

ZLATKO KVAČEK

CUTICULAR STUDIES IN ANGIOSPERMS OF THE BOHEMIAN  
CENOMANIAN

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Epidermal patterns so far encountered in Cenomanian plants of the Bohemian Massif suggest the presence of the following more or less natural independent lineages: *Platanus-Credneria* group (stomata laterocytic, associated fructifications *Platanus*-like), "*Aralia*"-*Debeya* group (stomata laterocytic to anomocytic), *Myrtophyllum* group (stomata paracytic with the sunken guard cells, fructifications aggregate), *Cocculophyllum* group (stomata paracytic, partly with subdivided subsidiary cells, mesophyllous secretory bodies) and "*Diospyros*" group (stomata cyclocytic). Except *Platanus-Credneria* lineage no modern counterparts have been found for the studied early angiosperms.

**Key words:** Cenomanian, leaf anatomy, angiosperms.

Zlatko Kvaček, *Institute of Geology and Geotechnics, Czechoslovak Academy of Sciences, 18009 Praha 8, V Holešovičkách 41. Received: September 1981.*

## INTRODUCTION

The fossil flora found in the lowest member of the Bohemian Cenomanian, the so-called Peruc Formation, belongs to the richest records of mid-Cretaceous vegetation of Europe. The local assemblages vary in their composition from one locality to another but they all may in general be characterized by an abundant occurrence of angiosperms. This particular component of the ecosystems gave undoubtedly new features of the whole landscape. In spite of recent palaeobotanical studies (see Knobloch and Konzalová 1978) the taxonomy of the plant megafossils is still poorly understood partly due to overemphasized affinities to modern taxa by earlier authors (Velenovský, Bayer, Vinikláš and others). The flora is ranged by Pačtová (1977) on palynological evidence to the upper part of the Middle Cenomanian and correlated with the lower Raritan Formation of the North American Cretaceous. The following attempt has been made to characterize the obviously extinct early angiosperms on the

basis of leaf anatomy and to aid towards their natural grouping. Leaf epidermal and physiognomic features are employed to help explain palaeo-ecological aspects, the stomatal types are discussed in terms of evolutionary trends.

MAIN GROUPS OF EARLY ANGIOSPERMS IN THE BOHEMIAN  
CENOMANIAN ACCORDING TO THE STOMATAL TYPES

PLATANUS-CREDNERIA GROUP

Leaf blade more or less palmately lobed to palmatifid, venation suprabasal palinactinodromous, base partly peltate. Stomata laterocytic to "anomocytic", compound polycellate and/or simple rounded hair bases.

*Platanus laevis* (Velenovský) Velenovský (pl. 3:1; pl. 4:1; fig. 1A, B).

The species with deeply lobate leaves is well distinguished by fine undulation of anticlinal cell walls, striated upper leaf cuticle and frequent hair bases compound of 4 or more cells on either leaf side; the broadly oval stomata in the lower epidermis are often laterally bordered on one or both sides by very narrow subsidiary cells, which subtend the guard cell pair, i.e. laterocytic type. The same structure as in the type specimen (Velenovský 1882: pl. 2: 2) has been found in deeply palmatifid leaves known so far as *Aralia saportanea* Lesquereux or *Credneria purkyněi* Velenovský and Viniklář (Němejc and Kvaček 1975:61, pl. 23:5,6).

*Platanus velenovskiana* Krasser (syn. *Platanus rhomboidea* (Velenovský) Velenovský non Lesquereux) (pl. 4:2; fig. 1C, D).

Otherwise quite similar to the above described structure of *P. laevis*, *P. velenovskiana* differs by the lower epidermis with finely undulating anticlinal cell walls, which is thickly covered by small rounded hair bases and the stomata with thickened periphery (stomatal rim) which obscures the arrangement of subsidiary cells. The species is similar but probably not conspecific with *Platanus cuneifolia* Bronn in view of different cuticular structure (Rüffle 1968).

*Credneria bohémica* Velenovský

Due to poor preservation only the structure of the upper epidermis has been obtained, which seems to be faintly striated, beset by large compound hair-bases, the anticlinal cell walls being slightly wavy. Other cuticular features of this very peculiar large-leaved species have not been observed.

