



FOLIAGE OF A BROAD LEAVED CONIFER *DAMMAROPHYLLUM* FROM THE CENOMANIAN OF BOHEMIA

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Abstract. The morphogenus *Dammarophyllum* VELENOVSKÝ is validated and emended to accommodate broad-leaved coniferous foliage with an affinity to Araucariaceae or Podocarpaceae. It shows characteristic parallel venation consisting of simple veins, arising from the base and gradually converging to the apex. Cuticle of hypostomatic leaves shows haplocheilic stomata without dorsal lamellae arranged irregularly or longitudinally in short rows. The genus *Dammarophyllum* is so far monospecific. It is compared to other genera of similar leaf morphology *Dammarites* PRESL, *Lindleycladus* HARRIS, *Nageiopsis* FONTAINE, and *Podozamites* C.F.W. BRAUN.

■ Araucariaceae, Podocarpaceae, conifers, Cenomanian, Cretaceous.

INTRODUCTION

Broad-leaved conifers are rare elements of mid-European Cretaceous floras. Their fossil remains have been traditionally associated with the family Araucariaceae, although similar foliage is known e. g. in the family Podocarpaceae. Unequivocal remains of the Araucariaceae showing a cone scale with one centrally arranged inverted seed were recorded in the Upper Cretaceous of the Czech Republic in the Březno Formation by Bayer (in Frič 1893). Other fossils found in the Bohemian Cretaceous Basin and interpreted as araucariaceous, e.g. *Dammara borealis* HEER and *Brachyphyllum squamosum* (VELENOVSKÝ) PALIBIN, are considered here as doubtful. *Dammara borealis* is probably related to the recently described family Doliostrobaceae (Z. Kvaček 2002).

Although the Araucariaceae, in contrast to the Podocarpaceae, has been recorded in the European Cretaceous the morphogenus *Dammarophyllum* is suggested to include foliage of the both families.

MATERIAL AND METHODS

The material studied comes from the Peruc-Korycany Formation of the Bohemian Cretaceous Basin as defined by Čech et al. (1980). It occurs at two localities – Bohdánkov near Hodkovice nad Mohelkou and Prague – Malá Chuchle. The material from the type locality Bohdánkov consists of poorly preserved leaf impressions. The specimen from Malá Chuchle is a leaf impression with adhering small pieces of cuticle. The cuticle was prepared by the standard technique (e.g. J. Kvaček 1999) for both observations in light microscope and SEM. All the material comes from old museum collections housed in the National Museum, Prague.

Genus: *Dammarophyllum* VELENOVSKÝ gen. nov.

syn: 1889 *Dammarophyllum* VELENOVSKÝ, pp. 7, 49, 53, nom. nud.

Type: *Podozamites striatus* VELENOVSKÝ 1885: 10, pl. 2, fig. 8

Description: Leaf oblong to ovate-rhombic, entire-margined, apex obtuse; leaf base abruptly narrowing to the short robust petiole; veins simple, dense, arising from the petiole over the base of the lamina gradually converging towards the apex. Leaves hypostomatic; adaxial cuticle showing tetragonal or polygonal isodiametric cells forming short rows; abaxial cuticle consisting of costal and intercostal bands, anticlinal walls undulate, haplocheilic stomata without dorsal lamellae irregularly or longitudinally orientated in short rows.

Discussion: The generic name *Dammarophyllum* was published invalidly by Velenovský (1889) without any diagnosis or description in invalid combination *Dammarophyllum striatum* (VELENOVSKÝ.) VELENOVSKÝ. Velenovský (1889) only pointed out that “*Dammarophyllum striatum* VEL. Zprávy král. Česk. spolku nauk r. 1886 [i.e. Velenovský (1887)] is in indirect association with *Dammara boraelis* HEER in the locality of Bohdánkov”. The name of the genus *Dammarophyllum*, although frequently used, was not validated even in the later publications (Frič et Bayer 1902, 1903; Seward 1919; Andrews 1970; Hlušík 1980). The genus is therefore described herein to be validated.

The genus *Dammarophyllum* differs from the genera *Podozamites* C.F.W. BRAUN and *Lindleycladus* HARRIS in epidermal structure. *Lindleycladus* has stomata orientated longitudinally with leaf margin. *Podozamites* has stomata orientated perpendicularly. *Dammarophyllum* shows irregularly orientated stomata.

