

## Plant reproductive structures and other mesofossils from Coniacian/Santonian of Lower Silesia, Poland

Zuzana Heřmanová, Jiří Kvaček, Jiřina Dašková, and Adam T. Halamski

### ABSTRACT

Mesofossils from the Upper Cretaceous of Lower Silesia are described from the Nowogrodzic Member of the Czerna Formation. The investigated strata are part of the North Sudetic Synclinorium and are of either late Coniacian or early Santonian age. The flora comprises megaspores of lycophytes, conifer and angiosperm mesofossils, and insect-related fossils (coprolite, eggs). Megaspores are assigned to the genus *Ricinospora*. Fragments of the sterile conifer twigs *Cunninghamites* sp. and *Geinitzia formosa* are associated with isolated seeds of the conifer genera *Seletya* and *Alapaja*. The greatest diversity is found among reproductive structures of angiosperms within the Normapolles complex. They are assigned to *Caryanthus communis*, *Caryanthus trebecensis*, *Caryanthus triasseris*, *Caryanthus* sp., *Zlivifructus vachae*, and *Zlivifructus microtriasseris*. Additionally, there are several unidentified reproductive structures showing affinities with plants of the Normapolles complex. Finally, there is a single insect coprolite and a few possible insect eggs assigned to *Costathea striata*.

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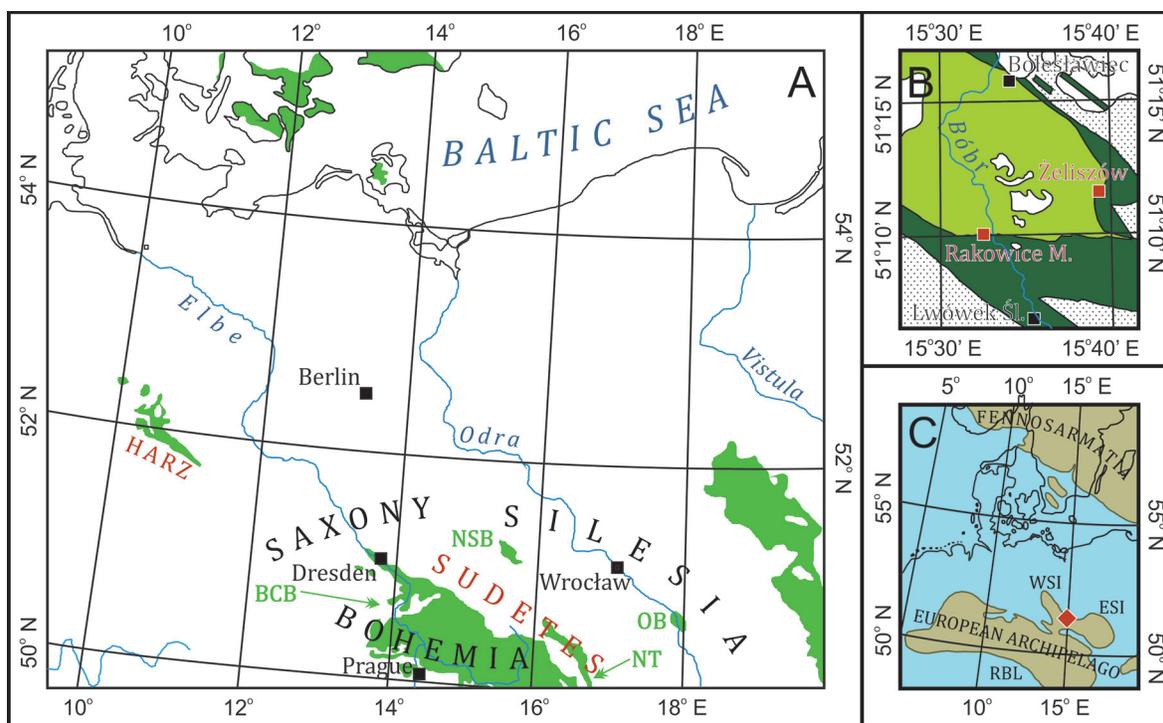
## INTRODUCTION

Mesofossils related to the Late Cretaceous vegetation of Lower Silesia (south-western Poland; Figure 1) are investigated in this study both as interesting study object in themselves and as a proxy for vegetation reconstruction. A previous study providing an overview of megafossils and palynospectra has been prepared by some of the present authors (Halamski et al., 2020). The paper by Halamski et al. (2020) deals with the mega- and the microflora, whereas mesofossil data are summarized there only as a part of a more extensive palaeoecological analysis of several assemblages (Turonian to middle Santonian). The focus of the present paper is on the systematic description of mesofossils, not given in Halamski et al. (2020).

The present study is a continuation of our interest in fossil plant material from Lower Silesia (Heřmanová et al., 2019). The studied mesofossils expand our understanding of the plant fossil diver-

sity, particularly angiosperms of the Normapolles Complex. The diversity of this group is reflected in previously-published dispersed palynospectra from the same area and stratigraphic level (Halamski et al., 2020). The mesofossil material described in the present paper comes from two sources, “old” material stored for several decades in museum collections on the one hand and the material newly collected in the field on the other hand. The “old” material comes only from Rakowice Małe locality (Knobloch and Mai, 1986). The “new” material, collected in 2017–2019, comes from two localities: Rakowice Małe and Żeliszów. We assume that the material collected recently at Rakowice Małe is from approximately the same place where it was collected in the 1980s by Knobloch and Mai (1986).

Fossil reproductive structures from the Rakowice Małe and Żeliszów localities are mostly fruits assigned to the Normapolles complex. The Normapolles complex includes flowers and young or fully developed fruits associated with pollen grains



**FIGURE 1.** Geographic and geologic context of the studied mesoflora. A. Extent of Cretaceous outcrops in Central Europe modified after von Gaertner and Walther (1971). Geographic regions in black typeface, mountains in red, waters in blue, geologic units with Cretaceous sediments in green. BCB, Bohemian Cretaceous basin; NSB, North Sudetic Basin; NT, Nysa Trough; OB, Opole Basin. B. Simplified geologic map of the North Sudetic Basin with main towns (black) and the two outcrops with mesoflora (red). Pre-Cretaceous stippled; Cenomanian to lower–middle Coniacian in dark green; upper Coniacian? to Santonian (Czerna Formation) in light green; post-Cretaceous white. C. Palaeogeography of Central Europe in the Late Cretaceous compared to the present geographic setting after Ron Blakey from Csiki-Sava et al. (2015), modified after data in Chatziemmanouil (1982), Surlyk in Voigt et al. (2008) Janetschke and Wilmsen (2014), and Halamski et al. (2016). ESI, East Sudetic Island; RBL, Rhenish-Bohemian Land; WSI, West Sudetic Island.