## MYRTOPHYLLUM GROUP

Leaf blade simple, oblong-ovate to lanceolate (to narrow lanceolate), entire-margined, venation pinnate, brochiodromous, in narrow leaf forms attaining eucalyptoid venation patterns. Stomata paracytic with the sunken guard cells, hair bases, if present, simple, small rounded, mesophyllous secretory bodies rare.

The group is most significantly represented in all localities. Their highly uniform epidermal patterns suggest they form a common lineage in a stage of progressive differentiation. The fructifications partly found in natural connection with foliage are aggregate ("*Eucalyptus*", *Ephedropsis sensu* Velenovský). More morphological forms (rather than species) can be recognized. A similar stomatal type was noted by Dilcher, Potter and Reynolds (1978) in the *Myrtophyllum*-like leaves from the Dakota group of the USA.

*"Magnolia" amplifolia* Heer (incl. "*Magnolia*" *speciosa* Heer)

The largest form of this group exhibits loose secondary venation that loops at the margin in form of an intralaminar vein. Intersecondaries may sometime occur suggesting a tendency to the eucalyptoid venation pattern, but the higher order venation is very thin and hardly visible. Although the type material lacks cuticles (imprints in sandstone) some specimens of the same morphology later found in claystones bear the epidermal characters described above, i.e. paracytic stomata, straight-walled ordinary cells, but lacking hair bases (Kvaček 1978). Some specimens attain up to 70 mm in width and at least 150 mm in length.

*Daphnophyllum crassinervium* Heer (incl. *Daphnophyllum ellipticum* Heer) (pl. 3:7; pl. 4:4; fig. 1L, M)

The entity is more likely to be treated as smaller leaves of the previously mentioned "*Magnolia*" *amplifolia*. Some well preserved specimens from Malá Chuchle show clear tendency of secondaries to form an intramarginal vein. By the paracytic type of stomata and small scattered hair bases they fit well within the *Myrtophyllum* group.

*Myrtophyllum geinitzii* Heer (incl. *Myrtophyllum schubleri* Heer, *Ficus krausiana* Heer)

The elongate leaf form has a typically developed eucalyptoid venation and the intramarginal vein. The secondaries are usually steeper than in

the previously mentioned entities, arising at the angles of about  $45-30^\circ$ . The thin cuticles suggest a chartaceous nature of the blade. The epidermal patterns conform those of *Daphnophyllum crassinervium*.

*Myrtophyllum angustum* (Velenovský) Knobloch (incl. *Proteophyllum laminarium* Velenovský) (pl. 3:6; pl. 4:3; fig. 1K)

