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A NEW RECORD OF THE GENUS *CARYANTHUS* FROM THE CRETACEOUS OF SOUTH BOHEMIA (CZECH REPUBLIC)

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Abstract. An inflorescence / infructescence of *Caryanthus* sp., a member of the Normapolles complex, is described from the clay pit at Zliv-Řídká Blana (Klikov Formation, Upper Cretaceous) South Bohemia (Czech Republic). It represents the first more complete specimen of *Caryanthus* showing the arrangement of flowers / fruits and thus allowing for a more precise interpretation of the genus. In the arrangement of flowers / fruits it is similar to the Cretaceous genus *Budvaricarpus* and to a minor degree also to *Endressianthus*, *Normanthus* and to the extant genus *Rhoiptelea*. The similarity of these genera provides additional support for the interpretation of *Caryanthus* as belonging to the juglandoid clade in the order Fagales.

■ *Caryanthus*, Normapolles complex, fossil flowers, Cretaceous

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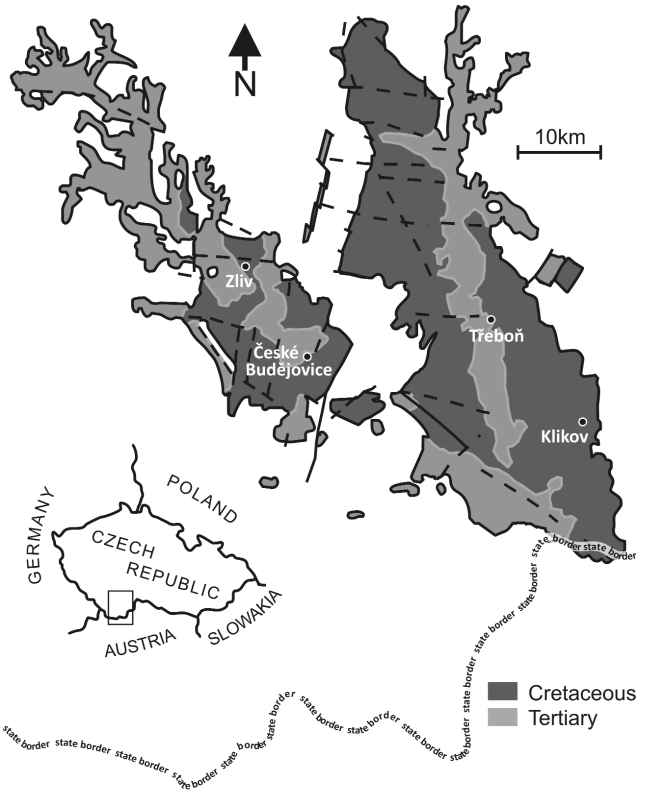
Introduction

The genus *Caryanthus* represents one of the most common Late Cretaceous reproductive structures bearing pollen of the Normapolles type. In this paper we describe new material from the genus – a single fragment of an inflorescence / infructescence, which sheds light on the structure of the inflorescence in *Caryanthus.* Representatives of the Normapolles complex were detected for the first time as fossil pollen (e.g. Pflug 1953, Pacltová 1981). This group of morphologically diverse pollen, characteristic of the Late Cretaceous of Europe and North America is distinguished from other early triporate forms by an internally complex pore structure (Góczán et al. 1967, Batten and Christopher 1981). About 80 genera of pollen taxa have been defined in the Normapolles complex (e.g. Batten and Christopher 1981). They were attributed to a number of families of extant Junglandales (Juglandaceae and Rhoipteleaceae), Betulales, Urticales, Casuarinales, Myricales, Myrtales, Sapindales, and Santalales, based on similarities of pollen characteristics (e.g. Pflug 1953, Walker and Doyle 1975, Zavada and Dilcher 1986, Pacltová 1987, Batten 1989).

