



Fossil angiosperm fruit *Allericarpus parvivalvis* (Ericales) from the Coniacian of the Bohemian Cretaceous Basin

Jiří Kvaček & Zuzana Heřmanová

National Museum, Václavské náměstí 68, 115 79 Praha, Czechia

Kvaček J. & Heřmanová Z., 2017: Fossil angiosperm fruit *Allericarpus parvivalvis* (Ericales) from the Coniacian of the Bohemian Cretaceous Basin. – Journal of the National Museum (Prague), Natural History Series 186: 117–124.

Abstract: An anatomically preserved fossil fruit *Allericarpus parvivalvis* (Bayer) J. Kvaček et Heřmanová comb. nov. is described from the Coniacian of Březno (Březno Formation), from the Bohemian Cretaceous Basin. Its morphology is characterised based on x-ray and SEM studies. It shows a pentamerous fruit consisting of loculicidally dehiscent capsules. The fruit is subtended by thin persistent sepals. The taxon is compared to other similar taxa, particularly to two earlier described fossil species of *Allericarpus*. All its characters indicate relationship with the family Pentaphylacaceae of the order Ericales.

Key words: angiosperm, fruit, Pentaphylacaceae, Ericales, Coniacian, Late Cretaceous.

November 30, 2017 | Accepted: December 18, 2017 | Issued: December 30, 2017

Introduction

Fossil flora of the Březno Formation, although described quite early (Bayer 1893), has not been revised so far. One of the most interesting specimens is a plant fossil interpreted by Bayer as a conifer cone, but reinterpreted herein as an angiosperm reproductive structure. The Březno Flora consists of gymnosperms, particularly conifers, e.g. *Frenelopsis* cf. *alata* (K. Feistmantel) Knobloch, *Geinitzia reichenbachii* (Geinitz) Hollick et Jeffrey, *Pagiophyllum brachyphyllum* (Bayer) Kunzmann including reproductive structures of *Araucaria fricii* Bayer (Araucariaceae) and *Sequoia lepidota* Bayer (Cupressaceae). *Frenelopsis* cf. *alata* was revisited by Hlušík (1974, 1978, 1990), while the material of Araucariaceae was revised by Kunzmann (2007). Angiosperms comprise the majority of the Březno flora. They are present as leaf impressions showing affinities to lauroids, platanoids and juglandoids. Finally, there are also angiosperm reproductive structures described as *Anthocephale bohémica* Bayer.

Material and Methods

The studied material comes from the Březno Formation, a lithostratigraphic unit of the Bohemian Cretaceous Basin, which is mid-early to late Coniacian in age. This stratigraphic position was confirmed by the presence of two index ammonites, *Texanites pseudotexanuscon-*



Fig. 1. *Allericarpus parvivalvis* (Bayer) J. Kvaček et Heřmanová comb. nov., holotype NMP F363, complete specimen showing one well-preserved sepal (arrow), Březno Formation, Coniacian, x-ray image, scale bar 5 mm.

firms (de Grossouvre) and *Paratexanites serratomarginatus* (Redtenbacher), and nanofossils indicating zone UC11 (Svobodová et al. 2014). The material comes from the mudstone-dominated facies of the Březno Formation, formerly referred to as the Březno Beds (Bayer 1893; Frič 1893, 1894; Halamski & Kvaček 2016), while the sandstone-dominated facies was termed the Chlomek Beds (Bayer 1896; Frič 1897, 1898). The general geological and palaeogeographic setting of the “Březno Beds” is similar to the “Chlomek Beds”, the latter being particularly well documented in Idzików, and defined as mid-Coniacian by the presence of *Scaphites kieslingwaldensis* (Langenhan & Grundey) - nanofossil zone UC10. Stratigraphy of the Idzików flora was described in detail in the papers by Halamski & Kvaček (2015, 2016). Kvaček et al. (2015) referred to its palaeoecology.

The fossil material was observed and documented

using an Olympus SZX12 binocular microscope equipped with an Olympus DP72 digital camera. For studies of internal structures, it was scanned with a Skyscan 1272 microCT, and analysed using N-Recon and Avizo 9.1.1. software. For SEM studies, the specimen was mounted on a SEM holder and observed with a Hitachi S-3700N SEM. The material is housed in the National Museum Prague.