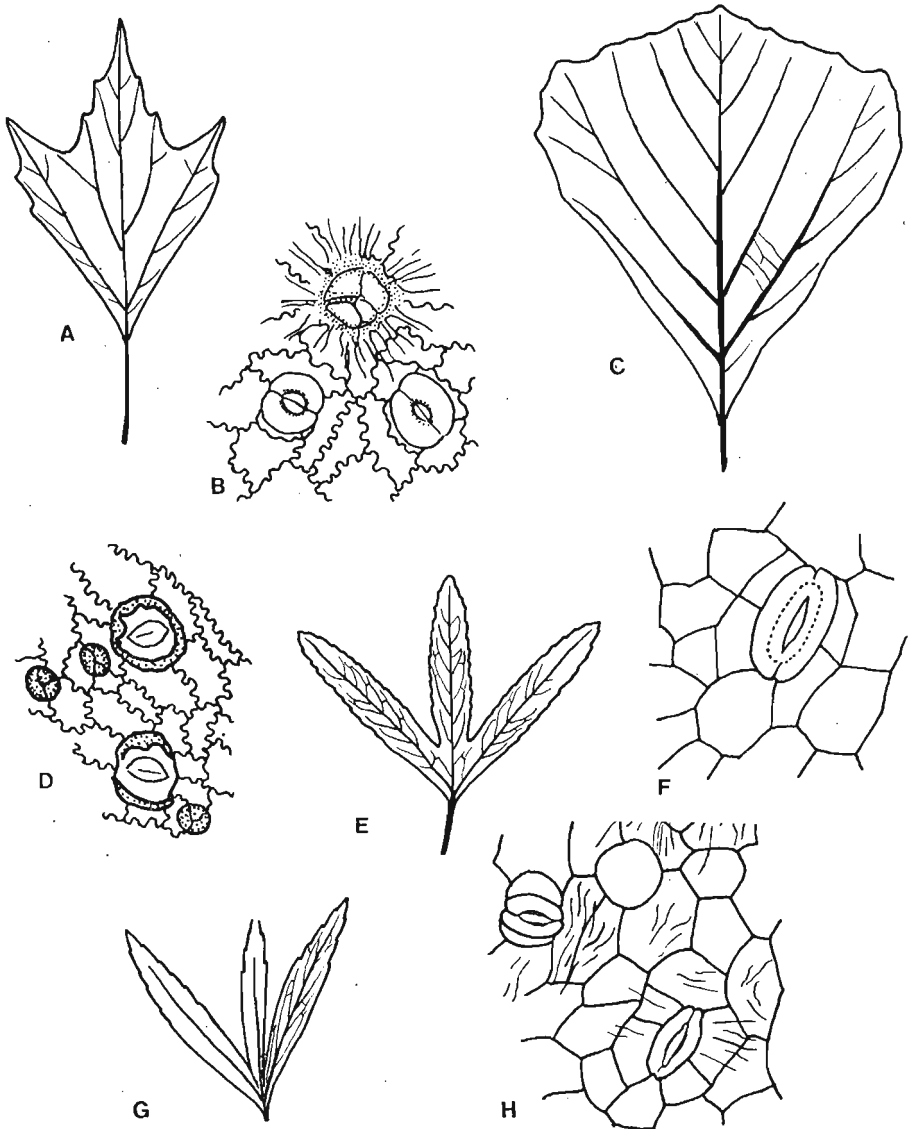
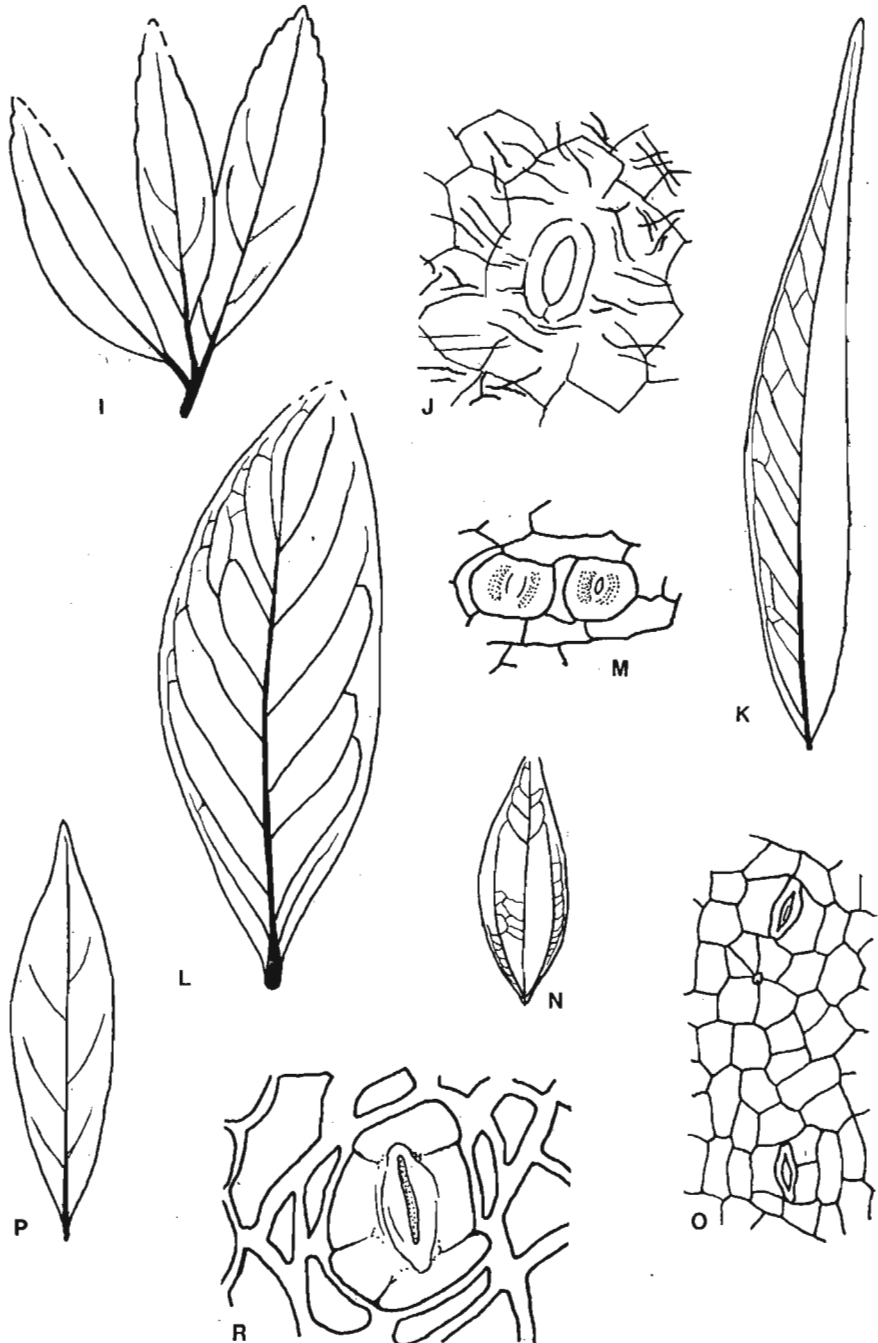