The first fossil plants bearing or associated with pollen Normapolles were mesofossils described by Friis (1983) as *Caryanthus*, *Manningia* and *Antiquocarya*. Friis (1983) interpreted these plants as being a part of juglandalean / myricalean clades. Later Knobloch and Mai (1986) described 20 species of mesofossils of the Normapolles complex, including eight species of *Caryanthus* from Cen-



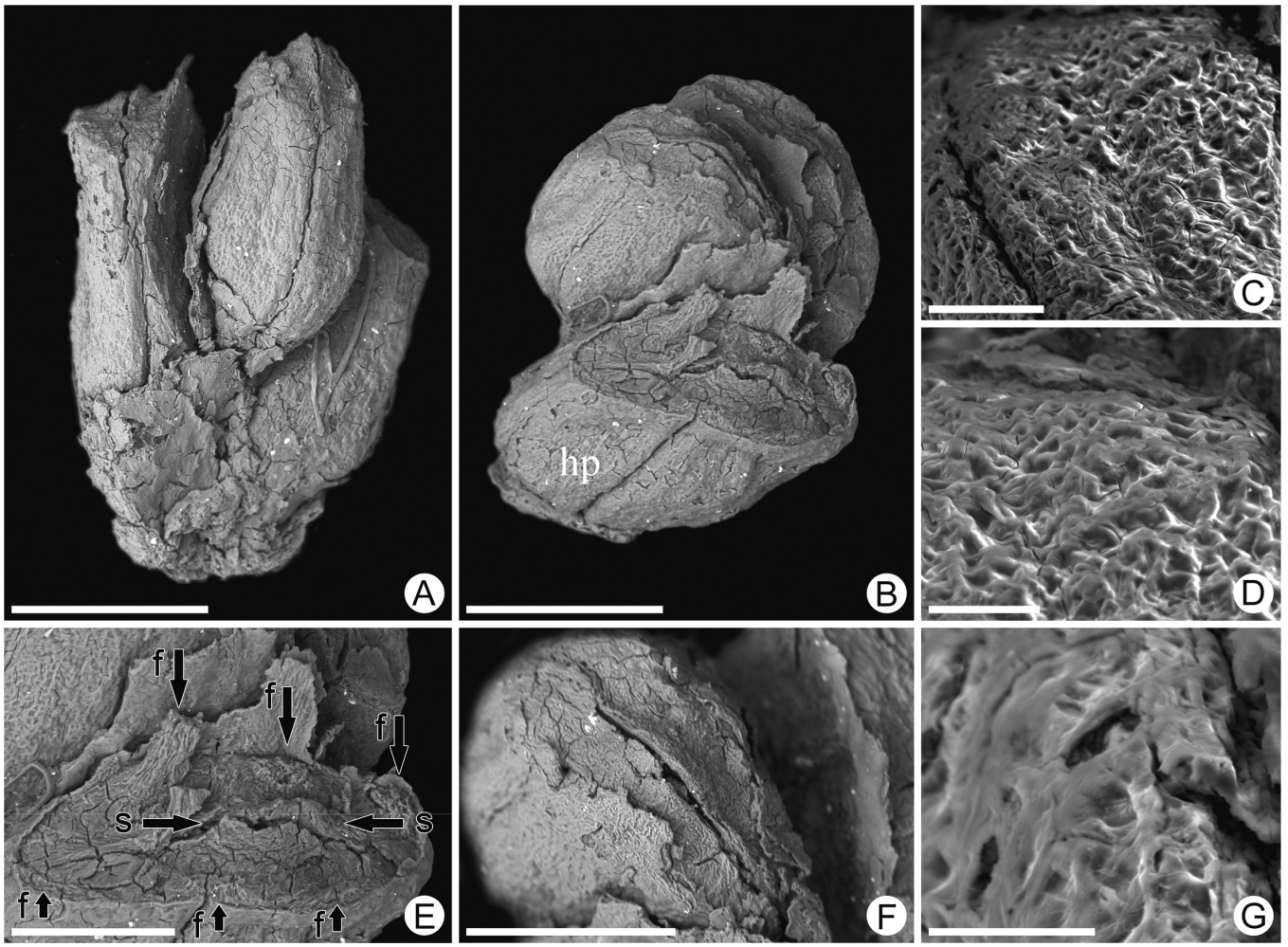
Text-fig. 1. Geographical position of the locality Zliv – Řídká Blana in the South Bohemian Basins.