The genus *Nageiopsis* (Fontaine 1890) differs in the venation pattern. Its veins do not converge into the apex reaching the leaf margin in sharp angles. Leaves of *Nageiopsis* are usually decurrent (Berry 1910).

The genus *Dammarites* Presl differs from *Dammarophyllum* in long linear leaves without petioles attached to short tuberous stems. Using these characters Hlušík (1976) argued for its non-coniferous affinity.

The type of stomata rules out affinities to cycads, which have stomata with dorsal and partly ventral lamellae and monocots, in which the stomata are not hidden in pits and have well preserved guard cells.

Dammarophyllum striatum (VELENOVSKÝ) VELENOVSKÝ comb. nov.

Figs 1–5

B a s i o n y m: *Podozamites striatus* VELENOVSKÝ 1885: 10, Die Gymnospermen der böhmischen Kreideformation, pl. 2, fig. 8

1885 *Podozamites striatus* VELENOVSKÝ: 10, pl. 2, fig. 8

1887 *Podozamites striatus* VELENOVSKÝ: 41, pl. 1, fig. 17

1889 *Dammarophyllum striatum* (VELENOVSKÝ) VELENOVSKÝ: 7, 49, 53, comb. inval. Art. 43.1

1889 *Dammarophyllum bohemicum* VELENOVSKÝ: 56, 71, 73, nom. altern. Art. 34.2

1902 *Dammarophyllum striatum* (VELENOVSKÝ) VELENOVSKÝ; Frič et Bayer: 96, text-fig. 48, nom. inval.

1903 *Dammarophyllum striatum* (VELENOVSKÝ) VELENOVSKÝ; Frič et Bayer: 95, text-fig. 48, nom. inval.

1906 *Dammarophyllum striatum* (VELENOVSKÝ) VELENOVSKÝ; Seward et Ford: 381, nom. inval.

1919 *Dammarophyllum striatum* (VELENOVSKÝ) VELENOVSKÝ; Seward: 246, nom. inval.

1919 *Dammarophyllum bohemicum* VELENOVSKÝ; Seward: 246, nom. inval.

1980 *Dammarophyllum striatum* (VELENOVSKÝ) VELENOVSKÝ; Hlušík: 27, nom. inval.

