylophyllum* sp. 5. more transverse. Given these differences, the material is described as separate morphotypes; it may have been, however, that the number of biologic species was smaller than that of morphotypes.

*Dicotylophyllum* sp. 5

Fig. 6C.

1907 *Fagus prisca* Ettingsh. (?); Nowak 1907a: 49, pl. 1: 2.  
non 1962 *Fagus* cf. *prisca* Ett.; Cieśliński and Milaković 1962: 254, pl. 3: 1.

**Material.**—A subcomplete leaf JS 8 from Krasnobród, a fragmentary leaf from Chełmowa Góra KrS 2, a fragment L PB-K.18 (formerly 153) from Potelych.

**Description.**—Blade attachment marginal, laminar size notophyll (the blade is 7 cm long and 5 cm wide), blade medially slightly asymmetric, basally symmetric. Base shape convex, angle obtuse. Margin probably entire. Venation pinnate, secondaries straight for about half of the blade width, then poorly preserved, eucamptodromous?; their attachment excurrent, angle constant, about 50°, spacing regular. Tertiaries not preserved.

**Remarks.**—*Dicotylophyllum* sp. 5 differs from other taxa described herein under the generic name *Dicotylophyllum* in smaller length to width ratio (and from *Dicotylophyllum* sp. 4 moreover in distinct secondary venation). Once again, it is not excluded that this morphotype does not represent a separate biologic species.

The fragmentary leaf of “*Magnolia polysperma* Karczmarz, 1966” (MZ VII/37/31, Karczmarz and Popiel 1966: fig. 3; refigured by Kohlman-Adamska 1975: pl. 1: 1) might represent either *Dicotylophyllum* sp. 4 or *Dicotylophyllum* sp. 5. For the status of this name and of *Fagus* cf. *prisca* sensu Cieśliński and Milaković (1962) see below, under Unidentified taxa.

## Class Monocotyledoneae de Candolle, 1819 (= Liliopsida Brongniart, 1843)

## Order and family unknown

Genus *Eolirion* Schenk, 1869

**Type:** *Eolirion primigenium* Schenk, 1869; Lower Cretaceous, “Urgonian”; Grodischtz, Silesia (= Hradišče, Silesia), Czech Republic.

*Eolirion*? sp.

Fig. 7D.

?1967 *Eulirion nervosum* Hosius et Marck; Malicki et al. 1967: 231, pl. 10: 29.

**Material.**—A single leaf fragment ZPAL Pl 4/1/9 from Krasnobród.

**Description.**—The fragment is 12 mm long and 25 mm wide. Traces of parallel veins, 1–2 per mm, can be observed; there is no midvein. The margin is poorly preserved and it is uncertain whether the observed absence of serration corresponds to the original condition.

**Remarks.**—This fragmentary plant remain is tentatively interpreted as a monocotyledonous leaf. However, the specimen described under the same generic name (erroneously as *Eulirion*) by Malicki et al. (1967) is more probably a twig fragment.

## Unidentified taxa

The following section contains taxa reported by previous authors for which the material is either lost, unidentifiable, or not a plant.

*Myrica latifolia* Karczmarz in Karczmarz and Popiel, 1966—holotype (and only specimen, Krasnobród) lost, figure poorly legible, description too general.

*Magnolia polysperma* Karczmarz in Karczmarz and Popiel, 1966—the type material (syntype) of *M. polysperma* consists of an poorly preserved leaf (about 1/3 of the blade preserved, only secondary venation, no cuticular features available) and of an infill of (bivalve or crustacean?) burrows interpreted by the previous authors as an infrutescence (both from Krasnobród). This name, if emended to represent a leaf morphotaxon, might be used only for the lectotype and thus of no palaeobiologic use. The present author, acting as the first reviewer, here selects the presumed “infrutescence” (MZ VII/33/110) as the lectotype of *Magnolia polysperma*. In this way the name falls out of palaeobotanic interest. A similar case (presumed palm fruitbodies reinterpreted as traces of wood-boring bivalves) was reported from the Oligocene of Tatra Mts. in southern Poland (Radwański 2009).

*Sphaerococcites affinis* Sternberg, 1833 sensu Malicki et al. (1967: 222)—probably sponges (specimen MZ VII/33/16) (Andrzej Pisera, personal communication 2011).