Systematic Palaeontology

Order: Ericales

Family: Pentaphragaceae

Genus: *Allericarpus* Knobloch et Mai 1984

Type: *Allericarpus pentaphragacoides* Knobloch and Mai 1984, p. 5, pl. 1, figs 1–6.

Emended diagnosis

Pentamerous to hexamerous loculicidally dehiscent pedicelate fruit consisting of solid valves, with broad basal discus, subtended by 5–6 persistent sepals. Central columella fibrous,

typically missing. Placentation central, each locule containing one, rarely two seeds. Seeds ovoid with subapical hillum, basilateral chalaza and apical micropyle, testa unilayered.

Remarks

The genus *Allericarpus* is used here to accommodate fruits of affinity to Pentaphylacaceae of the Ericales (Knobloch & Mai 1984, 1986). Contrary to Knobloch & Mai (1984), the genus is now understood in a slightly larger extent. It accommodates pentamerous to hexamerous valvate fruits, subtended by 5–6 sepals with locules containing 1(2) seeds. Surfaces of the seeds are not only reticulate, as suggested by Knobloch & Mai (1984), but can be also smooth or transversally ribbed. *Allericarpus* is in general similar to representatives of the Pentaphylacaceae. It differs from *Pentaphylax* in having typically only one instead of two seeds per locule, in the absence of well-pronounced central columella, and in having a transversally ribbed surface of the outer integument. *Pentaphylax* is an extant genus widespread in China, Vietnam and Indonesia. As indicated by Friis et al. (2011), current knowledge of relationships in Ericales is based on molecular studies (Soltis et al. 2005), but morphologically, Pentaphylacaceae and Theaceae are difficult to distinguish from each other. The family Pentaphylacaceae was traditionally described as monotypic (Engler & Prantl 1897). However, all recent phylogenetic studies indicate Pentaphylacaceae to be much broader, including a large part of Ternstroemiaceae within the order Ericales, close to (Schönenberger et al. 2005) or as a sister group of the Sladeniaceae Airy Shaw (APG IV, 2016). *Allericarpus* may be included also in Theaceae, however Theaceae are generally recorded from the Cenozoic (Friis et al. 2011). Their presence (particularly *Palaeoschima*) in the Late Cretaceous, suggested by Knobloch & Mai (1986) is questioned by Friis et al. (2011). *Allericarpus* differs from *Palaeoschima* Knobloch et Mai (described from the Maastrichtian of Eisleben (Knobloch & Mai 1984)) in having smoother, not so deeply pitted, reticulate surfaces of seeds and well-preserved columella. *Allericarpus* also differs from *Protovisnea* Knobloch et Mai (described from the Maastrichtian of Walbeck (Knobloch & Mai 1984)) in lacking seeds with spines. The genus *Epacridicarpum* Chandler, described originally from the Eocene of Great Britain (Chandler 1960) differs from *Allericarpus* in lacking persistent sepals, having broadly oblate shape, and short and flat-topped style. *Andrewsiocarpon* Grote et Dilcher of the Theaceae represents a fruit consisting of five loculicidally dehiscent capsules. It was described originally from the middle Eocene of south-eastern North America (Grote & Dilcher 1989). It differs from *Allericarpus* in having a thicker valve wall.

Allericarpus parvivalvis (Bayer) J. Kvaček et Heřmanová comb. nov.

Figs 1–3

- 1893 *Widdringtonia parvivalvis* Bayer, p. 14, 40, fig. 11.
1894 *Widdringtonia parvivalvis* Bayer; Frič, p. 125; fig. 182.

Basionym

Widdringtonia parvivalvis Bayer Věst. král. Čes. spol. nauk, Tř. math.-přír., 1893, p. 14, 40, fig. 11.

Holotype

NMP F363 (Bayer, 1893, fig. 11; Frič, 1894, fig. 182; re-figured herein).