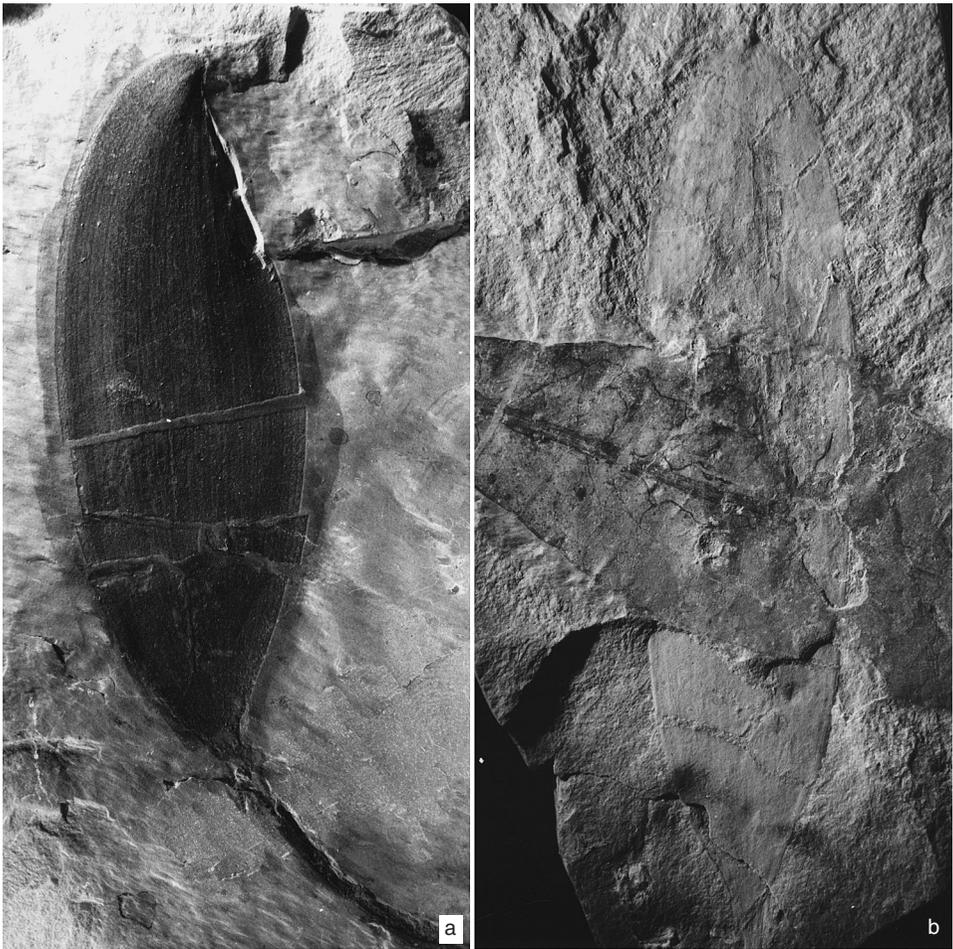


Fig. 1. *Dammarophyllum striatum* (VELENOVSKÝ) VELENOVSKÝ comb. nov. a – Holotype, Bohdánkov; F 241, $\times 1.5$; b – Leaf figured by Velenovský (1887, pl. 1, fig. 17), Bohdánkov; F 108, $\times 1.5$.

Holotype: F 241, F 107 (part and counterpart), Velenovský 1885 pl. 2, fig. 8, (herein fig. 1), housed in the National Museum, Prague.

Type locality: Bohdánkov (Liebenau), near Hodkovice nad Mohelkou.

Type horizon: Late Cretaceous, Cenomanian, Peruc-Korycany Formation.

Description: Leaf coriaceous, ovate-rhombic, entire-margined, apex rounded, partly asymmetrical; leaf base abruptly narrowing to the short robust petiole, born on a twig; primary veins simple, arising from the area at the base without forking, gradually converging to the apex. Leaves hypostomatic; adaxial cuticle showing tetragonal or polygonal isodiametric cells forming short rows; abaxial cuticle consisting of costal and intercostal bands, anticlinal walls bent or slightly undulate, stomata haplocheilic, irregularly or longitudinally orientated, surrounded by 5–6 subsidiary cells forming oval circle, bordering broad rounded stomatal pit with slightly raised rim.

Specimens studied: F 107, F 108, F 241, F 2355.

Occurrence: Bohdánkov, Prague-Malá Chuchle.

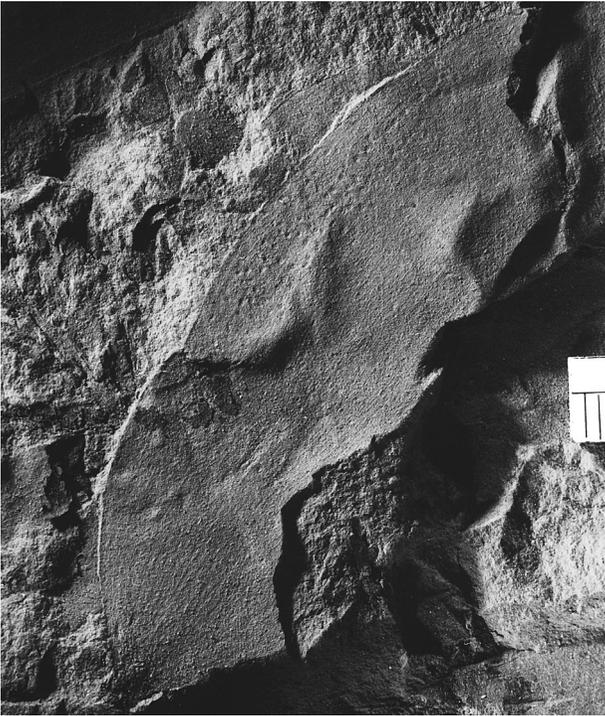


Fig. 2. *Dammarophyllum striatum* (VELENOVSKÝ) VELENOVSKÝ comb. nov. Leaf compression, Prague-Malá Chuchle; F 2355, $\times 2$.