*Podozamites eichwaldii* Schimper, 1870 sensu Malicki et al. (1967: 222–223, fig. 3)—poorly preserved specimen MZ VII/33/7 may be a leaf (possibly the same as *Eolirion*? sp.) or a twig.

*Dewalquea groenlandica* Heer, 1882 sensu Nowak (1907a)—the leaf L PB-K.12, formerly 151 from Potelych, is too fragmentary to be identifiable.

The following species reported by Cieśliński and Milaković (1962) from the Nida Trough are based on unidentifiable material: *Sequoia maior* from Liśnik, *Dryophyllum* cf. *dewalquea* from Zgubieniec, *Fagus* cf. *prisca* from Łysa Góra near Imielno, and *Aralia formosa* from Dalechowy.

## Frequencies of taxa

Out of twenty six taxa described above (three ferns, five conifers, seventeen dicots and a single probable monocot), only two (*Geinitzia reichenbachii* and *Debeya paulinae*) are represented by more than ten specimens. Three more (*Cunninghamites squamosus*, *Rarytkinia polonica*, and *Dicotylophyllum* cf. *proteoides*) are known from five or more specimens, whereas all the others (21 taxa) are represented by four or fewer specimens, including twelve (46%) taxa known only from single specimens. This means that our knowledge of the latest Cretaceous flora of southern Poland and western Ukraine is still incomplete; new forms will very probably be found if more specimens are gathered. Any conclusions based solely on absences of taxa should therefore be considered as provisory.



## Dynamics of the flora

Malicki et al. (1967) observed that early Maastrichtian (now late Campanian to early Maastrichtian) floras of Roztocze differ significantly from late Maastrichtian floras of the Lublin Upland in their composition, the former containing a large amount of angiosperms, whereas the latter are composed solely of conifers. In their opinion the main factor explaining this difference was palaeogeography, namely the shorter distance of the Roztocze region from the Carpathian land in conjunction with presumably higher resilience to transport degradation exhibited by conifers (Malicki et al. 1967: 220). This interpretation must be rejected for two major reasons: first, the transport of the floral remains was certainly very short (see Taphonomy above); moreover, modern palaeogeographic reconstructions indicate that there was no land in the northern Carpathians at the end of the Cretaceous (Golonka et al. 2006: fig. 15).

The described floral assemblages are not sufficiently diverse to allow an analysis of the vegetation in relationship to climate and palaeogeography, especially that the Maastrichtian climate was evolving particularly rapidly, including both the coolest interval of the Late Cretaceous (Wolfe and Upchurch 1987: 44) and two warmer intervals (Nordt et al. 2003). Moreover, a major reorganisation of oceanic circulation patterns took place at the early/late Maastrichtian boundary, resulting in global cooling and continentalisation of the climate, as well as in extinctions in marine the domain (Frank and Arthur 1999 and references therein). Lastly, the greatest changes in palaeogeography of the Mid-Polish Trough took place in the Maastrichtian–Palaeocene interval (Lamarche et al. 2003: 76); the gradual formation of the Mid-Polish Swell must have strongly influenced local palaeogeographic conditions of the studied area. However, the abundance of angiosperm remains in the upper Campanian rocks (Krasnobród and Potelych) is explained relatively simply, namely by a well documented marine lowstand on a local scale (Jaśkowiak-Schoeneichowa and Krassowska 1988; Świdrowska 2007; Dubicka and Peryt 2011) (possibly not correlated with a global highstand; Hancock 1989). Such a situation must have exposed land surfaces larger than both earlier and later. This explains the short transport of leaves documented above, their highest frequency, and better preservation.