Fig. 1. Scheme of the main groups of angiosperms in the Bohemian Cenomanian according to the leaf morphology and epidermal structure. *Platanus-Credneria* group: A,B *Platanus laevis* (Velenovský) Velenovský C,D *Platanus velenovskiyana* Krasser. "Aralia"-*Debeya* group: E,F "*Aralia*" *formosa* Heer; G,H "*Aralia*" *dentifera* Velenovský; I,J *Debeya coriacea* (Velenovský) Knobloch. *Myrtophyllum* group: K *Myrtophyllum angustum* (Velenovský) Knobloch: L,M *Daphnophyllum crassinervium* Heer. *Cocculophyllum* group: N,O *Cocculophyllum cinnamomeum* (Velenovský) Velenovský. "Diospyros" group: P,R "*Diospyros*" *cretacea* Velenovský and Vinikiář. A,C,E,I —  $\times 0.33$ ; G,N,P —  $\times 0.43$ ; K,L —  $\times 0.66$ ; B,D,F,H,J,M,O,R —  $\times 235$ .

One of the most common angiosperm leaves in the Bohemian Cenomanian is characterized by a quite steep eucalyptoid venation with a distinct intramarginal vein. The cuticles are usually thick, the carbonized substance of the blade usually curls up from the matrix. The epidermal



(Fig. 1 continued)

patterns differ from the above form by more frequent hair-bases but otherwise coincide with the general scheme of *Myrtophyllum* (straight-walled ordinary cells, paracytic stomata).

*"Grevillea" constans* Velenovský

Needle-like coriaceous leaves occur in quantities at different localities (Hloubětín). The venation when visible in imprints, is very steep, the secondaries running subparallelly with the midrib. Although they correspond to the *Myrtophyllum* group in the form of paracytic stomata, they vary in the frequency of hair-bases and the stomatal size.

COCCULOPHYLLUM GROUP

Leaf blade oblong to ovate, entire-margined, venation acrodromous. Stomata paracytic occasionally with transversely subdivided subsidiary cells. Remains of secretory mesophyllous bodies frequent.

After the acrodromous venation such leaf forms have been previously suggested as the ancestors or members of Lauraceae or Menispermaceae. The comparison of epidermal characteristics show closer resemblance to Lauraceae though the subdivided subsidiary cells in the stomatal apparatus are not known in this family (Němejc and Kvaček 1975). The secretory elements testify a higher specialized metabolism and can be explained as defense against herbivorous animals (Stebbins 1974).