Remarks: The holotype (Fig. 1a) represents nearly an entire leaf impression (21×61 mm) with a 3 mm long petiole attached to a twig (brachyblast?). The density of veins varies within the leaf. The densest venation is in the basal and apical parts, the least dense is the medial part, 1 vein per mm (Fig. 3). Leaf impression F 108 (18×81 mm) figured by Velenovský (1887, fig. 17) shows the well-preserved apex and the basal part attached to 5 mm long twig or petiole (Fig. 1b). Its veins are poorly preserved. The only specimen from the locality of Prague-Malá Chuchle represents a fragment of leaf impression/compression (Fig. 2). Several remnants of cuticle have been observed and used for preparations showing the described anatomical structures. The leaf is over 55 mm long and 18 mm wide. Veins run from a short petiole (2 mm) without forking. It is not clear, if the leaf was more complete when Bayer was studying it. Bayer's sketch attached to the back part of the specimen shows the entire leaf.

The leaf is hypostomatic and has cuticle of medial thickness. The adaxial cuticle bears polygonal cells ($15\text{--}30 \times 20\text{--}50$ μm) with straight or bent anticlinal walls $0.8\text{--}1$ μm thick. Cells of costal areas tend to be more tetragonal forming short rows (Fig. 4b). The abaxial cuticle consists of costal and intercostal bands (Fig. 4a). Costal bands show quadrangular cells ($10\text{--}20 \times 20\text{--}35$ μm) in rows, their anticlinal walls are straight or slightly sinuous ($1\text{--}2$ μm thick). Intercostal bands display irregularly orientated polygonal ordinary cells ($10\text{--}25 \times 15\text{--}40$ μm) with sinuous anticlinal walls ($0.8\text{--}1$ μm). Haplocheilic dicyclic stomata (Fig. 5e) are obliquely or sometimes longitudinally orientated to the leaf margin. They are most likely arranged in short rows, as it is apparent on tiny pieces of cuticle (Fig. 4a). They are surrounded by 5–6 subsidiary cells ($10\text{--}20 \times 20\text{--}35$ μm), sunken in pits (Figs 5a, b, d). The external surface of the pit shows slightly arisen cutinized rim (Figs 5b, d), which is rarely well pronounced (Fig. 5a).

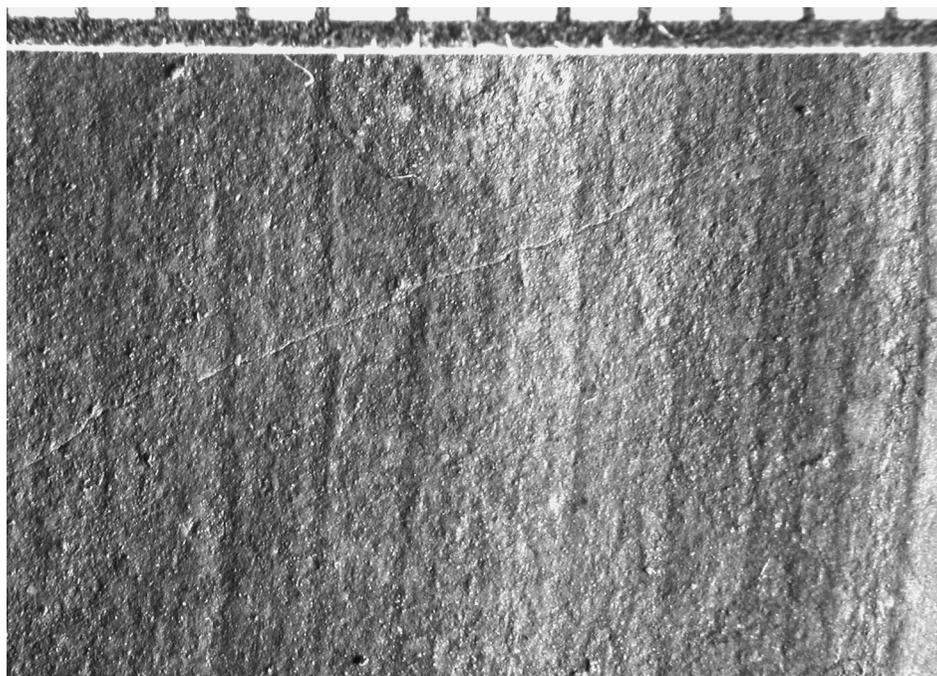


Fig. 3. *Dammarophyllum striatum* (VELENOVSKÝ) comb. nov. Holotype, detail of venation, Bohdánkov; F 241, $\times 10$.