There exist two palaeogeographic reconstructions for the Maastrichtian of Poland, by Jaśkowiak-Schoeneichowa and Krassowska (1988) and by Świdrowska and Hakenberg (1999), the former proposing several relatively small land areas in the Mid-Polish Trough, the latter interpreting this area as entirely marine. Here we shall not enter the much debated problem of the chronology of the inversion of the Mid-Polish Trough (see Leszczyński 2010 for a recent review). However, as shown above, at least small patches of land must have existed in several places within the Polish Trough (not only the Roztocze but also the southern border of the Holy Cross Mts., as proven by the specimen of *Debeya insignis* from Zgubie-

niec (Fig. 9E) situated ca. 200 km westwards from Krasnobród) during the marine lowstand in the late Campanian. So, for this period (namely the late Campanian), the former reconstruction would be better for explaining the development of the vegetation. These small islands were probably situated in the area corresponding to the present Mid-Polish Swell (Leszczyński 2010). The palaeogeographic situation in the Maastrichtian was most probably different with the maximum extent of the sea in the Polish Basin taking place at the end of the late Maastrichtian (Krassowska 1997).

A comparison of the distribution of the fossil floras in the studied area and in the approximately coeval rocks of the same marine facies in Limburg (southern Netherlands), might allow us to determine if the above-mentioned pattern of replacement of a mixed angiosperm-gymnosperm flora by a predominantly coniferous one is a regional or a supraregional phenomenon. The rarity of angiosperms in Limburg is a serious hindrance for such a comparison; yet the single late Maastrichtian plant fossil from that region is an angiosperm leaf (Raymond van der Ham, personal communication 2010). This is a meagre indication; however, if one has to choose between a regional and a supraregional interpretation, the former will be preferred.

To sum up, the difference between the late Campanian to early Maastrichtian mixed taphocoenoses and late Maastrichtian conifer-dominated assemblages resulted, arguably, mainly from regional factors. The greatest abundance of fossil angiosperms in the late Campanian is correlated with a local marine lowstand.

## Palaeoecology

The examined material is both allochthonous and numerically far too small to allow any palaeophytosociological study. Nonetheless it is tempting to place the recognised taxa within palaeocommunities described elsewhere where more favourable taphonomic contexts existed.

Representatives of the genus *Debeya* are considered to have formed xerophytic associations (*Debeya*–*Dryophylletum* sensu Krassilov 1997b), especially in the proximity of oceanic and marine coasts, e.g., associations described from the Cenomanian of Crimea (Krassilov 1984) or the Senonian of Sakhalin (Krassilov 1979). In the former case, similarly to our material, the terrestrial flora is preserved in marine strata, whereas in the latter terrestrial and marine strata are intercalated. Xeromorphic conifers were a subordinate member of these associations (Krassilov 1997b). Such an ecological situation corresponds well to the abundance of *Debeya insignis* which is the commonest angiosperm in our material. The nearly monospecific accumulation of *Geinitzia reichenbachii* in Kazimierz Dolny might also be referred to a community of this kind, although in this case taphonomic bias has probably been stronger. A rough Recent analogy would be coastal forests of *Araucaria columnaris* in New Caledonia.

Representatives of Platanaceae show a strikingly constant ecology since the mid-Cretaceous up to the present day

(Doyle and Hickey 1976; Wing and Boucher 1998; Wing 2000), being present in disturbed, freshwater-related environments, i.e., forests growing along braided rivers (Coiffard et al. 2006) or channels (Upchurch et al. 1994). In Europe today, such a formation is represented by forests from the *Platanion orientalis* alliance (southern Balkan Peninsula). Contrary to the Recent *Platanus* forests, in the Cretaceous platanoids were often accompanied by representatives of Lauraceae (Upchurch et al. 1994; Coiffard et al. 2006). The Cenomanian “*Aralia*” *formosa* is reconstructed as belonging to the floodplain vegetation (Coiffard et al. 2007); this might be true also about *Araliopsoides*? cf. *minor* from our material. A forest growing in a humid environment along the river, containing (probably among other species, given our imperfect knowledge of the vegetation) *Ettingshausenia lublinensis*, *Araliopsoides*? cf. *minor*, aff. *Eucalyptolaurus* sp. and possibly *Dicotylophyllum* cf. *proteoides* (that might also represent Lauraceae), may be tentatively suggested as another source of the studied material.

*Cladophlebis* probably represents wetland vegetation. In contrast, members of Matoniaceae belonged to the floodplain communities (Coiffard and Gomez 2010).