characterized by the presence of a short polar axis and three complex apertures with three germinals (Pflug, 1953). Currently the Normapolles complex comprises about 160 species (Góczán et al., 1967; Batten, 1981; Batten and Christopher, 1981; Pačtová, 1981; Polette and Batten, 2017) and the following “flower” genera: *Antiquocarya* Friis, *Bedellia* Sims, Herendeen, Lupia, Christopher et Crane, *Budvaricarpus* Knobloch et Mai, *Calathiocarpus* Knobloch et Mai, *Caryanthus* Friis, *Dahlgrenianthus* Friis, Pedersen et Schönenberger, *Endressianthus* Friis, Pedersen et Schönenberger, *Manningia* Friis and *Normanthus* Schönenberger, Pedersen et Friis, *Zlivifructus* Heřmanová, Dašková et J. Kvaček (Friis, 1983; Friis et al., 2003, 2006, 2011; Knobloch and Mai, 1986; Schönenberger et al., 2001; Sims et al., 1999).

The present paper is based on micro-CT, a relatively new technology, which allowed a detailed description and in some cases a reinterpretation of the “old” material. Standard observation under a scanning electron microscope was used first, then, the fossils were further investigated using Micro-computed tomography (micro-CT). Micro-CT uses X-rays to visualize internal structures and provides 3D reconstructions of the studied fossils. The main benefit of this method is its non-destructive nature. This method allows the study of the internal structures without damaging the specimen and at the same time retains the possibility of a complete repetition of the procedure.

## MATERIAL AND METHODS

The “old” material from the Rakowice Małe locality is a part of Ervín Knobloch’s collection gathered in the 1980s, partly published by Knobloch (1984) and Knobloch and Mai (1986). The “new” material was collected in Rakowice Małe and Żeliszów during the 2017 and 2019 field seasons, by two of the authors (JK and ATH).

Ervín Knobloch’s collection is housed in the National Museum Prague (NMP), and encompasses megaspores, flowers, fruits, seeds, insect eggs, and coprolites from Lower Silesia and other regions. The greater part of that material was sieved about 50 years ago but never published. In the collections of the National Museum Prague, there were several small boxes labelled “Rakowice Małe – nicht bearbeitet”, meaning “not described”. This particular part of the collection is described in the present paper.

All studied specimens (from both old and new collections) are charcoalified or lignified mesofossils, gathered using standard bulk maceration. The

mesofossil material was treated with hydrofluoric acid and hydrochloric acid, rinsed in water, and dried in air. Preliminary studies were carried out using an Olympus SZX 12 binocular microscope. Specimens for SEM observations were mounted on aluminum stubs using nail polish, coated with gold and studied using a Hitachi S3700 field emission scanning electron microscope at 2 kV. Uncoated specimens were studied in low vacuum at 15 kV.

Specimens NMP K2768, K2905, K2906 and K2951 were studied using X-ray micro-tomography with the SkyScan 1172 equipment (Bruker). The effective pixel size was ca. 0.5  $\mu\text{m}$ . Tube voltage was set to 40 kV, and the current source was 250  $\mu\text{A}$ . No filter was used. The acquired data were processed using flat field correction and reconstructed by the supplied software NRecon (Bruker). Photographs were created by Avizo 9.1 software. The presented figures were edited in Adobe Photoshop CS5. Plates were formed using Adobe InDesign CS5.5.

Under the “Range” we understand the stratigraphic range of the material described in the paper, not the total range of the species.

## GEOLOGY

The mesofossils described in the present paper from the Rakowice Małe and Żeliszów localities were collected in Lower Silesia (Dolny Śląsk, Niederschlesien), more precisely, in the North Sudetic Synclinorium (Walaszczyk, 2008), situated approximately between the towns of Lwówek Śląski (Löwenberg in Schlesien) and Bolesławiec (Bunzlau) in south-western Poland (Figure 1). They all come from a single stratigraphic unit, the formal name of which is the Nowogrodziec Member of the Czerna Formation, which is a characteristic coaly-clayey decametre-scale intercalation between two predominantly sandstone parts of the succession. The Nowogrodziec Mb. is a regressive unit. Its deposition took place in an embayment subject to limited marine influence, as testified by the palynomorph assemblage dominated by terrestrial pollen and spores, with only relatively few dinocysts (Halamski et al., 2020).

The “new” mesofossils material was collected from the only two outcrops of the Nowogrodziec Member existing at present. These are the Rakowiczki mine at Rakowice Małe (Wenig-Rackwitz) (several levels with mesoflora within sections RK-2 at 51°9.967'N 15°32.482'E and RK-4 at 51°9.962'N 15°32.525'E) and an open-cast mine east from Żeliszów (Giersdorf), where a single mesoflora-

yielding level was found in a trench dug at 51°11.049'N 15°38.892'E (Halamski et al., 2020). A detailed sedimentological account of the Rakowiczki site was given by Leszczyński (2010), whereas the outcrop of the Nowogrodziec Mb. at Żeliszów was discovered only recently (Halamski et al., 2018) and as yet has no comprehensive interpretation. Notable variations in thickness and lithological details are evident both between and within the two outcrops. For example, Halamski et al. (2020, figure 20) observed marine-influenced levels alternating with levels devoid of marine palynomorphs, whereas a section in the same quarry described by Leszczyński, (2010, fig. 4) was interpreted in terms of a general transgressive trend (first a lake, then a lagoon, finally shoreface).

The age of the Nowogrodziec Member is close to the Coniacian–Santonian boundary. It was dated to the early Santonian by Mitura et al. (1969) and Milewicz (1997), but according to Walaszczyk (2008) and Leszczyński (2010), it should be rather treated as late Coniacian, but details have not been provided. Palynological data (Halamski et al., 2020) are inconclusive, but indicative, if anything, rather of the Santonian than the Coniacian.