*Cocculophyllum cinnamomeum* (Velenovský) Velenovský (pl. 3:8; pl. 4:10; fig. 1N, O)

Apart from the narrow and small leaf form there occur in some localities broad leaves of the same venation patterns, which have been designated as *Aralia daphnophyllum* Velenovský. They exhibit the same epidermal structure as the type material of *C. cinnamomeum* and seem conspecific. Similar leaf form of early angiosperms are often assigned to *Cinnamomoides* Seward (Samylina 1968).

"ARALIA"-DEBEYA GROUP

Leaf blade palmately divided, mostly trilobate to trifoliate, with palinactinodromous venation. Stomata laterocytic to anomocytic (the stomatal type partly obscured by cuticular striation). Rare hair-bases large; partly heavily cutinized.

Not all *Debeya* species fit in the above concept by their epidermal structure. Beside the entities described below also the Senonian *D. tikhonovichii* (Kryshtofovich) Krassilov (1973) and *Debeya aquisgranensis* (Saporta et Marion) Knobloch *sensu* Stockmans (1946) are united here into this rather heterogenous group of uncertain systematic position while the Senonian *Debeya insignis* (Hos. et Marck) Knobloch *sensu* Němejc and Kvaček (1975) and the Paleogene *Debeya hibernica* (Johnson et Gilmore)

Knobloch show by the kind of hair-bases and stomata affinities to the Cainozoic lineage of *Platanus neptuni* (Ettingshausen) Bůžek, Holý and Kvaček.

"*Aralia*" *formosa* Heer sensu Velenovský (incl. *Proteophyllum araliopsis* Velenovský et Viniklář) (pl. 3:4; pl. 4:6; fig. 1E, F).

The form of which the epidermal structure has become known (Velenovský 1882: pl. 7: 4 from Kozákov) differs from the type specimen by narrower lobes, the venation of the lobes being brochiodromous, rather steep, with obliquely arranged elongate meshes of the higher-order veins. It is hardly distinguishable from *Proteophyllum araliopsis* described by Velenovský and Viniklář (1927, 1931) the only difference given by the authors, i.e. a very distinct higher-order venation being clearly due to the state of preservation. The epidermal remains bear massive cutinized hair-bases similar to those described by Krassilov (1973) in *Debeya tikhonovichii*. The outer surface of the polygonal straight-walled ordinary cells is faintly striated. The broadly elliptic stomata with thickened elliptic outer ledges seem to be bordered by two or more subsidiary cells in the laterocytic manner though their arrangement is not quite clearly seen.

"*Aralia*" *anisoloba* Velenovský (pl. 3:2; pl. 4:7)

The epidermal structure has been obtained from the type specimen (Velenovský 1882: pl. 3: 4) of this form peculiar by the reduced medial lobe. It differs from that of *Aralia formosa* by the lack of hair-bases and by smaller stomata whose type is obscured by a distinct striation.

"*Aralia*" *dentifera* Velenovský (pl. 3:9; pl. 4:5; fig. 1G, H)

The leaves are usually deeply lobate to tripartite with finely crenulate margin and a very steep and dense venation of the lobes. Both epidermides are striated, compound of polygonal straight-walled cells. The narrow elliptic stomata with a *Pseudonaviculla*-shaped outer pore have prevalently two parallel subsidiary cells, though occasionally the stomata with more subsidiary cells occur. The large hair-bases are less cutinized than in "*Aralia*" *formosa*.

*Debeya pentaphylla* Velenovský (pl. 3:5; pl. 4:8)

A very rare and incompletely known species has very thin cuticular remains (obtained from the type specimen from Lanšperk, Velenovský 1884: pl. 8:12). Among the straight-walled ordinary cells in the lower epidermis only small oval probably anomocytic stomata have been noticed though the arrangement of cells is very poorly visible.

*Debeya coriacea* (Velenovský) Velenovský (pl. 4:9; fig. 1I, J)

Its pedatiform tri- to pentafoliate leaves have been rarely found complete at Vyšehořovice (Velenovský 1889), while detached entire-margined or loosely crenulate lanceolate leaflets occur commonly at more localities. The venation is very vaguely seen due to a thick coriaceous leaf membrane. The ordinary cells in both upper and lower leaf sides are straight-walled, polygonal with heavily striated outer walls. The type of stomata, which are the largest among the "*Aralia*"-*Debeya* group, is obscured by the striation.