## Palaeoclimatology

Only a qualitative palaeoclimatological analysis, based on seminal observations by Bailey and Sinnott (1915), is attempted here. Quantitative formalisations of the foliar physiognomic analysis either as the Leaf Margin Analysis (LMA; Wilf 1997; Steart et al. 2010) or the Climate Leaf Analysis Multivariate Programme (CLAMP; Wolfe 1993) require, respectively, at least either fifteen or twenty woody dicots from a single locality. Such a number is hardly attained even if all the material described here is regarded as a single assemblage. Neither can the Nearest Living Relative method (NLR; Heer 1859; Mosbrugger 1999, 2009) be used for our material insofar as it is composed mostly of taxa of uncertain affinities.

The seventeen dicotyledonous taxa in our material may be grouped as follows according to the character of the margin: (i) eight taxa with lobate or serrate margins (*Protodhedycarya* sp., *Ettingshausenia lublinensis*, *Debeya insignis*, *Grewiopsis* sp., *Araliopsoides*? cf. *minor*, *Rarytkinia polonica*, *Dicotylophyllum zubaense*, and *D. varienerve*); (ii) eight taxa with entire margins (aff. *Eucalyptolaurus* sp., *Cinnamomoides*? sp. nov., *Debeya haldemiana*, *Dicotylophyllum* cf. *proteoides*, *Dicotylophyllum* sp. 1, 2, 7, and 8); (iii) one taxon with unknown type of margin (*Dicotylophyllum* sp. 3).

Taxa with serrate or lobate margins are therefore equally numerous to those with entire margins ( $P = 50\%$ ). LMAT should not be calculated using these incomplete data for two major reasons: first, because the taxa do not come from a single assemblage; secondly, coastal plants were most probably experiencing a degree of water stress brought about by saline groundwater, whereas the method assumes

there is none in the analysed samples (Herman and Kvaček 2007: 43). If, nonetheless, we disregard these limitations the estimated LMAT would be between 14.3 and 16.5°C depending on which regression model was used (see Váchová and Kvaček 2009 for methodology details). However, it should be noted that entire-margined taxa are in a large part poorly known forms represented by single specimens, whereas lobate and serrate forms include the most numerous and characteristic species *Debeya paulinae* and *Rarytkinia polonica*. The values calculated for the analysed flora are evidently too high if one considers the CLAMP LMAT of 14.4°C for more thermophilic Grönbach flora (Spicer and Herman 2010).

## Palaeobiogeographic relationships

The described flora belongs to the middle latitude floras sensu Spicer et al. (1993), i.e., neither polar forests nor xeromorphic low latitude vegetation. In the two richest localities (Krasnohřd and Potelych) angiosperm are clearly the most numerous element of the flora which suggests their dominance. Given the something particular taphonomic setting of the studied flora, this should not be, however, taken as a proof of angiosperms necessarily forming either canopy or climatic vegetation. In a very general way it can be said that the Cretaceous vegetation was “dominated by a mixture of microphyllous conifers, (...) ferns, cycadophytes, pteridosperms, and sphenophytes” (Spicer et al. 1993: 277), although probably less so at the very end of the period. Late Campanian mid-latitude forests included both conifer- and angiosperm-dominated communities, the former exemplified by a nearly monospecific *Cupressinoxylon* community from New Mexico (Davies-Vollum et al. 2011), the latter by a dicotyledonous forest from Texas (Wheeler and Lehman 2000; Lehman and Wheeler 2001).

According to the reconstruction of Maastrichtian vegetation presented by Upchurch et al. (1998), in which the zone about 40° N palaeolatitude is on the southern edge of a “subtropical broad-leaved evergreen forest and woodland” dominated by angiosperms, with only small evergreen leaves, and few or no drip tips, not far from the northern limit of a “subtropical semi-deciduous forest”. The Late Cretaceous situation in North America is even more complicated, the zone between 40° and 50° N palaeolatitudes being covered by either tropical forest, paratropical rain forest, or notophyllous broad-leaved evergreen forest, according to the palaeoclimatic peculiarities of the region (Graham 1999: 153, 2011: 337). The described flora of either unstable or water-deficient environments is, however, quite difficult to place in these schemes of climatic zonal vegetation. Unstable environments favour deciduousness (Wolfe and Upchurch 1987). The described flora has a notable “Northern” aspect due to absence of palms and presence of taxa with clear polar relationships (*Rarytkinia*).