#### SYSTEMATIC PALAEONTOLOGY

Kingdom PLANTAE Linné, 1753 sensu Cavalier-Smith, 1981

Division LYCOPHYTA Zimmermann, 1959

Class LYCOPODIOPSIDA Bartling, 1830

Order SELAGINELLALES Prantl, 1874

Genus RICINOSPORA Bergad, 1978 emend. Li et al., 1987

**Type species.** *Ricinospora cryptoreticulata* (Bergad, 1978), pp. 48, 50, pls. 4, 5.

**Remarks.** The studied material shows a diagnostic character of the genus *Ricinospora*: the apical spongiöse wall sculpturing typical for this genus (Bergad, 1978) in which it differs from similar megaspores.

*Ricinospora* sp.  
Figure 2A-C

v 1984b aff. *Istisporites inornatus* (Miner) Potonié; Knobloch, p. 172

**Description.** Trilete megaspore, 400–530 µm in diameter, flattened in lateral direction, protruding Y mark, reaching one-third of proximal side (Figure 2B, 2C), body of spore delicately reticulate with low muri, polygonal lumina ca 10 µm. Exoexine reticulate, on the proximal face covered with complex three-dimensional network of exinal strands arising

from muri. Sometimes complex spongiöse material covers nearly whole megaspore (Figure 2C).

**Remarks.** The studied megaspores were identified by Knobloch (1984) as aff. *Istisporites inornatus* (Miner) Potonié. The material is mentioned in his review of mid-European Cretaceous megaspores. However, the complex spongiöse material is much more characteristic for the genus *Ricinospora*. The type *R. cryptoreticulata* Bergad (1978) described from the Maastrichtian of North Dakota, USA, is of similar size, the trilete body is also round and the surface is reticulate, it also shows similar spongiöse material on the surface (Bergad, 1978). Our material differs in the presence of reticulum with larger lumina and more pronounced muri. *Ricinospora* sp. differs from *R. laevigata* Li et al. (Li et al., 1987): *Ricinospora* sp. has delicately reticulate body that can be completely covered by spongiöse material, while *R. laevigata* has a smooth body covered with spongiöse material only in the apical part. A similar “irregularly lobed substance” in the apical part is mentioned by Dijkstra (1959) in *R. pileata* (Dijkstra) Singh, 1983, from the Maastrichtian of Limburg. The studied material is covered by this substance over nearly whole body, except for the distal apex. However, Lupia (2015) found out that megaspores can lose substantial portions of this spongiöse structure. A similar structure has been described in spores of Recent *Selaginella* by Korall and Taylor (2006), particularly in species *S. pygmaea* and *S. gracillima*. Unlike these species, two of our fossil specimens have this mass more extended (Figure 2A, C).

**Range.** Late Coniacian or early Santonian age.

**Occurrence.** Rakowice Male locality.

**Material studied.** K 3014-3019; the material is housed in the National Museum Prague.

Division GYMNOSPERMAE (Lindley, 1830) Prantl, 1874

Class CONIFERAE (de Jussieu, 1789) Engler, 1892

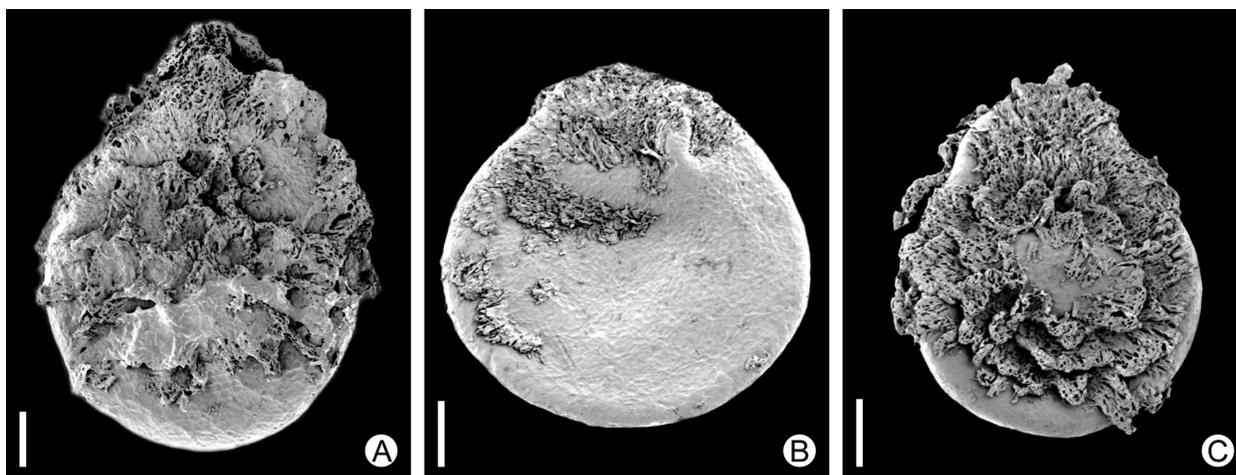
Order PINALES Gorozhankin, 1904

Family CUPRESSACEAE Gray, 1821

Genus CUNNINGHAMITES Presl in Sternberg, 1838

**Type species.** *Cunninghamites oxycedrus* Presl in Sternberg, 1838, p. 203, pl. 48, figs. 3a-c, pl. 49, figs. 1a, b from Late Cretaceous, Cenomanian; Niederschöna, Saxony, Germany.

**Remarks.** The leaves are dorsiventrally flattened with expanded leaf cushions, and adaxially showing two distinct bands of stomata, characters that indicate the genus *Cunninghamites* Presl in Sternberg.



**FIGURE 2.** *Ricinospora* sp. (A) and (C) showing that nearly the whole megaspore is covered with spongiose material, (B) spongiose exinal strengthenings is mainly in the proximal part of spore, a fragment of the trilete laesure is visible. Scale bar for all images 0.1 mm. All specimens from Rakowice Male locality.

*Cunninghamites* cf. *squamosus* Heer, 1871

Figure 3A-C

- 1871 cf. *Cunninghamites squamosus* Heer, p. 9, pl. 1, figs. 5-7.  
 1880 cf. *Cunninghamites recurvatus* Hosius et von der Marck, p. 178, pl. 37, figs. 143, 144.  
 1905 cf. *Cunninghamites pulchelles* Knowlton, p. 136, pl. 16, fig. 1.  
 1910 cf. *Cunninghamites elegans* (Corda) Endlicher; Berry, p. 186, pl. 20, figs. 1-4  
 1919 cf. *Elatocladus elegans* (Corda) Seward, p. 433, figs. 804, 805.  
 1922 cf. *Elatocladus elegans* (Corda) Seward; Kräusel, p. 10, pl. 1, figs. 4-10; pl. 2, figs. 1-5; pl. 3, figs. 1,2; Text figs. 4,5.  
 1925 cf. *Cunninghamites elegans* (Corda) Endlicher; Berry, p. 33.  
 2000 cf. *Elatocladus elegans* (Corda) Seward; Rufflé and Trostheide, p. 434, pl. 1, fig. 6; pl. 2, fig. 2; pl. 3, fig. 1.  
 2009 cf. *Cunninghamites squamosus* Heer; Bosma et al., p. 486, fig. 4c-f; fig. 5.  
 2012 cf. *Cunninghamites squamosus* Heer; Bosma et al., p. 24, pl. 1, figs. 5-6, pl. 2, figs. 4, 7.