Type locality and stratum

Březno; Březno Formation, Coniacian, Upper Cretaceous.

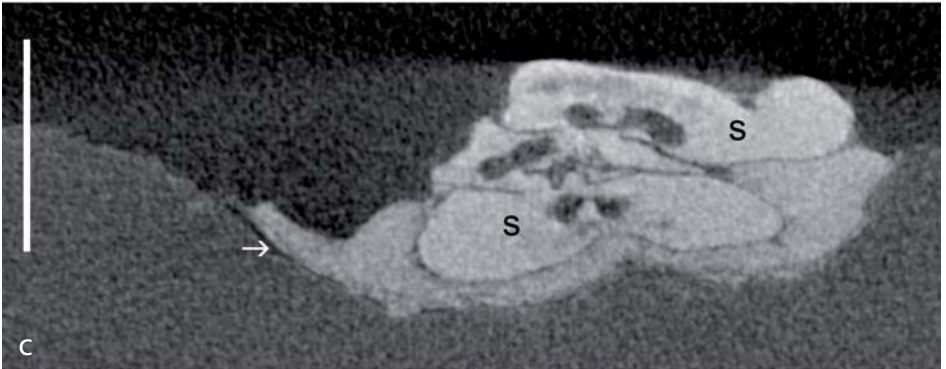


Fig. 2. *Allericarpus parvivalvis* (Bayer) J. Kvaček et Heřmanová comb. nov., holotype NMP F363, Březno Formation, Coniacian.

- a) Complete specimen showing seed details, translucent x-ray image, scale bar 5 mm.
- b) Apical view, x-ray image, scale bar 5 mm.
- c) Internal surface of fruit showing delicate sepals (arrows indicate impressions of apex and lower sinus of sepal), x-ray image, scale bar 5 mm.
- d) Detail of fruit wall, SEM, scale bar 0.5 mm.
- e) Holotype showing buried parts of fruit, x-ray image, scale bar 5 mm.

Fig. 3. *Allericarpus parvivalvis* (Bayer) J. Kvaček et Heřmanová comb. nov., holotype NMP F363, Březno Formation, Coniacian, x-ray images.

- a) longitudinal section showing two seeds, arrow indicates basilateral chalaza, scale bar 1 mm.
- b) longitudinal section with two seeds and one sepal, arrow indicates horseshoe-shaped embryo, scale bar 1 mm.
- c) transversal section displaying two seeds (s), arrow indicates sepal adpressed to fruit wall, scale bar 1 mm.



Emended diagnosis

Fruit pentamerous, consisting of loculicidally dehiscent capsules subtended by five persistent sepals, nearly reaching apex of fruit. Central columella fibrous, generally missing; pedicel persistent. Each elongate locule contains typically one drop-shaped seed. Valves of capsule built by relatively thin homogenous layer. Embryo horseshoe-shaped.

Description

The holotype, the only specimen available, represents a longitudinally broken pentamerous fruit (5 × 4 mm; Figs 1, 3a–c). As it is clear from the impression, the fruit originally consisted of five loculicidally dehiscent elongate capsules; only two are preserved (2 × 5 mm), each containing one seed (1.8 × 3.75 mm). In the basal part of the fruit, there are more clearly visible fragments of persistent sepals (up to 4 mm long) subtending the capsule (Figs 1, 3c). Two more complete, but poorly preserved impressions of sepals are seen on the capsule outer surface, documented by x-ray (Figs 2b, 3c). The capsule wall is 240 µm thick, generally smooth, with slightly pronounced keels formed by sepal mid-veins. It consists of about five layers of cells arranged in palisade (10–25 × 25–80 µm, Fig. 2d). Seeds are ovoid to drop-shaped, narrow apically, broad basally, with hilum situated on the dorsal part of the seed below the apex (Fig. 2a). The exposed part of the seed shows a surface with transversal ribs (Fig. 2a,c). The micropyle is not preserved. The funicle runs dorsally to the basilateral chalaza (Fig. 3a). X-ray investigation has revealed a horseshoe-shaped embryo (Fig. 3b).