The most similar floras to the one described in the present paper are those from Westphalia (Hosius and von der Marck



1880) and from the Netherlands (Miquel 1853, van der Ham et al. 2001, 2007; Raymond van der Ham, personal communication 2010). Taxa in common (either genera or species) include *Geinitzia reichenbachii*, *Cunninghamites lignitum*, *C. ubaghsii*, *Debeya insignis*, and *D. haldemiana*. The flora of Westphalia contains several forms that do not occur in Poland (e.g., those described by Hosius and von der Marck 1880 as species of *Quercus*). The Dutch flora is of comparable numeric size and broadly similar composition; however, marine tracheophytes, including seagrasses (van der Ham et al. 2007) and putative lycophytes (van der Ham and van Konijnenburg-van Cittert 2010, van der Ham et al. 2011), known from the Netherlands have not been found in Poland up to now.

In comparison with approximately coeval floras from Grünbach in Austria and Russian Far East, the flora from southern Poland and western Ukraine occupies an intermediate position. The former is more thermophilic (palaeolatitude 32°N; Preisinger et al. 1986) with a dominance of integrimarginate species (e.g., the commonest *Juglandiphyllites pelagicus*, numerous *Theiaiphyllum kollmannii*) and presence of palms (*Sabalites longirhachis*) (Herman and Kvaček 2010), although the absolute number of serrate/lobate morphotypes is smaller at Grünbach, contrarily to the general aspect of the flora (P = 48% for Grünbach, 50% for our material; Herman and Kvaček 2007). Only *Dicotylophyllum* cf. *proteoides* might be a species common to the Polish-Ukrainian and Grünbach floras; this low number of species in common is, however, due also to ecologic discrepancies, the latter flora coming from wetlands. The Far East assemblages represent specific polar forests communities (Spicer 2003 and references therein). The genus *Rarytkinia* is most probably the only taxon linking the studied floras with polar forests. Thus, taxa in common between the Polish-Ukrainian floras and both Grünbach and Far East assemblages are quite scanty.

## Conclusions

- The latest Cretaceous (Campanian to Maastrichtian) marine rocks of southern Poland and western Ukraine contain a moderately diverse terrestrial flora composed of ferns (3 species), conifers (5 species), dicotyledonous angiosperms (17 species) and a single presumed monocot. The flora is evidently allochthonous but more or less complete leaves of *Debeya* strongly argue against a long transport distance prior to burial.
- The highest diversity is recorded in the late Campanian which may be explained by a local marine lowstand resulting in nearby emergent vegetated areas.
- The eudicot clade is formalised as supersubclass Eudicotyledoneae Doyle and Hotton ex Halamski, hoc loco.
- The genus *Dicotylophyllum* de Saporta, 1894 cannot be maintained in the present sense due to the identification of its type, *D. cerciforme*, as a nymphaealean. Either the type choice by Andrews (1970) must be superseded or *Dico-*

*tylophyllum* Bandulska, 1923 has to be conserved against *Dicotylophyllum* de Saporta, 1894.

- The most numerous angiosperm in the studied material is described as *Debeya (Dewalquea) paulinae* sp. nov. It differs from other European representatives of the genus in wide leaflets. It is most similar to North American *D. smithii*, from which it differs in the form of median lateral leaflets.
- Among seventeen dicotyledonous taxa eight have serrate or lobate margins and also eight (but these are in a large part poorly known taxa known from single specimens) are integrimarginate. This attests to an intermediate character of the flora between more thermophilic and polar vegetation.
- The studied material may have come from at least two communities: xeromorphic mixed *Debeya*-conifer forests (*Debeya* spp. and possibly *Geinitzia reichenbachii*) and platanoid-Lauraceae forests growing in disturbed environments along rivers (*Ettingshausenia? lublinensis*, *Araliopsoidea? cf. minor*, aff. *Eucalyptolaurus* sp., *Dicotylophyllum* cf. *proteoides*, and *Matonidium* sp.). *Cladophlebis* sp. possibly represents wetland vegetation.
- The studied assemblage is most similar to approximately coeval floras from Westphalia and the Netherlands.