Discussion: Leaves similar to *D. striatum* were described by LESQUEREUX (1883) from the Cenomanian of the Dakota Formation (Kansas, USA). They were later figured (Lesquereux 1891, pl. 1, figs 9–11) and placed to the genus *Dammarites* (*Dammarites caudatus* (LESQUEREUX) LESQUEREUX, *Dammarites emarginatus* (LESQUEREUX) LESQUEREUX). Both these leaves differ from *D. striatum* in larger size (140 \times 40–50 mm). Probably the same leaves occurring in the Upper Cretaceous Nanaimo Group (Vancouver Island, British Columbia) were figured by Bell (1957, pl. 19, figs 2, 4, 6) as *Dammarites robinsii* (DAWSON) BELL. *Dammarites bayeri* ZEILLER (1905, pl. 2, figs 8–11) from the Cretaceous of Bulgaria resembles *D. striatum* in its size (100–120 \times 15–30 mm). Nevertheless, all four species mentioned above (*D. caudatus*, *D. emarginatus*, *D. bayeri*, *D. robinsii*) were published without cuticles. Therefore, a more precise comparison is now impossible.

Leaves very similar to *D. striatum* were described by Cookson et Duigan (1951) as *Agathis yellournensis* COOKSON et DUIGAN from the Palaeocene of south-eastern Australia. The leaf shape and size, 35–95 \times 10–20 mm, correspond well with *Dammarophyllum striatum*. The anatomical characters are also similar. Both taxa are hypostomatic showing abaxially similar stomatal structure and arrangement. *D. striatum* differs from *A. yellournensis* in poorly distinguished costal and intercostal zones and in well pronounced continuous stomatal rows.

The genus *Araucarioides* GIGWOOD et R. HILL (1985) is intermediate between *Araucaria* and *Agathis*, having many characters in common with *Araucaria*, but resembling *Agathis* in transversally orientated stomata to leaf margin. It is now compared with the recent genus *Wollemia*. *Araucarioides* resembles *Dammarophyllum* in lack of the Florin

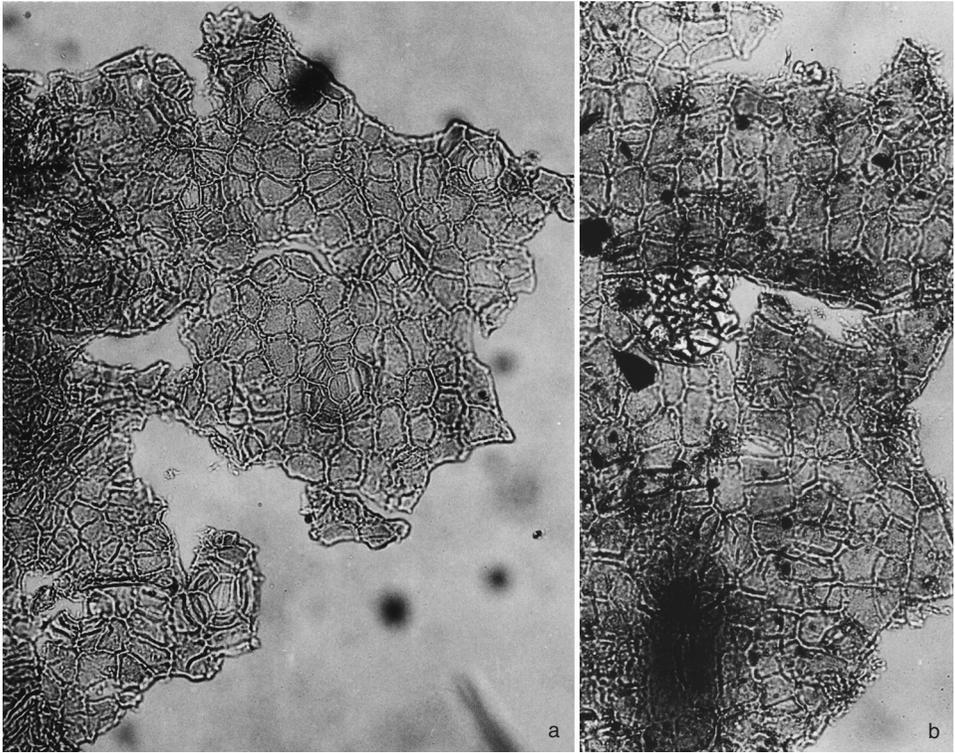


Fig. 4. *Dammarophyllum striatum* (VELENOVSKÝ) comb. nov. a – Abaxial cuticle, Prague-Malá Chuchle; F 2355b, $\times 200$; b – Adaxial cuticle, Prague-Malá Chuchle; F 2355b, $\times 200$.

