



Caryanthus diversity in the Late Cretaceous

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ABSTRACT

Genus *Caryanthus* with fourteen species represents the most diversified genus in the Normapolles complex. Detailed review of material from Central Europe allowed accurate study of its geographic and stratigraphic distribution. An emended diagnosis of *Caryanthus communis* Knobloch et Mai, *Caryanthus deltoides* (Knobloch) Friis, *Caryanthus microtriasseris* Knobloch et Mai, *Caryanthus multiasseris* (Knobloch) Knobloch et Mai, *Caryanthus pseudoctocostatus* (Knobloch) Knobloch et Mai, *Caryanthus trebecensis* Knobloch et Mai, *Caryanthus triasseris* (Knobloch) Knobloch et Mai is presented. A single specimen of Cenomanian age has been reinterpreted as *Caryanthus* sp. This earliest known record of the genus *Caryanthus* comes from the Peruc–Korycany Formation in the Czech Republic. Rapid radiation of the genus *Caryanthus* is documented in the Turonian of North Bavaria and southern part of the Czech Republic. The most diverse community comes from the Klikov Formation (Late Turonian–Santonian) of the Czech Republic. During the Santonian/Campanian, the genus *Caryanthus* occurred widely in Central and Northern Europe; one species is also documented from North America. *Caryanthus* species diversity clearly decreased in the Maastrichtian.

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1. Introduction

Remains of fossil plants assigned to “Normapolles complex” form an important part of many Late Cretaceous floras. They are recognized as an important group of the higher fagalean clade of eudicot angiosperms (Friis et al., 2006, 2011; Manchester, 1987; Schönenberger et al., 2001). The term Normapolles was first used for a group of pollen grains characterized by the presence of a short polar axis and three complex apertures with three pores and three colpi (Góczán et al., 1967; Pacltová, 1981; Pflug, 1953). Flowers associated with the Normapolles pollen were described for the first time by Friis (1983), who defined three genera from south Sweden: *Manningia*, *Antiquocarya* and *Caryanthus*. Subsequently six species of *Caryanthus* were described from the Czech Republic (Knobloch and Mai, 1983) and a summary of *Caryanthus* species from Central Europe was presented in Knobloch and Mai (1986). The first report on mesofossils of the Normapolles complex from North America was published by Sims et al. (1999), who described *Caryanthus* sp. and *Bedellia*, both fossil flowers from the Late Cretaceous of Gaillard in Georgia, USA.

“Normapolles complex” at present comprises nine genera: *Antiquocarya*, *Bedellia*, *Calathiocarpus*, *Caryanthus*, *Dahlgrenianthus*, *Endressianthus*, *Manningia*, *Normanthus* and recently described genus *Budvaricarpus* from the Czech Republic (Heřmanová et al., 2011). The last mentioned genus shows remarkable similarities to the recent

monotypic genus *Rhoiptelea* (Rhoipteleaceae), which occurs in southwest China and northern Vietnam.

Although *Caryanthus* is well described at the genus level, a clear definition at the species level is still lacking, and only a small number of specimens from central Europe have been documented using a scanning electron microscope. We decided to study *Caryanthus* using nondestructive techniques, to assemble a more accurate description and show newly observed features. This revision also provides new information on *Caryanthus* distribution.

2. Material and methods

This study is based on material collected by Ervín Knobloch from numerous boreholes and opencast quarries in Central Europe (Knobloch and Mai, 1986), as well on the new material collected by the authors in the locality Zliv-Řídká Blana (49°04'43"N, 14°23'04"E). A list of the *Caryanthus* species and their occurrences is in the appendix. The material is currently housed in the National Museum (Prague). Specimen no. RGM.JMS.61620 (*Caryanthus trebecensis* Knobloch et Mai) comes from the collection of Naturalis Biodiversity Centre, Leiden, the Netherlands. All specimens are about 1 mm in diameter, charcoalified or coalified three-dimensionally preserved mesofossils. The new material was extracted from gray claystone by bulk maceration, followed by washing on a 90 µm sieve. After sieving, the organic residue was treated with hydrofluoric acid and hydrochloric acid, rinsed in water, and dried in air. Sorting and preliminary studies were carried out using an Olympus SZX 12 binocular microscope. Specimens for SEM observations were