**Lectotype.** Designated by Bosma et al. (2012), No. 6166 (ex coll. Schenk in the Würzburg University), Late Cretaceous, late Santonian, "Altenburg" near Quedlinburg, Germany.

**Description.** The material consists of fragments of branches. The terminal part of the sterile twig 8 mm long and 4.0 mm broad shows needles packed in a pointed bud (Figure 3A). A fragment of an axis (4.0 mm long) shows helically arranged basal parts of needle-like leaves. A nearly complete isolated leaf 5.0 mm long, shows basally broadened leaf

cushion (Figure 3B). Its cuticle shows adaxially two clearly distinct stomatal bands (Figure 3C). Stomata tend to be orientated perpendicularly to the leaf margin.

**Remarks.** The material resembles the type material designated by Bosma et al. (2009). However, it is too fragmentary to allow precise comparison. We found minor differences in the studied material from the type, so open nomenclature is used. Particularly the leaves of the studied material show only one rib/keel and contained probably only one vein. Its stomata are orientated perpendicularly to the leaf margin, while the type material shows a random orientation (Bosma et al., 2012, 2009).

**Range.** Late Coniacian or early Santonian age.

**Occurrence.** Żeliszów locality.

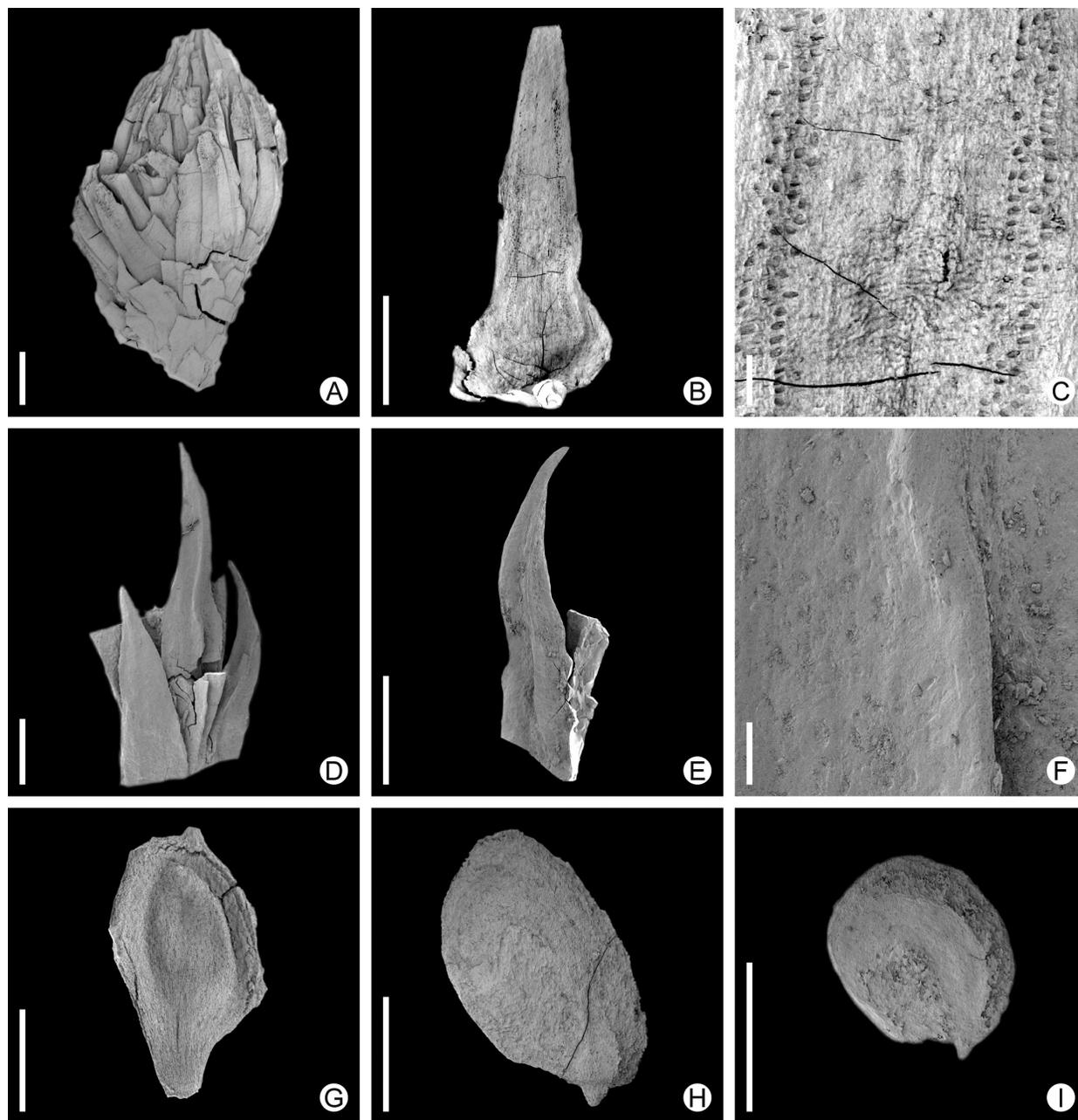
**Material studied.** K 2940, K 2948, K 2953, K 2956; the material is housed in the National Museum Prague.

Genus *ALAPAJA* Dorofeev, 1979

**Type species.** *Alapaja uralensis* (Dorofeev, 1979), p. 314, figs 1, 5-10, fig. 7, 1-10

**Remarks.** Based on the presence of a structure very probably representing a curved embryo, asymmetric wings, pronounced funiculus and due to the overall shape of the seed, we assign the seed to the genus *Alapaja*. *Alapaja* differs from *Seletya* Dorofeev and *Kozykorpeshia* Dorofeev in having a marginal crest, being less curved, and lacking a basiventral micropyle (Dorofeev, 1979; Kunzmann and Friis, 1999).