rings and differs in transversely orientated stomata. *Dammarophyllum striatum* is similar to the recent broad-leaved araucarians in irregularly to longitudinally orientated stomata to the leaf margin that are arranged in discontinuous rows. *Dammarophyllum* resembles *Agathis* in having similar arrangement of stomata, but differs in lack of the typical Florin rings. The same applies for most of the broad-leaved Podocarpaceae, additionally their stomata are arranged longitudinally to leaf margin (Stockey et al. 1998).

Due to the lack of any fructification the systematic position of *Dammarophyllum striatum* is uncertain as already pointed out by Velenovský (1887). When mentioning the genus *Dammarophyllum* for the first time, Velenovský (1889) suggested the connection between cone scales of “*Dammara*” *borealis* HEER = *Sciadopityes borealis* (HEER) SEWARD et CONWAY and leaves of *Dammarophyllum striatum*. This hypothesis was not verified. In my opinion, the frequently occurring cone scales of *S. borealis* do not seem to allow an association with the very rare leaves of *D. striatum*. On the other hand, the cuticle pattern of *D. striatum* argues for its araucarian affinity (Hlušík 1980, see also Stockey 1994).

It should be stressed that certain members of the family Podocarpaceae also have similar appearance of leaves. Although broad-leaved species of this family, (e.g. *Podocarpus* L’HÉRITIER ex PERSOON and *Nageia* GAERTNER), as pointed out already by Cookson et Duigan (1951) and Florin (1931), differ in clearly longitudinally orientated stomata to the leaf margin.

The name *Dammarophyllum bohemicum* VELENOVSKÝ 1889 is considered here as only Ve-