#### "DIOSPYROS" GROUP

Leaves simple, ovate to lanceolate, entire-margined, venation brochiodrome, stomatal type cyclocytic.

These thick coriaceous leaf compressions with a vaguely seen venation but with a characteristic epidermal structure occur more frequently in an association of *Frenelopsis*, *Nehvizdya*, *Dammarites* at Hloubětín, Lobeč, more rarely elsewhere. Their affinities are uncertain.

*"Diospyros" cretacea* Velenovský et Viniklář (pl. 3:3; pl. 4:12; fig. 1 P, R).

The epidermal features of these simple entire-margined leaves vary as to the size of ordinary cells, but the stomata are invariably surrounded by one or two rings of small subsidiary cells. There are no other epidermal characters like hairs etc. that would aid at solving the systematic position of these fossils.

The following scheme is by far not complete, many forms of the Bohemian Cenomanian flora are not yet well known (pl.3:10; pl.4:11), partly preserved as impressions without cuticles (*Proteophyllum*, *Halyserites*, "*Myrica*", *Cussoniophyllum*, *Diplophyllum* etc.) but with peculiar dissected leaf lamina (Knobloch 1978). Even some plants assigned by Velenovský to non-angiospermic groups may belong in fact after the stomatal types to angiosperms (e.g. *Pseudoasterophyllites* Velenovský), but additional work is needed to elucidate their nature.

#### PALAEOECOLOGICAL CONSIDERATION

Considering the leaf morphology and anatomy the response of angiosperms to climatic conditions may not have changed much through their evolution so that we are able to interpret with caution leaf anatomical and physiognomical data of early angiosperms ecologically.

Quantitatively the entire-margined, coriaceous leaves prevail in most of the local assemblages, but they belong only to few entities — *Myrto-phyllum*, "*Diospyros*", *Cocculophyllum* group and partly *Debeya coria-*



cea. In the richest assemblage at Vyšehořovice more than 30% of forms are probably deciduous (with very thin, chartaceous leaves). Leaf margin analysis is at the moment hardly reliable, for the number of the species in the whole flora is uncertain. Judging after the leaf forms that are distinct enough to be recognized as separate entities it appears that the dentate leaf forms slightly prevail over the entire-margined ones. The density of fine venation is rather low in most forms except in the *Platanus-Credneria* group but it is mostly due to the low degree of venation organisation (mostly the 2nd rank in sense of Hickey 1977) rather than due to ecological pressure and cannot be used as Manžer (1967) attempted in the Tertiary floras.

The lack of drip-tips in most of the forms attests to lower humidity of climate. The average leaf size in some localities (Vyšehořovice) is higher (certainly more than 20 cm of length) than one would expect in seasonally dry climate (see Dilcher 1973) while some of the local assemblages are notophyll to microphyll with xeromorphic aspects (Lipenec). Thus for the entire area of the Bohemian Cenomanian we must expect the varied humidity of climate from the dry seasonal to the moist type while the temperature regime might not exceed subtropical conditions. One is tempted to look for a modern analogon of the Cenomanian landscape in the subtropics of Mexico today. Such a concept would correspond to the palaeogeographical and palaeoecological scheme of the Upper Cretaceous given by Vakhrameev *et al.* (1978) for the European-Turansk region within Eurasia.

#### STOMATAL TYPES OF EARLY ANGIOSPERMS AND THEIR BEARING ON PHYLOGENY

Four types of stomata have been recognized among Cenomanian angiosperms studied. A peculiar xeromorphic type is represented by the cyclocytic stomata in the "*Diospyros*" group. The subsidiary and the guard cells probably arose from the only mother cell, so that the stomatal ontogeny is mesogenous. The *Myrtophyllum* group and also the *Cocculophyllum* group are characterized by the paracytic type. Ontogenetically the stomata are also clearly mesogenous.

In the *Platanus-Credneria* group which represents an independent well stabilized lineage, the laterocytic type is developed together with a specific kind of hair bases. The ontogeny of stomata might not change till present, i.e. the subsidiary cells are partly formed by division of some of the neighbouring cells. Brett (1979) describes the *Platanus* ontogeny as hemiperigenous. A similar arrangement of subsidiary cells corresponding principally to the laterocytic type but with a tendency towards the anomocytic type (probably with a perigenous ontogeny) occurs in the "*Aralia*"-*Debeya* group. This situation seems most ancient as it was stated

in the oldest known angiosperm cuticles of the lower Potomac Group (Aptian to early Albian) by Upchurch (1978).