*Alapaja* sp.  
Figure 3G



**FIGURE 3.** Conifers (A) *Cunninghamites* cf. *squamosus* terminal fragment of twig, no. K2948, scale bar 1 mm (B) *Cunninghamites* cf. *squamosus* isolated leaf with leaf cushion, no. K2956, scale bar 1 mm (C) *Cunninghamites* cf. *squamosus* adaxial cuticle showing two bands of stomata, no. K2956, scale bar 100  $\mu$ m (D) *Geinitzia formosa*, fragment of twig, no. K2958a scale bar 1 mm (E) *Geinitzia formosa*, isolated leaf with keel, no. K2958b scale bar 1 mm (F) *Geinitzia formosa*, detail of abaxial cuticle showing two irregular stomatal bands, no. K2958b scale bar 100  $\mu$ m (G) *Alapaja* sp. seed, no. K2962 scale bar 1 mm (H) *Seletya* sp. seed no. K 3012 scale bar 1 mm (I) *Seletya* sp. seed no. K 3013, scale bar 1 mm. All specimens from Źeliszów locality.

**Description.** Seed is 2.7 mm long, 1.4 mm broad, flattened, ovate, asymmetric, showing fragments of one narrow, inconspicuous wing and one wider wing (Figure 3G). Margin shows both large and smaller projections, forming a crest. Larger projections frequently broken off. Micropyle pointed and

partly broken in terminal part. Basal part formed by distinctive funicle. Central part of the seed relatively smooth, showing a central depression and a curved structure representing an embryo.

**Remarks.** Although the seed is not well preserved, we decided to publish it here as unequivocally doc-

umenting the presence of the genus at Rakowice Małe. Our seed is more similar to the type material of (Dorofeev, 1979) from the Cenomanian–Turonian of Alapayevsk (Yekaterinburg, east Ural). Our seed is smaller than *Alapaja uralensis* from the Turonian of Kazakhstan (Frumina et al., 1995)

**Range.** Late Coniacian to early Santonian age.

**Occurrence.** Żeliszów locality.

**Material studied.** K 2962; the material is housed in the National Museum Prague.

Genus SELETYA Dorofeev, 1979

**Type species.** *Seletya kryshstofovichii* Dorofeev, 1979, p. 315, pl. 2, figs. 1-6, pl. 3, fig. 1, 2, pl. 8, figs. 1-6.

**Remarks.** Seeds of *Seletya* differ from *Alapaja* in having a smooth margin and a clearly projecting hilum. The type *S. kryshstofovichii* was transferred to *Geinitzia* by Knobloch and Mai (1986), but *Geinitzia* is based on sterile foliage, so from a nomenclatorial point of view this need not be accepted. We therefore applied a more conservative approach, and separated the seeds (and ovuliferous cones) from the sterile twigs *Geinitzia formosa*.

*Seletya* sp.  
Figure 3H, I

**Description.** Seeds small, 2.0–2.6 mm long, 1.6–1.4 mm broad, flattened, ovate to sub-circular showing a very narrow inconspicuous wing (Figure 3H, I). Locule curved campylotropous, hilum and micropyle basiventral, hilum circular, broad, micropyle pointed and conspicuous. Seed coat rugulose, pits quadrangular or polygonal, rarely oblong, arranged in regular parallel grooves following curvature of seeds.

**Remarks.** The described seeds are reminiscent of *Seletya krishtofovichii* from the Cenomanian of Kazakhstan (Dorofeev, 1979) and Santonian of Quedlinburg (Knobloch and Mai, 1986) in number of characters e.g. in having a very narrow wing and a conspicuous micropyle. An ovuliferous cone comparable to that described by Kunzmann (1999) attached to twigs of *Geinitzia formosa* was described from the studied area and stratigraphic horizon (Rakowice Małe) by Halamski et al. (2020). The seeds of similar shape are found in ovuliferous cones *Fricia nobilis* Velenovský, described from the Turonian of the Bohemian Cretaceous Basin (Kvaček, 2013).

**Range.** Late Coniacian or early Santonian age.

**Occurrence.** Żeliszów locality.

**Material studied.** K 3012, K 3013; the material is housed in the National Museum Prague.

Family GEINITZIACEAE Kunzmann, 1999

Genus GEINITZIA Endlicher, 1847

**Type species.** *Araucarites reichenbachii* Geinitz, 1842, p. 98, pl. 24, 4 = *Geinitzia reichenbachii* (Geinitz) Hollick and Jeffrey, 1909, p. 38, pl. 5, figs. 7-10, pl. 8, figs. 3, 4, pl. 16 figs. 2-4, pl. 17 figs. 1-4, pl. 18, figs. 1-4

**Remarks.** The material of sterile shoots is assigned to this genus, as suggested by Harris (1969) and Harris et al. (1979). It is characterised by helically arranged needles that are triangular in cross-section, and having a conspicuous keel. Our material shows all those characters very clearly.

*Geinitzia formosa* Heer, 1871

Figure 3D-F

v 1871 *Geinitzia formosa* Heer, p. 6, pl. 1, fig. 9, pl. 2, figs. 1-6

v.1999 *Geinitzia formosa* Heer, Kunzmann, p. 114, pl. 26, figs. 1-8, pl. 27, figs. 1, 5-10, pl. 28, figs. 1-6

2003 *Geinitzia formosa* Heer, Kunzmann, p. 13, fig. 4A-D, pl. 4, figs. 1-9

**Lectotype.** No. UW 3936, designated by Zijlstra et al. (2010), based on Kunzmann (1999), pl. 27, fig. 1, coll. University of Würzburg, Germany, Late Cretaceous, Santonian, Quedlinburg.

**Description.** Fragments of sterile twigs 1.0–2.0 mm broad, 4.0–13.0 mm long, with helically arranged needle-like leaves (Figure 3D), 1.5–4.5 mm long and 0.6–0.8 mm broad. Leaves triangular in cross section, showing a conspicuous keel (Figure 3E). Sometimes amber droplets preserved adhering to twigs. Abaxial cuticle shows two bands of stomata 200–500 µm broad (Figure 3F), the same arrangement is on abaxial cuticle. Stomata surrounded by 5–6 subsidiary cells. Stomatal axes irregularly orientated. Ledges of guard cells sunken in shallow stomatal chambers, sometimes surrounded by a slightly raised stomatal rim.