Discussion

Bayer (1893) interpreted the studied specimen as a conifer cone. However, a detailed study, particularly using x-ray, revealed its angiospermous nature, with clear affinities to Pentaphylacaceae. The studied species is similar to the extant genus *Pentaphylax*, particularly in similar morphology and anatomy of its seed. It shows a similar drop-shaped seed with horseshoe-shaped embryo. *Allericarpus parvivalvis* differs from *Pentaphylax protogaea* from the Maastrichtian of Walbeck (Knobloch & Mai 1986), particularly in lacking central columella, in having persistent calyx lobes of the same length. Furthermore, it differs in a thicker capsule wall – 0.25 mm, instead of the roughly 0.1 mm that has been observed in *P. protogaea*.

The genus *Allericarpus* is based on *A. pentaphylacoides* and contains one more species: *A. clausenispermus*. Both species come from the Maastrichtian of Walbeck, Germany (Knobloch & Mai 1986). They differ from *A. parvivalvis* in having a reticulate surface on their seeds. The seeds are more oval and broad basally in both species from Germany. Moreover, *A. parvivalvis* differs from *A. clausenispermus* Knobloch et Mai in having thinner and shorter sepals, and in lacking unification of pericarp and seed.

Conclusions

Widdringtonia parvivalvis Bayer is reinterpreted herein as an angiosperm fruit: *Allericarpus parvivalvis* (Bayer) J. Kvaček et Heřmanová comb. nov. Its systematic relationship is discussed based on x-ray and SEM studies. Showing pentamerous fruits, consisting of loculicidally dehiscent capsules subtended by five persistent sepals and seeds with horseshoe-shaped embryo, it is assigned to the family Pentaphylacaceae, and adds more information to our understanding of early evolution of the order Ericales.

Acknowledgements

We are grateful to Edoardo Martinetto (University of Torino) for fruitful discussions, Jaromír Váňa (NMP) for preparation of the material, and Lenka Váchová (NMP) for the photo-documentation. The paper greatly profited from reviews by Steven Manchester and Alexei Herman. This study was supported by the Czech Science Foundation (grant No. 15-049875S).