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mounted on aluminum stubs using nail polish, coated with gold and studied using Hitachi S-4300 and JEOL JSM 6380 field emission scanning electron microscopes at 2 kV. Uncoated specimens were studied at low vacuum using Hitachi S3700 scanning electron microscope at 15 kV. Selected specimens were studied using MicroCT SkyScan 1172 without filter, using 250 µA at 40 kV.

3. Terminology

All specimens in this work are plant reproductive structures. All flower/fruit samples are flattened to some degree, some almost completely, like a pancake, some retain a more ovoid shape. Two flat sides are herein called 'lateral faces', and no distinction is made between the sides. We use the term 'hypanthium' for perianth parts fused to the ovary. Tepals attached on top of the hypanthium are usually preserved as fragments. When detached, tepals leave a scar at the former attachment point. These characters are termed tepal attachment scars (or only scars, where the meaning is clear from context). In some cases, scars are immediately adjacent to each other, with indistinct boundaries, and it is difficult to determine where one ends and the next begins. In such cases, the scars form a ring, and are here termed a scar ring. The genus is defined as having exactly four tepals, in two decussate pairs. The two tepals are referred to here as the lateral pair, for those on the lateral faces, and median pair, for those on the edges.

4. Geology

4.1. Czech Republic

Specimens of *Caryanthus* were extracted from several sedimentary units in the Bohemian Cretaceous Basin, the South Bohemian Basins and the Carpathian Flysch in Moravia.

The Bohemian Cretaceous Basin, as defined by Čech et al. (1980); Čech (2011), located in the Bohemian Massif, is represented by Late Cretaceous non-marine and marine deposits of Cenomanian to Campanian age (for detailed stratigraphy see Uličný et al., 1997). The *Caryanthus* specimens come from two formations in the basin: the basal Peruc-Korycany Formation (Greguš and Kvaček, 2016) and the topmost Březno/Merboltice Formation. Biostratigraphic studies based on pollen spectra (Pacltová, 1977) date the Peruc-Korycany Formation to later stages of the middle Cenomanian. The locality Vyšehořovice-Kamenná Panna (Fig. 1) yielded one unique specimen of *Caryanthus* sp. from gray claystone near the top of the Peruc Member (Knobloch and Mai, 1986). The Březno and Merboltice Formations (Fig. 1) form the topmost part of the Bohemian Cretaceous Basin. The Březno Formation ranges from early/middle Coniacian through earliest Santonian in age (Čech, 2011). According to Knobloch and Mai (1986), the plant fossils occur in the lowermost part of the Březno Formation, originally named the Chlomek Beds by Bayer (1886); Halamski and Kvaček (in press) described the flora and indicate its age as Coniacian (Halamski and Kvaček, 2015). The Santonian Merboltice Formation consists mostly of coarse clastics that generally do not yield any plant remains. However, the material described by Knobloch and Mai (1986) probably comes from silty beds present in the coarse clastic sequences (Čech et al., 1980, p. 295). The regressive, irregularly cyclic, mostly marine sediments of Coniacian to Lower Santonian age yield mesofossil flora, including *Caryanthus* material. They come from boreholes located near the villages of Chřibská, Kerhartice, Markvartice, Mášovice, Stará Hut', Studený, Veselý and Žandov.