**Remarks.** We assign the studied material to *Geinitzia formosa*, as described from the type locality at Quedlinburg by Kunzmann (1999), particularly on account of leaves that are amphistomatic and triangular in cross section in terminal parts. *G. formosa* differs from *G. reichenbachii* in having shorter needles, which are frequently s-shaped. The needles of *G. formosa* are rhomboidal only in their basal parts, they are triangular terminally. *G. formosa* differs from *Cunninghamites* cf. *squamosus*, in having more three dimensional leaves. Leaves of *Cunninghamites* cf. *squamosus* are flattened in cross section, and their cuticle shows irregularly orientated stomata forming two bands. We also collected *Seletya* seeds in

association, similarly to the situation described by Kunzmann (1999). However, Kunzmann did not make the nomenclatorial distinction between seeds and twigs, assigning seeds described herein under *Seletya* directly to *Geinitzia* (Kunzmann, 1999) along with sterile shoots.

**Range.** Late Coniacian or early Santonian age.

**Occurrence.** Żeliszów locality.

**Material studied.** NMP K 2933-5, 2942-6, 2947, 2955, 2958, 3009; the material is housed in the National Museum Prague.

Division ANGIOSPERMAE Brown and Doell ex  
Doell, 1857

Class Dicotyledoneae de Candolle, 1824

Order FAGALES Engler, 1892 s.l.

Genus CARYANTHUS Friis, 1983

**Type species.** *Caryanthus knoblochii* Friis, 1983, p. 172, pl. 5, 6, 7, figs. 1-4

**Remarks.** Fruits of the genus *Caryanthus* are small, ribbed, bisymmetrical and epigynous, nuts supported by a bract showing single erect seed (Friis, 1983; Friis et al., 2011, 2006; Heřmanová et al., 2016). In some cases, remains of perianth are preserved. They show a perianth consisting of four tepals arranged in two decussate pairs. The androecium is built 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.

*Caryanthus communis* Friis, 1983  
Figure 4A-C

v1964 *Microcarpolithes triasseris* Knobloch, (Knobloch, 1964) p. 170, pro parte.

v1983 *Caryanthus communis* Knobloch and Mai, (Knobloch and Mai, 1983) p. 308, pl. 8, figs. 5, 8, 11-13.

v1986 *Caryanthus communis* Knobloch et Mai, (Knobloch and Mai, 1986), p. 75, pl. 5, figs. 18, 19.

v2006 *Caryanthus communis* Knobloch et Mai; (Friis et al., 2006) p. 113.

v2016 *Caryanthus communis* Knobloch et Mai; (Heřmanová et al., 2016) p. 36, pl. 1, figs. 1-9.

**Holotype.** No. NMP F 3577, published by Knobloch and Mai (1983); pl. 8, fig. 5, stored in the National Museum Prague, Late Cretaceous, Upper Turonian–Santonian, České Budějovice – Rožnov borehole GB-3190.0–3190.1 m, Czech Republic.

**Description.** Single specimen from Rakowice Małe locality, flat fruit of ovoid shape (Figure 4A). Length 1.3 mm; breadth 0.8 mm. Apical part of fruit concave (Figure 4B). Persistent perianth fused basally, forming hypanthium. Tepals attached on

the top of hypanthium. Tepals not preserved; their insertion indicated by attachment scars, indicating four tepals in two decussate pairs. Lateral face of fruit shows a long concave tepal attachment scar, placed mid-way between the base and the apex. Medial scars small, close to the base. The lateral face of the fruit shows a diamond shaped area. Length of this area 0.9 mm; breadth of fruit 0.7 mm. Epidermis of the fruit composed of small irregular cells (Figure 4C).

**Remarks.** The specimen from the Rakowice Małe locality is slightly longer than other fruits of *Caryanthus communis* (Heřmanová et al., 2016). The species *Caryanthus communis* is described as having a concave base, but the specimen from Rakowice Małe has slightly pointed base. However, absence of this character may be due to poor preservation of the specimen.

**Range.** Late Coniacian or early Santonian age.

**Occurrence.** Rakowice Małe locality.

**Material studied.** K2899; the material is housed in the National Museum Prague.

*Caryanthus trebecensis* Knobloch and Mai, 1983  
Figure 4D-F

v1983 *Caryanthus trebecensis* Knobloch et Mai; Knobloch and Mai, 1983, p. 309, pl. 8, figs. 1-4, 10, 14.

v1986 *Caryanthus trebecensis* Knobloch et Mai; Knobloch and Mai, 1986, p. 76, pl. 5, fig. 4.

v2006 *Caryanthus trebecensis* Knobloch et Mai; Friis et al., 2006, p. 113.