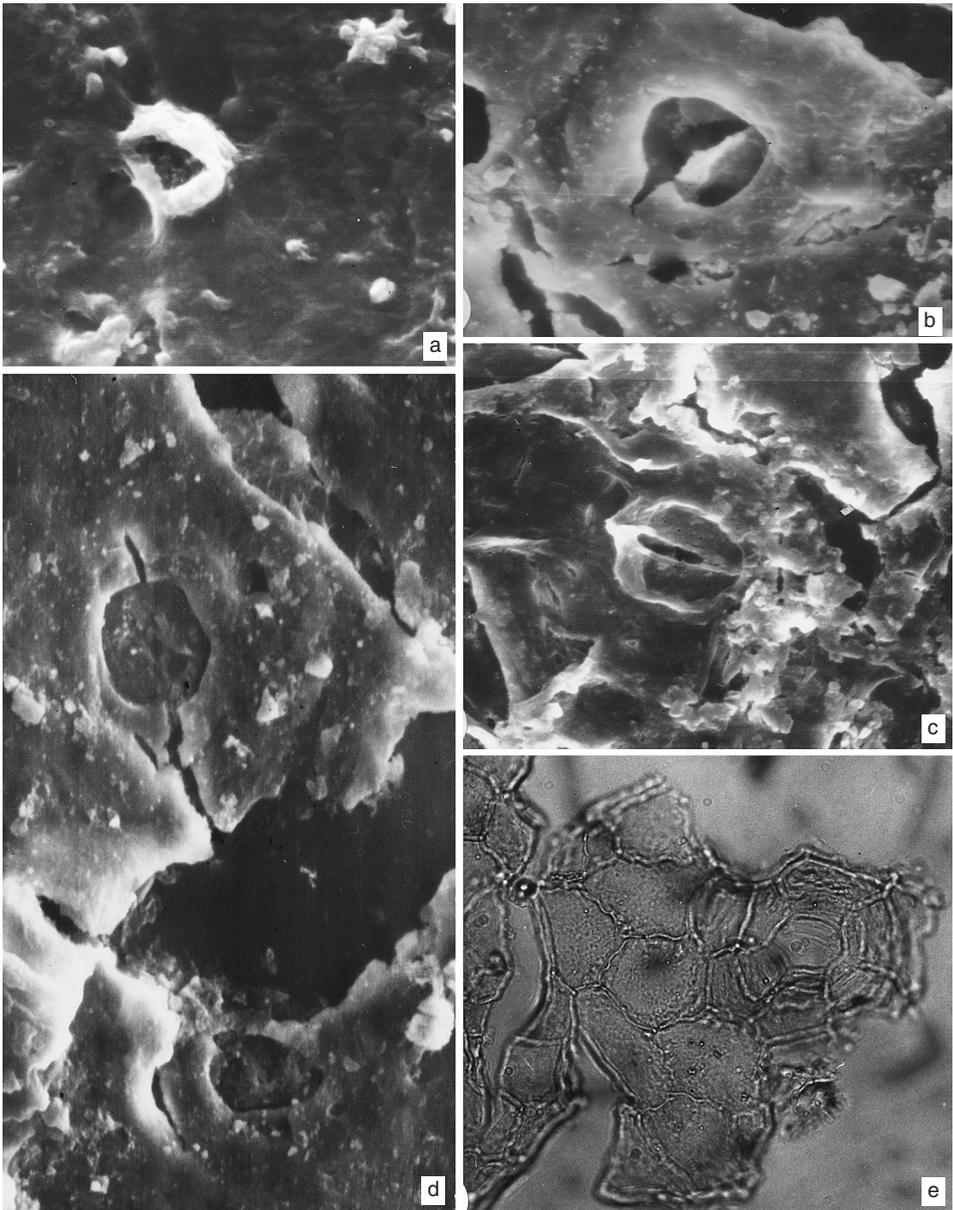


Fig. 5. *Dammarophyllum striatum* (VELENOVSKÝ) VELENOVSKÝ comb. nov. a – Abaxial cuticle, possible stoma, SEM of outer surface, Prague-Malá Chuchle; F 2355c (4217), $\times 1500$; b – Abaxial cuticle, stoma, Prague-Malá Chuchle; F 2355c (5131), $\times 1000$; c – Abaxial cuticle, stoma, SEM of inner surface, Prague-Malá Chuchle; F 2355b, $\times 400$; d – Abaxial cuticle, ?stoma, SEM of outer surface, Prague-Malá Chuchle; F 2355c (5133), $\times 1000$; e – Abaxial cuticle, stoma, Prague-Malá Chuchle; F 2355c (5226), $\times 800$.

lenovský's confusion with *D. striatum* mentioned in the same publication, as it follows from the context (Velenovský 1889). Moreover, there is no diagnosis or figure of *D. bohemicum* in Velenovský (1889), so the name is definitely an alternative name for *D. bohemicum*.