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## Appendix 1

An alphabetic description of localities follows; their geographic position is signalled briefly through abbreviations: N, Nida Trough (Poland); L, Volhynia-Podolia Upland, L'viv region (Ukraine); P, Polesie (Poland); R, Roztocze: Rp, Polish part, Ru, Ukrainian part; V, Vistula valley (Poland).

**Bliżów (Rp).**—A small quarry in the eastern part of the village, 50°36'6"N, 20°7'39"E. Exposed rocks (about ten metres of opokas) belong to the *Endocostea typica* (inoceramid) Zone (early Maastichtian; Stolarski and Vertino 2007) and *Belemnella obtusa* (belemnite) Zone sensu Remin (2012) as defined for the Vistula and Krons-moor sections (Remin 2012). This is the locality 3 of Kin (2010). Despite large excavations, this outcrop yielded only two identifiable leaflets, one of *Debeya paulinae* (leg. Marcin Machalski), one of *D. haldemiana*.

**Chełm (P).**—A large quarry in the town of Chełm, approximate coordinates 51°9'N, 23°29'E, exposing ca. 40 m of white chalk (our only locality having this kind of rock). The age of the strata is early late Maastichtian (Machalski 2005 and references therein; Machalski et al. 2008; Dubicka and Peryt 2011). The fauna is abundant while the flora is very rare (two twigs of *Cunninghamites squamosus* with cuticle imprints preserved; the only such material in the studied area).

**Cierno (N).**—A small quarry, approximate coordinates 50°39'N, 20°12'E. The exposed opokas are lower Maastichtian according to Cieśliński and Milaković (1962; possibly upper Campanian). Rare vegetal remains.

**Dalechowy (N).**—A small quarry, approximate coordinates 50°36'N, 20°23'E. The exposed opokas are lower Maastichtian according to Cieśliński and Milaković (1962; possibly upper Campanian according to the Tercis definition). Rare vegetal remains.

**Hrebenne (Rp).**—Temporary excavations during the construction of a new border pass between Poland and Ukraine in 2006, approximate coordinates 50°16'N, 23°35'E. The age is late early Maastichtian (*Belemnella sumensis* Zone; Kin 2010). The opokas yielded a very rich marine fauna (locality 7 of Kin 2010).

**Ignacówka (N).**—A small quarry, approximate coordinates 50°40'N, 20°21'E. The exposed opokas are lower Maastichtian according to Cieśliński and Milaković (1962; possibly upper Campanian according to the Tercis definition). Rare vegetal remains.

**Janowiec (V).**—The outcrops are situated on the west bank of the Vistula opposite the town quarry in Kazimierz Dolny, approximate coordinates 51°19'N, 21°54'E; strata cropping out in both localities are coeval and similar in character (see below).

**Jasionna (N).**—A small quarry, approximate coordinates 50°37'N, 20°24'E. The exposed opokas are lower Maastichtian according to Cieśliński and Milaković (1962; possibly upper Campanian according to the Tercis definition). Rare vegetal remains.

**Jędrzejów (N).**—Temporary outcrops during the construction of the northern ring road in summer 2011, approximate coordinates 50°39'N, 20°17'E. The exposed opokas are upper Campanian according to the Tercis definition (Zbigniew Remin, personal communication 2011) and yielded the single specimen of *Cinnamomides?* sp. nov. (leg. Adrian Kin). Two further specimens, one of

*Debeya haldemiana* (Jagiellonian University, Institute of Geological Sciences, Cracow, UJ 220P/Jędrzej 1/3; leg. Agata Jurkowska), another of *D. cf. paulinae* (private collection, leg. Tadeusz Jurkowski; both from the "*Inoceramus*" *costaecus* Zone, upper Upper Campanian) have been made known to the author too late to be included in the systematic part (A. Jurkowska, personal communication April 2013).

**Kazimierz Dolny (V).**—The large town quarry, 51°18'59"N, 21°55'22"E, exposes about 25 m of opokas. The deposits belong to the *Belemnella kazimirovensis* Zone (late late Maastichtian); this is the locality 2 of Machalski (2005). The rocks, besides an abundant fauna, yielded several dozens of *Geinitzia reichenbachii*, which is the only vascular plant there. The presumed "algae" (Malicki et al. 1967: 222) are, as a matter of fact, sponge spicules, at least in major part.