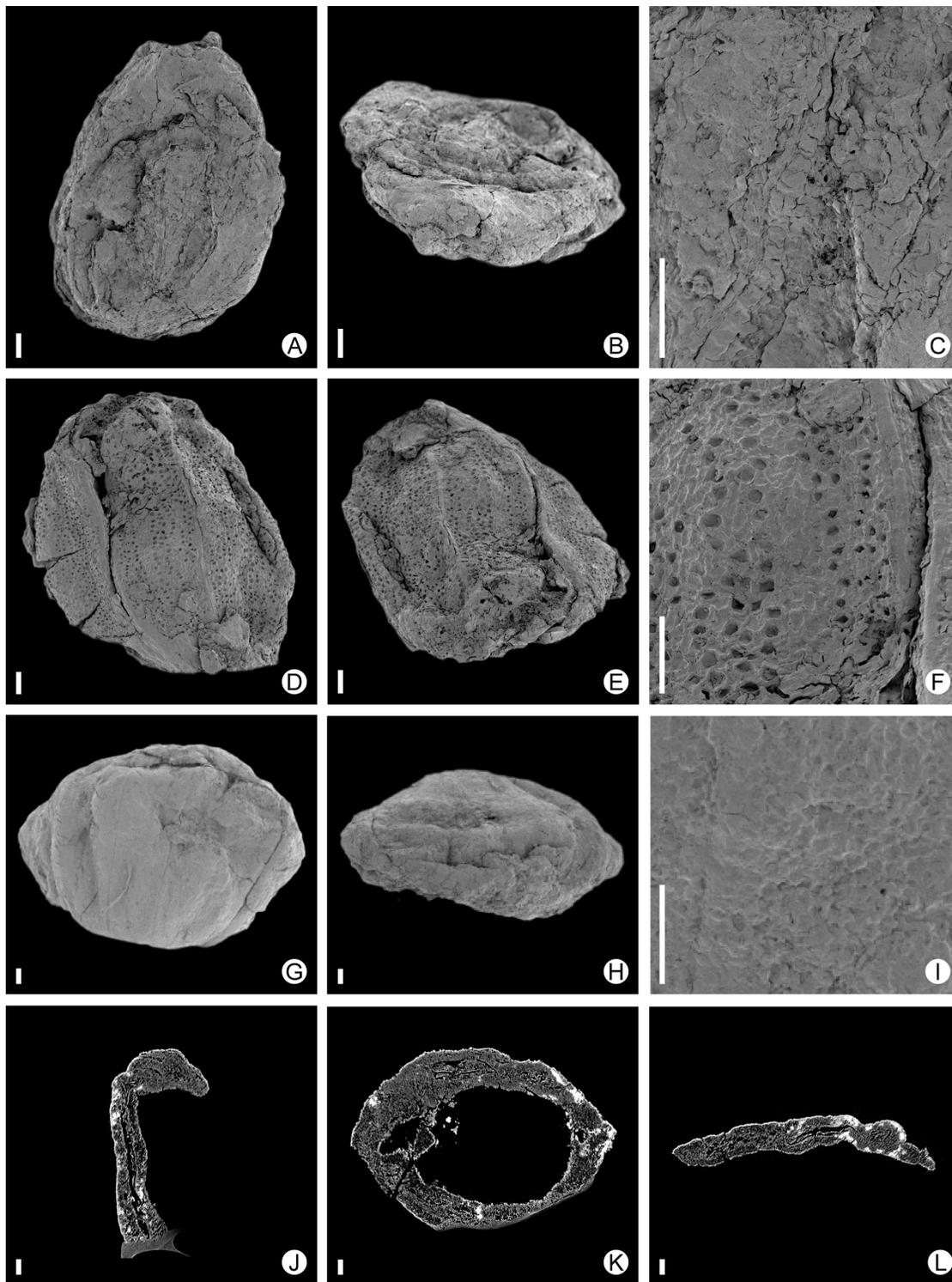
v2012 *Caryanthus* sp.; Heřmanová and Kvaček, 2012, p. 49, pl. 2, figs. A-G.

v2016 *Caryanthus trebecensis* Knobloch et Mai; Heřmanová et al., 2016, p. 42, pl. 6, figs 1-12.

**Holotype.** Published by Knobloch and Mai (1983), pl. 8, figs. 1-3, stored in the National Museum Prague NMP F3873, Late Cretaceous, Upper Turonian–Santonian, Branišov Br 21 borehole, 23.0–23.5 m, Czech Republic.

**Description.** The specimen from Rakowice Małe locality is a slightly deformed fruit of ellipsoid shape (Figure 4D). Length 1.4 mm; breadth 1.0 mm. Apical part of the fruit concave; persistent perianth fused basally forming hypanthium, which covers the entire fruit (Figure 4E). Lateral faces of the fruit show two deeply sunken ridges running from the base to the apex. Surface covered with irregularly shaped thick-walled cells. Periclinal wall of cells sometimes collapsed (Figure 4F).

**Remarks.** The specimen from the Rakowice Małe locality is slightly longer than other fruits of *Caryanthus trebecensis* (Heřmanová et al., 2016). The apical part of the specimen described here is



**FIGURE 4.** *Caryanthus* (A) *Caryanthus communis* broadly elliptical fruit, no. K2899; (B) *Caryanthus communis* apical part of fruit, no. K2899; (C) *Caryanthus communis* detail of epidermis, no. K2899 (D) *Caryanthus trebecensis* ribbed fruit, no. K2900; (E) *Caryanthus trebecensis* apical part of fruit, no. K2900; (F) *Caryanthus trebecensis* detail of epidermis, no. K2900; (G) *Caryanthus* sp. ribbed fruit, no. K2906; (H) *Caryanthus* sp. apical part of fruit, no. K2906; (I) *Caryanthus* sp. detail of epidermis, no. K2906; (J) *Caryanthus* sp. X-ray image, longitudinal/lateral section of fruit, no. K2906; (K) *Caryanthus* sp. X-ray image, transversal section of fruit, no. K2906; (L) *Caryanthus* sp. X-ray image longitudinal/adaxial-abaxial section of fruit, no. K2906. Scale bar for all images 0.1 mm. All specimens from Rakowice Male locality.

deformed, thus shape and position of tepals, usually attached on top of the hypanthium, are unclear.

**Range.** Late Coniacian or early Santonian age.

**Occurrence.** Rakowice Małe locality.

**Material studied.** K2900; the material is housed in the National Museum Prague.

*Caryanthus triasseris* Knobloch (Knobloch and Mai), 1983  
Figure 5A-F

- v1964 *Microcarpolithes triasseris* Knobloch; (Knobloch, 1964) p. 170, pl. 5, fig. 6.
- v1970 *Microcarpolithes octocostatus* Knobloch; (Knobloch, 1970), pl. 11, figs. 4, 16, 17.
- v1971 *Microcarpolithes octocostatus* Knobloch; (Knobloch, 1971) p. 27, pl. 6, figs. 1-5, 9, 11.
- v1971 *Microcarpolithes triasseris* Knobloch; (Knobloch, 1971) p. 21-5, pl. 3, figs. 1-8 (non figs. 9-14), non pl. 6, figs. 12-13, pl. 10, fig. 5.
- v1977 *Microcarpolithes triasseris* Knobloch; (Knobloch, 1977) p. 113-114, pl. 1, figs. 5, 9, 11, 13, 16, 18, 19, pl. 2, figs. 8, 10, pl. 4, figs. 25, 26, pl. 5 figs. 13, 21-23 pl. 11, 6-9.
- v1983 *Caryanthus triasseris* (Knobloch) Knobloch et Mai; (Knobloch and Mai, 1983) p. 309, pl. 6, figs. 4, 5 (non pl. 6 fig. 11), (non pl. 8 fig. 6), pl. 9, fig. 8, pl. 10 fig. 9.
- v1986 *Caryanthus triasseris* (Knobloch) Knobloch et Mai; (Knobloch and Mai, 1986) p. 76, pl. 5 figs. 1-3. non (figs. 7-10), (non pl. 6 fig. 18).
- v2006 *Caryanthus triasseris* (Knobloch) Knobloch et Mai; (Friis et al., 2006) p. 113.
- v2016 *Caryanthus triasseris* (Knobloch) Knobloch et Mai; (Heřmanová et al., 2016) p. 44 pl. 7 figs. 1-11.