tral Europe. One mores species was described by Sims et al. (1999) from the Late Cretaceous of Georgia (USA).

The present material was recovered in 2007 from the clay pit in Zliv-Řídká Blana (Klikov Formation, Upper Cretaceous). The locality has been known for many years, since the time of F. Němejc and E. Knobloch (Knobloch 1964, Knobloch and Mai 1986, Němejc 1961), but during past few decades, it was visited only rarely. The new flora comprises about 40 taxa, based on reproductive structures of fossil plants. All fossils are preserved as charcoal around 1 mm in size. The material includes remains of ferns, gymnosperms, and angiosperms. Their excellent preservation allows for a detailed description of the specimens and in several cases provided new information about already described taxa. More than half of these reproductive structures can be assigned to species or genera already described from the Klikov Formation from other strata in Europe. The largest part of the new material consists of fruits belonging to several genera assigned to the Normapolles complex. *Caryanthus* and *Budvaricarpus* represent the most common taxa in the complex. Although it was described decades ago, these new findings add interesting characters and improve our knowledge about this important group of plants.

Material and methods

The material described here consists of a single specimen with three fruits arranged in an inflorescence / infructescence (no. F 03286). In addition, several isolated fruits / flowers are available from newly collected material. They are housed in the National Museum, Prague. The material was collected and prepared by Z. Heřmanová and J. Kvaček from the clay pit Zliv–Řídká Blana Quarry (49_049430N, 14_239040E) in the South Bohemian Basins (Text-fig. 1). The specimen described here was extracted from gray claystones by bulk maceration using bicarbonate, followed by washing on a 90 μm sieve. After sieving, the residue was treated with hydrofluoric acid and hydrochloric acid in order clean the organic components from mineral remains, rinsed in water and dried in air. Sorting and preliminary studies were done using a binocular microscope (Olympus SZX 12). Subsequently, the specimen was mounted on an aluminium stub using nail polish, coated with gold and studied using a Hitachi S-3700 scanning electron microscope. For a direct comparison, we used material from Ervin Knobloch's collection housed in the National Museum, Prague.



Text-fig. 2. ***Caryanthus*** **sp., no. F03286, locality Zliv-Řídká Blana**
A – Inflorescence, three bisexual flowers / fruits, central flower inserted slightly higher than the two lateral ones, scale bar 0.5 mm; B – Lateral flowers arranged at an angle of about 45˚ relative to each other, hp. – hypanthium with grooves, scale bar 0.5 mm; C – Epidermal cells of hypanthium, scale bar 0.1 mm; D – Detail of epidermal cells, scale bar 50 μm; E – Lateral flower, basal parts of six filaments and basal parts of two anthers styles, f – filaments, s – styles, scale bar 0.3 mm; F – Central flower, scale bar 0.3 mm; G – Stoma, scale bar 30 μm.

Systematic part

Order *Fagales* Engler, 1892

Genus *Caryanthus* Friis, 1983

Flowers / fruits of *Caryanthus* are small, apparently sessile, about 1 mm long, bisymmetrical and epigynous, supported by a small bract and two lateral prophylls. The perianth consists of four tepals arranged in two decussate pairs. The androecium consists of six to eight stamens. The gynoecium is bicarpellate with a unilocular ovary and two free styles. Pollen is triaperturate and triangular in equatorial outline. A distinct Y–shaped mark extends between the apertures over the pole. The fruits are small, ribbed nuts with a single erect and apparently orthotropous seed as described by Friis (2006).