References

- APG IV, 2016: The Angiosperm Phylogeny Group IV (2016): An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. – *Botanical Journal of the Linnean Society*, 181: 1–20. <https://doi.org/10.1111/j.1095-8339.2009.00996.x>
- Bayer E., 1893: O rostlinstvu vrstev březenských. Die Flora der Priesener Schichten. – *Věstník královské české společnosti nauk, třída mathematicko-přírodovědecká*, [Sitzungsberichte der königliche böhmischen Gesellschaft der Wissenschaften in Prag, mathematisch-naturwissenschaftlichen Classe], 1893: 1–50.
- Bayer E., 1896: O rostlinstvu vrstev chlomeckých. Die Flora der Chlomeker Schichten. – *Věstník královské české společnosti nauk, třída mathematicko-přírodovědecká*, [Sitzungsberichte der königliche böhmischen Gesellschaft der Wissenschaften in Prag, mathematisch-naturwissenschaftlichen Classe], 1896, 27: 1–36.
- Chandler M.E.J., 1960: Plant Remains of Hengistbury and Barton Beds. *Bulletin of British Museum Natural History (Geology)*, 4: 193–238.
- Engler A., Prantl K., 1897: Die natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigeren Arten. – *Teilen 2–4, Nachträge 1*.
- Frič A., 1893: Studien im Gebiete der böhmischen Kreideformation. Paläontologische Untersuchungen der einzelnen Schichten. V. Die Priesener Schichten. – *Das Archiv für die naturwissenschaftliche Landesdurchforschung von Böhmen* 9, 1: 1–135.
- Frič A., 1894: Studie v oboru křídového útvaru v Čechách. Palaeontologické prozkoumání jednotlivých vrstev. V. Březenské vrstvy. – *Archiv pro přírodovědecké prozkoumání Čech* 9, 1: 1–129.
- Frič A., 1897: Studien im Gebiete der Böhmischen Kreideformation. Paläontologische Untersuchungen der einzelnen Schichten. 6. Die Chlomeker Schichten. *Das Archiv für die naturwissenschaftliche Landesdurchforschung von Böhmen* 10, 4: 1–83.
- Frič A., 1898: Studie v oboru českého útvaru křídového. Palaeontologický výzkum jednotlivých vrstev. VI. Chlomecké vrstvy. *Archiv pro přírodovědecké prozkoumání Čech*, 10, 4: 3–84.
- Friis E.M., Crane P.R., Pedersen K.R. 2011: Early flowers and angiosperm evolution. – Cambridge University Press, Cambridge, 585 pp. <https://doi.org/10.1017/cbo9780511980206>
- Grote P., Dilcher D.L., 1989: Investigations of angiosperms from the Eocene of North America: a new genus of Theaceae based on fruit and seed remains. – *Botanical Gazette* 150: 190–206. <https://doi.org/10.1086/337764>
- Halamski A.T., Kvaček J., 2015: The Late Cretaceous (Coniacian) leaf and cone flora from the Sudetes. – *Palaeontographica B*, 292: 95–171. <https://doi.org/10.1127/palb/292/2015/95>
- Halamski A.T., Kvaček J., 2016: The Coniacian leaf flora from the north-eastern part of the Bohemian Cretaceous Basin. – *Bulletin of Geosciences* 91: 297–318. <https://doi.org/10.3140/bull.geosci.1591>
- Hlušík A., 1974: New finds of *Frenelopsis* (Cupressaceae) from the Cretaceous of Czechoslovakia and their problems. – [In Czech, English summary] *Časopis pro mineralogii a geologii* 19: 263–268.
- Hlušík A., 1979: Frenelopsid plants (Pinopsida) from the Cretaceous of Czechoslovakia. – 129–141. In: Pokorný, V. (ed.), *Paleontologická conference '77 – Univerzita Karlova Praha*.
- Hlušík A., 1990: *Frenelopsis* Schenk: its possible value for Cretaceous stratigraphy in Czechoslovakia. 67–71. – In: Knobloch, E., Kvaček, Z. (eds), *Proceedings of the Symposium "Paleofloristic and paleoclimatic changes in the Cretaceous and Tertiary"*, 1989.
- Knobloch E., Mai D.H., 1986: Monographie der Früchte und Samen in der Kreide von Mitteleuropa. – *Rozprawy Ústředního ústavu geologického*, 47: 1–219.
- Knobloch E., Mai D.H., 1984: Neue Gattungen nach Früchten und Samen aus dem Cenoman bis Maastrichtian (Kreide) von Mitteleuropa. – *Feddes Repertorium*, 95: 3–41. <https://doi.org/10.1002/fedr.4910950103>

- Kunzmann L., 2007: Neue Untersuchungen zu *Araucaria* Jussieu aus der europäischen Kreide. *Palaeontographica B*, 276: 97–132. <https://doi.org/10.1127/palb/276/2007/97>
- Kvaček J., Halamski A.T., Svobodová M., Durska E., 2015: Coniacian flora of the Sudetes (south-western Poland): Palaeoecological and palaeoclimatic interpretations. – *Palaeogeography, Palaeoclimatology, Palaeoecology* 436: 178–187. <https://doi.org/10.1016/j.palaeo.2015.06.041>
- Schönenberger J., Anderberg A.A., Sytsma K.J., 2005: Molecular phylogenetics and patterns of floral evolution in the Ericales. – *International Journal of Plant Sciences* 166: 265–288. <https://doi.org/10.1086/427198>
- Soltis D.E., Soltis P.S., Endress P.K., Chase M.W., 2005: *Phylogeny and Evolution of angiosperms.* – Sinauer Associates, Sunderland, Massachusetts, 370 pp.
- Svobodová A., Košťák M., Čech S., Švábenická L., 2014: New biostratigraphic evidence (texanitid ammonites, inoceramids and calcareous nannofossils) for the Upper and the uppermost Coniacian in the Bohemian Cretaceous Basin. – *Zeitschrift der Deutschen Gesellschaft für Geowissenschaften* 165: 577–589. <https://doi.org/10.1127/zdgg/2014/0023>