**Kosobudy (Rp).**—An abandoned quarry (approximate coordinates 50°37'N, 23°04'E) with approximately 10 meters of opokas of early Maastichtian age – *Endocostea typica* (inoceramid) Zone and most probably *Belemnella obtusa* (belemnite) Zone sensu Remin (2012) as defined for the Vistula and Krons-moor sections (Remin 2012). This outcrop yielded *Dicotylophyllum* sp. 1.

**Krasnobród (Rp).**—A large quarry town quarry in Krasnobród (locality 4 of Kin 2010), situated between the centre of the town and Podzamek, 50°32'58"N, 23°12'14"E, exposes about 15 m of upper Campanian opokas belonging to the *Belemnella lanceolata* Zone sensu Remin (2012) (Zbigniew Remin, personal communication 2012) and showing rhythmic sedimentation of opokas alternating with thin marly intercalations (Zbigniew Remin and ATH, unpublished data). Marine fauna is very numerous, including cephalopods (nautiloids, *Pachydiscus neubergicus*, *Pachydiscus* sp., *Hoploscaprites* sp., *Acanthoscaphites quadrispinosus*; Kin 2010 and Adrian Kin, personal communication 2011), scaphopods, bivalves, and gastropods of broadly similar composition to that described from coeval deposits of the Middle Vistula Valley by Abdel-Gawad (1986), as well as brachiopods and fish scales. *Odontochitina* sp. (dinocysts) present in opokas in large number indicates restricted shallow marine conditions and varying salinity (Ewa Durska, personal communication 2011). This is the richest outcrop for angiosperms (see further details in Taphonomy section) and the type locality of *Rarytkinia polonica*, *Ettingshausenella lublinensis*, and *Debeya paulinae*.

**Liśnik (Rp).**—A borehole, approximate coordinates 50°53'N, 22°3'E. Lower Campanian (according to Cieśliński and Milaković 1962) marls yielded an unidentifiable conifer (reported by the above-mentioned authors as *Sequoia maior*).

**Lubycza Królewska (Rp).**—Temporary outcrops during the construction of the school in 2008, approximate coordinates 50°20'N, 23°31'E. The opokas (probably late Campanian in age given the presence of *Acanthoscaphites quadrispinosus* in the locality 6 of Kin 2010) yielded *Debeya haldemiana* (leg. Maciej Duda).

**L'viv (Lwów, Lemberg; L).**—Rocks exposed in temporary outcrops within the city of L'viv, approximate coordinates 49°52'N, 24°5'E, span at least the entire Maastichtian (Zofia Dubicka, personal communication 2011). Stratigraphic details of single outcrops are usually not available. They yielded several vegetal (mainly conifer) remains.

**Łysa Góra near Imielno (N).**—A small quarry, approximate coordinates 50°34'N, 20°26'E. The exposed opokas are lower Maastrichtian according to Cieśliński and Milaković (1962; possibly upper Campanian according to the Tercis definition). Rare vegetal remains.

**Majdan Nepryski (Rp).**—Outcrops north of the village of Majdan Nepryski, approximate coordinates 50°29'36"N, 23°5'1"E, show gaizes, the age of which is Campanian (Zbigniew Remin, personal communication 2010). They yielded *Dicotylophyllum* cf. *proteoides*.

**Nasiłów (V).**—A large quarry (now abandoned), situated on the left bank of the Vistula river opposite the town of Kazimierz Dolny, 51°21'9"N, 21°58'30"E. The age of the rocks is late late Maastrichtian (*Hoploscaphites constrictus crassus* Zone). A single specimen of *Elatocladus* sp. comes from this locality.

**Nemyriv (Niemirów; Ru).**—A borehole drilled in Nemyriv, approximate coordinates 50°6'N, 23°26'E, reached the "(lower?) Campanian", according to the label of the single *Pagiophyllum* sp. recovered from there.

**Obrocz (Rp).**—An unidentified outcrop reported by Malicki et al. (1967), approximate coordinates 50°36'N, 23°1'E. The age is lower Maastrichtian (upper Campanian?). Rare vegetal remains.