The inflorescence / infructescence from Zliv – Řídká Blana described here shows the above mentioned characters – juvenile fruits with tepals united basally forming a hypanthium, basal parts of filaments arranged in two rows and fragmentarily preserved styles. Pollen *in situ* was not found in stamens, but *Caryanthus* pollen has been described from the flora of Åsen, southern Sweden (Friis 1983).

Species *Caryanthus* sp.

The specimen described here is currently the only known *Caryanthus* inflorescence / infructescence. It is 1.4 mm long and 0.8 mm broad (Text-fig. 2A), and consists of three bisexual, epigenous postanthetic flowers / fruits. Two of them are in lateral positions, separated by about 45° from each other. They surround the central flower, which is positioned slightly higher in the inflorescence than the other two (Text-figs 2A, B). Each flower / fruit is supported by several bracts, but the number of bracts is uncertain due to the preservation of the fossil. The flowers / fruits have tepals united basally forming a hypanthium. Fruits in the inflorescence are closely spaced. The flowers / fruits are distinctly epigynous and have a hypanthium characterized by three distinct grooves on each side. The androecium of each flower consists of six stamens. Only basal parts of the filaments are preserved. The gynoecium is bicarpellate, bearing two free styles in the apical part (Text-fig. 2E). Epidermal cells in the apical part of the gyneceum show sinusoid anticline walls. The surface of the fruit is covered with small irregular thick-walled cells (Text-fig. 2C); sometimes round trichome bases occur. Stomata are very small and sunken (Text-fig. 2G). Two guard cells are surrounded by probably 6 cells; this number is uncertain due to the preservation of the fossil.

Discussion

The inflorescence / infructescence described here shows similarities to several species of *Caryanthus*: *Caryanthus triasseris* (Knobloch) Knobloch et Mai, *Caryanthus pseudooctocostatus* (Knobloch) Knobloch et Mai and *Caryanthus trebecensis* Knobloch et Mai. Based on the variability of the type collection of *C. triasseris* the new material may be similar to this species. It is round in shape and the fruit is characterized by a hypanthium, characteristics also observed by Knobloch and Mai (1986). In some characteristics, the new material is distinct from the holotype of *C. triasseris*. The new material differs in lacking a triangular projection in the apical part of each flower / fruit and having grooves instead of clear ridges on the hypanthium. As the holotype of *C. triasseris* does not show any remains of stamens and styles, further comparisons are not possible.

According to the description given for *C. pseudooctocostatus*, the structure described here also shows characteristics similar to this latter species: the rounded shape of the fruit and lack of distinct triangular apical protrusion. The holotype of *C. pseudooctocostatus* shows four indistinct ribs while the present material shows grooves. As stamens and styles of *C. pseudooctocostatus* are not known, no further comparisons are possible here either.

A third species that shares characteristics with the material described here is *C. trebecensis*, which also has grooves instead of ridges on the surface of the hypanthium. *C. trebecensis* differs from the present specimen in having epidermal cells of the hypanthium larger. The androecium of *C. trebecensis* is formed by six stamens, as well as the androecium of the new inflorescence. Moreover, its holotype is currently unavailable, because it was probably lost before the E. Knobloch collection arrived in the National museum in Prague.

For the time being, we refrain from assigning the specimen described here to any of the already described species.

During our studies of the genus *Caryanthus* we noticed an interesting feature present in several species (*C. communis, C. triasseris* and *C. trebecensis*). Within each species, specimens fall into two morphologically distinct groups, which differ in the shape of the apical part of the fruit / flower. One group is characterised by a blunt apex, and remnants of styles and stamens. The second group shows an apical tip, and lacks any traces of styles or stamens. One of our interpretations is that these two groups within each species represent two different stages of maturity. The younger stage corresponds to the flower at or shortly after anthesis, with styles and stamens partially preserved. It also usually shows a well preserved cuticle.