The existence of such widely diversified stomatal structures among Cenomanian plants supports the idea that at that time first primitive, mostly extinct groups (? of the family rank) were already formed, though their more precise definition will be possible when the characters of reproductive structures become better known (Dilcher *et al.* 1976).

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## EXPLANATION OF PLATES 3—4

## Abbreviations used:

NM — National Museum, Palaeontological Department, Praha

UGG — Institute of Geology and Geotechnics, Czechoslovak Academy of Sciences, Praha.

## Plate 3

1. *Platanus laevis* (Velenovský) Velenovský, NM F 283, the lectotype (see Velenovský 1882: pl. 4:2). Mělník.
2. "*Aralia*" *anisoloba* Velenovský, NM F 322, the lectotype (see Velenovský 1882: pl. 5:4). Lanšperk.
3. "*Diospyros*" *cretaceae* Velenovský and Viniklár, UGG H1 28 A. Praha—Hloubětín.
4. "*Aralia*" *formosa* Heer, NM F 327 (see Velenovský 1882: pl. 7:4). Kozákov.
5. *Debeya pentaphylla* (Velenovský) Knobloch, NM F 536, the lectotype (see Velenovský 1884: pl. 8:12). Lanšperk.
6. *Myrtophyllum angustum* (Velenovský) Knobloch, NM F 537. Praha—Malá Chuchle.
7. *Daphnophyllum crassinervium* Heer, NM F 539. Praha—Malá Chuchle.
8. *Cocculophyllum cinnamomeum* (Velenovský) Velenovský, NM F 500. Lipenec.
9. "*Aralia*" *dentifera* Velenovský, NM F 535. Praha—Malá Chuchle.
10. *Dicotylophyllum* sp. (aff. "*Diospyros*" *prosecta* Velenovský vel "*Laurus*" *plutonia* Heer), NM F 538. Praha—Malá Chuchle.

Scale-bar = 10 mm

## Plate 4

1. *Platanus laevis* (Velenovský) Velenovský, UGG Mě 2/1, lower epidermis. Mělník; ×500.
2. *Platanus velenovskyana* Krasser, UGG MCh 13/2, lower epidermis. Praha—Malá Chuchle; ×500.
3. *Myrtophyllum angustum* (Velenovský) Knobloch, UGG MCh 15/1, lower epidermis of the specimen in pl. 3:6. Praha—Malá Chuchle; ×200.
4. *Daphnophyllum crassinervium* Heer, UGG MCh 14/2, lower epidermis of the specimen in pl. 3:7. Praha—Malá Chuchle; ×200, phase contrast.
5. "*Aralia*" *dentifera* Velen., UGG MCh 21/2, lower epidermis of the specimen in pl. 3:9. Praha—Malá Chuchle; ×500.
6. "*Aralia*" *formosa* Heer, UGG Ko 1/1, lower epidermis of the specimen in pl. 3:4. Kozákov; ×500, phase contrast.
7. "*Aralia*" *anisoloba* Velen., UGG Ln 5/1, lower epidermis of the specimen in pl. 3:2. Lanšperk; ×500, phase contrast.
8. *Debeya pentaphylla* (Velenovský) Knobloch, UGG Ln 7/3, lower epidermis of the specimen in pl. 3:5. Lanšperk; ×500, phase contrast.
9. *Debeya coriacea* (Velenovský) Knobloch, UGG Vi 12/1, lower epidermis. Praha—Vidoule; ×500.
10. *Cocculophyllum cinnamomeum* (Velenovský) Velenovský, UGG Li 8/1, lower epidermis. Lipenec; ×500.
11. *Dicotylophyllum* sp., UGG Li 5A/2, lower epidermis of the specimen in pl. 3:10. Lipenec; ×200.
12. "*Diospyros*" *cretacea* Velenovský and Viniklář, UGG H1 28A/1, lower epidermis of the specimen in pl. 3:3. Praha—Hloubětín; ×200.