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REFERENCES

- Andrews, H. N., Jr. (1970): Index of Generic Names of Fossil Plants, 1820–1965. – U.S. Geological Survey Bulletin, 1300: 1–354.
- Bell, W. A. (1957): Flora of the Upper Cretaceous Nanaimo Group of Vancouver Island, British Columbia. – Geological Survey of Canada, Memoir, 293: 1–84.
- Berry, E. W. (1910): A revision of the fossil plants of the genus *Nageiopsis* of FONTAINE. – Proc. U.S. National Mus., 38: 185–195.
- Bigwood, A. J., Hill, R. (1985): Tertiary araucarian macrofossils from Tasmania. – Aus. J. Bot., 33: 645–656.
- Cookson, I. C., Duigan, S. L. (1951): Tertiary Araucariaceae from south-eastern Australia, with notes on living species. – Australian Journal of Scientific Research, Series B, Biological Series, 4(4): 415–449.
- Čech, S., Klein, V., Kříž, J., Valečka, J. (1980): Revision of the Upper Cretaceous stratigraphy of the Bohemian Cretaceous Basin. – Věstník Ústředního Ústavu geologického, 55(5): 277–296.
- Florin, R. (1931): Untersuchungen zur Stammesgeschichte der Coniferales und Cordaitales. – Kung. Svenska Vetensk. Handl. Ser. 3, 10 (1): 1–588.
- Fontaine, W. M. (1889): The Potomac or younger mesozoic flora. – U. S. Geol. Surv., Monogr., 15: 1–377.
- Frič, A., Bayer, E. (1902): Studien im Gebiete der Böhmisches Kreideformation. Peruczer Schichten. – Archiv naturwiss. Landesdurchforsch. Böhmen, 11(2): 1–180.
- Frič, A., Bayer, E. (1903): Studie v oboru křídového útvaru českého. Perucké vrstvy, [Study in Cretaceous strata of Bohemia]. – Archiv Přírodověd. Prozk. Čech, 11(2): 1–179. (in Czech)
- Frič, A. (1893): Studien im Gebiete der Böhmisches Kreideformation. Palaeontologische Untersuchungen der einzelnen Schichten. Priesener Schichten. – Archiv naturwiss. Landesdurchforsch. Böhmen, 9(1): 1–134.
- Greuter, W., McNeill, J., Barrie, F. R., Burdet, H. M., Demoulin, V., Filgueiras, T. S., Nicolson, D. H., Silva, P. S., Skog, J. E., Trehane, P., Turland, N. J., Hawksworth, D. L. (eds.) (2000): International Code of Botanical Nomenclature (Saint Louis Code). – Regnum Vegetabile, Königstein, pp. 474.
- Hlušítk, A. (1976): Contribution to the systematic and leaf anatomy of the genus *Dammarites* Presl in Sternberg. – Acta Mus. Nat. Pragae, ser. B., Hist. Nat., 30: 49–70.
- Hlušítk, A. (1980): Problematic *Podozamites* – like leaves from the Upper Cretaceous of the Bohemian Massif. – Acta Mus. Nat. Pragae, ser. B., Hist. Nat., 36(1): 21–33.
- Kvaček, J. (1999): New data and revision of three gymnosperms from the Cenomanian of Bohemia – *Sagenopteris variabilis* (VELENOVSKÝ) VELENOVSKÝ, *Mesenea bohemica* (Corda) comb. n. and *Eretmophyllum obtusum* (VELENOVSKÝ) comb. n. – Acta Mus. Nat. Pragae, Ser. B., Hist. Nat., 55(1–2): 15–24.
- Kvaček, Z. (2002): Novelities on *Doliosirobus* (Doliosirobaceae), an extinct conifer genus of the European Palaeogene. – Čas. Nár. Muz., ř. přírodověd., 171: 131–175.
- Lesquereux, L. (1883): The Cretaceous and Tertiary floras, Contribution to the fossil flora of the Western Territories, Part III. – Report of the United States Geological Survey of the Territories, 8: 1–283.
- Lesquereux, L. (1891): The Flora of the Dakota Group. – Monograph of the United States Geological Survey, 17: 1–256.
- Seward, A. C. (1919): Fossil plants, vol. IV. – 543 pp. Cambridge University Press, Cambridge.
- Seward, A. C., Ford, S.O. (1906): The Araucariaceae, recent and extinct. – Philosophical Trans. Roy. Soc., London, Ser. B, 198: 305–411.
- Stockey, R. A. (1994): Mesozoic Araucariaceae: morphology and systematic relationships. – J. Plant Res., 107: 493–502.
- Stockey, R. A., Frevel, B.J., Woltz, P. (1998): Cuticle morphology of *Podocarpus*, subgenus *Podocarpus*, section *Scytodopodium* (Podocarpaceae) of Madagascar and South Africa. – Int. J. Plant. Sci., 159: 923–940.
- Velenovský, J. (1885): Die Gymnospermen der böhmischen Kreideformation. – 34pp. E. Greger, Prag.
- Velenovský J. (1887): Neue Beiträge zur Kenntnis der Pflanzen des böhmischen Cenomans. – Sitz. König. Gesell. Wiss., Math.-naturwiss. Cl., (1886): 633–645.
- Velenovský, J. (1889): Květena Českého cenomanu [Flora of the Bohemian Cenomanian]. – Rozpravy Královské České Společnosti Nauk, 7(3): 1–75.
- Zeiller, M. R. (1905): Sur quelques empreintes végétales de la Formation Carbonese supracrétacée des Balkans. – Ann. des Mines, (1905): 1–28.