The older stage is clearly post-anthetic, and remains of stamens, styles and any tissue covering the fruit in its apical part have been lost. The fruit apex shows a triangular projection, which in some cases is divided by the apical dehiscence of the fruit. The openings also vary in size. The cuticles of older fruits are usually either lost, or present in the form of cracked remains. This may be due to the fact that the cuticles of younger fruits are more elastic, but become more fragile at older stages of fruit development. Other possibilities are abrasion and different preservation of individual specimens. Those which were longer in the transporting process might be more abraded than those specimens which were buried quickly with a minimum of transport.

Caryanthus seems closely related to *Budvaricarpus serialis*. Both are members of the Normapolles complex. *Budvaricarpus* represents an aggregation of three or four flowers / fruits arranged in a dichasium and enclosed in a common bract. Usually the central flower / fruit is bisexual, the lateral flowers / fruits are female. The inflorescence of *Caryanthus* consists also of three flowers / fruits, but there is no common bract preserved. The flowers / fruits of the present specimen are not as closely aggregated as those

of *Budvaricarpus* and all three flowers / fruits are bisexual. The androecium of *Budvaricarpus* consists of six stamens arranged in the same manner as in *Caryanthus*. The gynoecium of *Budvaricarpus* is also very similar to *Caryanthus*, bicarpellate with two free styles.

The Normapolles complex was established to include plants producing oblate and triaperturate Normapolles pollen grains. The complex consists of numerous pollen taxa and currently nine genera based on preserved flowers and / or fruits: *Antiquocarya* Friis*, Bedellia* Sims et al.*, Budvaricarpus* Knobloch et Mai*, Calathiocarpus* Knobloch et Mai*, Caryanthus* Friis*, Dahlgrenianthus* Friis et al.*, Endressianthus* Friis et al.*, Manningia* Friis*, Normanthus* Schönenberger et al.

The type of inflorescence is unknown for most of the "Normapolles flowers". In addition to *Budvaricarpus,* the type of inflorescences is also known in *Endressianthus* and *Normanthus*. *Endressianthus* from the Late Cretaceous of Portugal (Friis et al. 2003) shows flowers borne in four-flowered dichasia, which are spirally arranged along the main inflorescence axis and may be a part of a thyrse (Friis et al. 2003). In *Normanthus* from the Late Cretaceous of Portugal (Schönenberger et al. 2001), inflorescences have only been partially preserved. They also form dichasia, but the flowers are more loosely arranged than in *Endressianthus* (Friis et al. 2006).

Preliminarily, we interpret the inflorescence of *Caryanthus* sp. described here as a possible dichasium, although more detailed Micro Computer Tomography studies are necessary for unequivocal conclusions. However, this preliminary concept of the *Caryanthus* inflorescence is in good accord with other known Normapolles inflorescences such as *Endressianthus* and *Normanthus*.

A closer relationship between *Budvaricarpus* and extant *Rhoiptelea* was suggested and based on similarity between their inflorescences. *Rhoiptelea* is usually placed in its own family, Rhoipteleaceae, and resolved as a sister group to the Juglandaceae or sometimes placed in the Juglandaceae (APG III 2009). Therefore a closer similarity of *Caryanthus* and *Budvaricarpus* in terms of their inflorescence provides an additional link between these two genera and gives additional support to the hypothesis that *Caryanthus* is part of the juglandoid clade.

Summary

The Late Cretaceous Klikov Formation (South Bohemian Basins) has yielded a number of reproductive structures of fossil plants containing diverse assemblages of angiosperm flowers, fruits and seeds. Flowers / fruits of the Normapolles complex are the most common meso-fossils in the Klikov Formation. Here we report the first record of a *Caryanthus* inflorescence, and provide new insights in our understanding of the genus *Caryanthus* within the Normapolles complex.

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