Caryanthus is particularly common in the Klikov Formation (Late Turonian-Santonian age) (Knobloch, 1985), which is the basal stratigraphic unit of the South Bohemian Basins (the Třeboň and the Budějovice Basins; Fig. 1). The formation consists of three lithological types that occur in irregular cyclic sequences: (1) light gray or yellow conglomeratic sandstones; (2) red beds of poorly sorted sandstones, sandy mudstones, or sandy claystones; (3) gray plant-bearing

sandstones or claystones with variously distributed coalified plant fragments (Slánská, 1976). The sediments of the South Bohemian Basins are products of fluvial systems (J. Laurin personal communication). Palynological data from Pacltová (1981) suggest Coniacian to Santonian age. Knobloch (1985) suggest Late Turonian-Santonian, based on mesofossils.

The Carpathian Flysch Zone (Fig. 1) represents an extremely complicated unit formed during the Alpine-Carpathian Orogeny. Late Jurassic to early Miocene sediments were transformed by the orogeny, mainly during the middle Miocene, into two groups of nappes of external Western Carpathians. According to Knobloch (1977) and M. Bubík (personal communication), the mesofossil material from boreholes Bruzovice Br-4 and Štramperk NJ-50 comes from the Frýdek Formation (Campanian-Maastrichtian). Fossils from the Ráztoka, Řeka and Staré Hamry 3 localities are from the Godula Formation (Coniacian-Campanian). Fossils from Horní Bečva, Horní Bečva-Bůčkový potok, Klín, potok Mečůvka, Staré Hamry 1 & 2 localities are from the Istebna Formation (Campanian-Palaeocene) and the fossils from Rusava locality are from the Soláň Formation (Maastrichtian-Palaeocene).

4.2. Czech-Polish border area

Fossils from marine sediments of the Opole Cretaceous Basin (Fig. 1) were extracted from the borehole OS-5 near Slezské Pavlovice in Nížký Jeseník. Based on the marine fauna, the plant-bearing sediments are of Late Turonian to Coniacian age. This stratigraphic level corresponds to the Rakowice Wielke Formation of the Opole Cretaceous Basin (Kotaňski and Radvaňski, 1977; Voight and Wagleich, 2011). The borehole passes through sediments of Coniacian age with *Inoceramus* cf. *kleinii* G. Müll. and *I. ex gr. inconstans* Wood (223.3–413.0 m), and through sediments of late Turonian age with *Inoceramus waltersdorfensis waltersdorfensis* and *I. striatoconcentricus striatoconcentricus* Gumb (413.0–491.5 m) (Knobloch and Mai, 1986).

4.3. Poland

The specimens of *Caryanthus* studied by Knobloch and Mai (1986) from Rabka-Zaryte locality come from the Kanina beds, Campanian (Bak and Oszczypko, 2000). The specimens from Rakowice Małe locality, Żerkowice Member come from the Rakowice Wielkie Formation and the Czerna Formation including the Nowogrodziec Member, North Sudetic Basin, Coniacian-?Santonian (Leszczyński, 2010). From Knobloch and Mai (1986) it is not clear whether the fossils were picked up from the Czerna Formation or Rakowice Wielkie Formation in quarry at Rakowice Małe (Fig. 1). The Cretaceous succession of the North Sudetic Basin comprises marine sediments of marls, limestones, and sandstones (Greguš et al., 2013).

4.4. The Netherlands-Germany borders

Rich coalified mesofossil flora containing *Caryanthus* was recovered from the Hergenrath Member (Santonian) of the Aken Formation from the Liege-Limburg Basin, (Voight and Wagleich, 2011). The Hergenrath Member (Fig. 1), 10–35 m in thickness comprises a sequence of alternating light to dark gray, sandy and silty clays with silty and clayey, light gray fine- to coarse-grained sands, with subordinate fine-grained gravel, silts, minor red clays, and ferruginous horizons (Jagt, 1999). Locally these beds contain increased amounts of wood debris and root horizons, in parts associated with thin lignite deposits, as well as rich assemblages of autochthonous and parautochthonous gymnosperm and angiosperm fossil remains (Bosma et al., 2009). Where this member rests on a carbonate basement, variegated sandy and silty clays occur at the base. This formation is interpreted as fluvial to limnic in origin, with probable marine incursions (Jagt, 1999).

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