**Pidtemne (Podciemno; L).**—Temporary outcrops in the village, approximate coordinates 49°40'N, 24°03'E. The rocks may be dated to *Belemnella junior* Zone (Daniel Drygant, unpublished data). Animal (not uncommon) and rare plant fossils were collected by Daniel Drygant between 1957 and 1997. The fossil flora was described by Drygant (1998) and the types were re-illustrated by Mamčur (2006).

**Pińczów (N).**—An unidentified outcrop reported by Roemer (1870); approximate coordinates of the town are 50°32'N, 20°32'E. Limestone and marl with *Belemnitella mucronata* yielded a *Debeya* sp. (possibly *D. insignis*; specimen not traced).

**Piotrawin (V).**—A quarry situated in the Vistula valley, approximate coordinates 51°5'35"N, 21°48'10"E. The age of the exposed opokas spans the "*Inoceramus*" *altus* and "*Inoceramus*" *inkermanensis* Zones (Peryt 2000, Walaszczyk 2004) and therefore is late Campanian. A single *Dicotylophyllum* cf. *proteoides* comes from there.

**Potelych (Potylicz; Ru).**—A very large quarry, approximate coordinates 53°13'N, 23°33'E, abandoned for about ten years. The lower part of the exposed opokas is late Campanian in age but the upper part may already belong to the lower Maastrichtian (Zofia Dubicka, personal communication 2011). Fossil plants (ferns, coni-

fers, and angiosperms) are relatively numerous and were described by Nowak (1907a) who is also the author of a paper on the fossil fauna from the same locality (Nowak 1907b).

**Rachodoszcze (Rp).**—An unidentified outcrop reported by Malicki et al. (1967), approximate coordinates 50°37'N, 20°16'E. The age is early Maastrichtian (upper Campanian?). It yielded *Geinitzia reichenbachii*.

**Raków (N).**—A small quarry, approximate coordinates 50°38'N, 20°24'E. The exposed opokas are lower Maastrichtian according to Cieśliński and Milaković (1962; possibly upper Campanian according to the Tercis definition). Rare vegetal remains.

**Szozdy (Rp).**—A small outcrop, approximate coordinates 50°34'N, 22°55'E. The exposed gaizes may be dated to the middle part of the Campanian (Zbigniew Remin, personal communication 2010). They yielded *Matonidium* sp. (leg. Zbigniew Remin).

**Tarnawatka (Rp).**—An unidentified outcrop, approximate coordinates 50°32'N, 23°24'E. According to Nowiński (1967), it belongs to the late late Maastrichtian (*Belemnella kasimiroviensis* Zone). It yielded *Geinitzia reichenbachii*.

**Wieprzecka Góra (Rp).**—A small quarry near the road from Kąty II to Wychody, 50°40'42"N, 23°7'37"E. The exposed opokas are either upper Campanian or lower Maastrichtian and yielded a single specimen of *Geinitzia reichenbachii* (Piotr Chmielewski, personal communication 2011).

**Wola Pawłowska (V).**—Small quarries on the left bank of the Vistula, approximate coordinates 51°2'N, 21°50'E. The exposed opokas are late Campanian in age (*Didymoceras donezianum* Zone according to Błaszkiwicz 1980). They yielded fragmentary material of *Cunninghamites ubaghsii* (leg. Zbigniew Remin).

**Wolica (N).**—A small quarry, approximate coordinates 50°37'N, 20°22'E. The exposed opokas are lower Maastrichtian according to Cieśliński and Milaković (1962; possibly upper Campanian according to the Tercis definition). Rare vegetal remains.

**Zashkiv (Zaszków; L).**—An outcrop in the village, approximate coordinates 49°57'N, 23°59'E. The exposed opokas are of late late Maastrichtian age (*Hoploscaphites constrictus crassus* Zone; Zofia Dubicka, personal communication 2011). They yielded *Geinitzia reichenbachii* (leg. Zofia Dubicka).

**Zgubieniec (N).**—A small quarry, approximate coordinates 50°33'N, 20°21'E. The exposed opokas are lower Maastrichtian according to Cieśliński and Milaković (1962; possibly upper Campanian according to the Tercis definition). Rare vegetal remains, including a subcomplete leaf of *Debeya insignis*.