**Holotype.** Published by Knobloch (1964); pl. 5, fig. 6, stored in the National Museum Prague No. NMP F 3611, Late Cretaceous, Upper Turonian–Santonian, Včelná borehole GB2 119.5–119.8 m, Czech Republic.

**Description.** Four specimens from Rakowice Małe locality are fruits, round to elliptical in shape. Length 0.9–1.3 mm (arithmetic mean 1.0 mm); breadth 0.7–1.1 (arithmetic mean 0.1). Three specimens round (Figure 5A), one elongated (Figure 5D). Apical part of fruit pointed or slightly pointed (Figure 5B, E), as well as its base. Perianth persistent, fused basally, forming a hypanthium, which extends for almost the entire length of fruit. Lateral faces of fruit have three very indistinct ribs running from the base to the margin of hypanthium.

**Discussion.** Specimens of *Caryanthus triasseris* from the Rakowice Małe locality are above average in size of the fruits, compared to the type material (Knobloch and Mai, 1986). The ribs that are very

characteristic for the species run from the base to the margin of the hypanthium. However, this character is very indistinct in material from Rakowice Małe.

**Range.** Late Coniacian or early Santonian age.

**Occurrence.** Rakowice Małe locality.

**Material studied.** NM K2898; K2901; K2902; K2907; the material is housed in the National Museum Prague.

*Caryanthus* sp.  
Figure 4G-L

**Description.** The single specimen from the Rakowice Małe locality is a slightly deformed flattened fruit, ellipsoid in shape (Figure 4G). Length 1.4 mm; breadth is 2.0 mm. Apical part of the fruit concave and strongly deformed (Figure 4H). Basal part convex. Persistent perianth fused basally, forming hypanthium, which covers the entire fruit. Lateral faces of fruit show five slightly sunken ridges running from base to apex, surface covered with irregular thick-walled cells (Figure 4I). Distinct compact outer and inner layers of the fruit wall consist of small cells. The middle layer has larger cells (Figure 4J-L).

**Remarks.** Lateral face of *Caryanthus trebecensis* shows two to four sunken ridges, lateral face of *Caryanthus triasseris* shows three parallel ribs and lateral face of this fruit shows five slightly sunken ridges so it is difficult to decide to which species this specimen belongs, either to *C. trebecensis* or *C. triasseris*.

**Range.** Late Coniacian or early Santonian age.

**Occurrence.** Rakowice Małe locality.

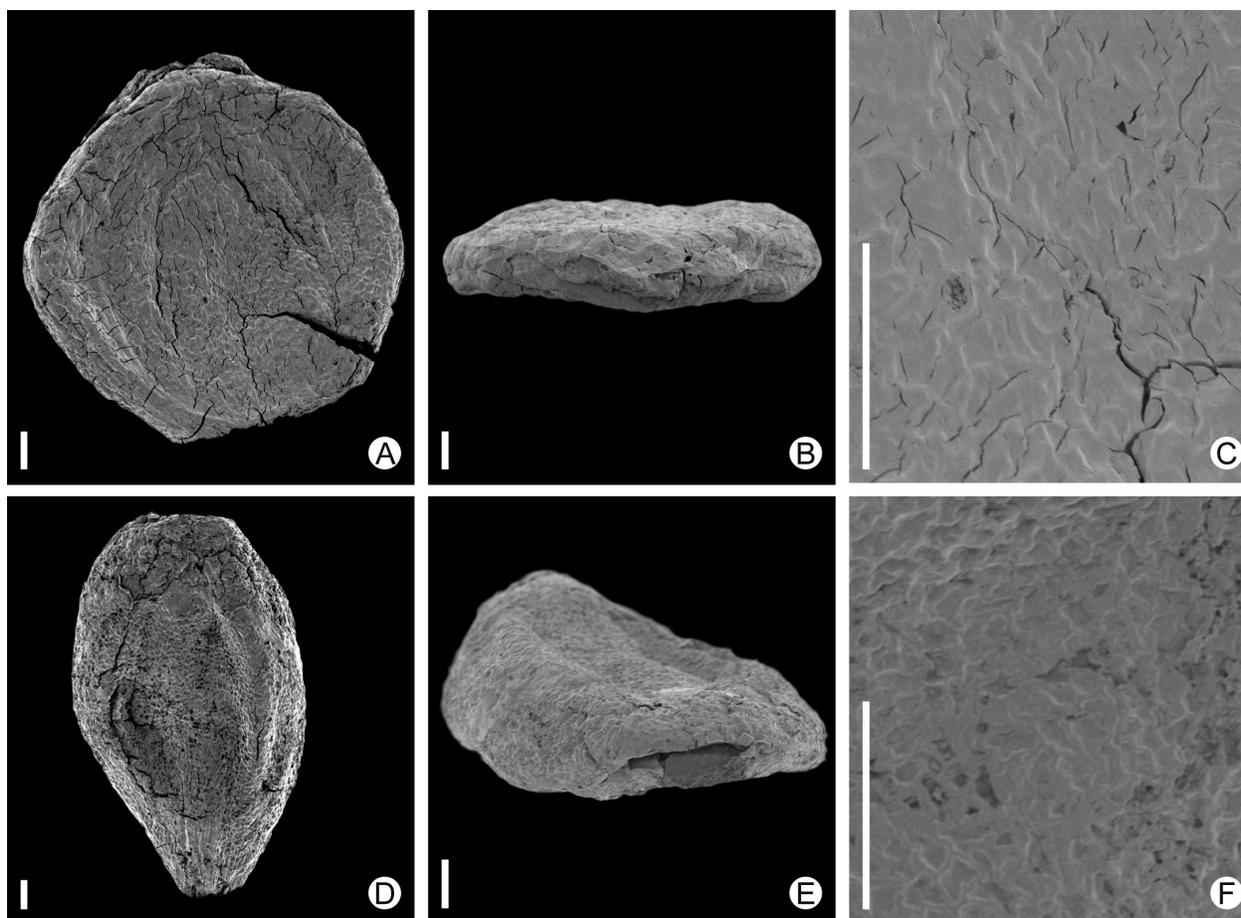
**Material studied.** K2906; the material is housed in the National Museum Prague.

Genus ZLIVIFRUCTUS Heřmanová, Dašková et J. Kvaček, 2017

**Type species.** *Zliviifructus vachae* Heřmanová, Dašková et J. Kvaček (Heřmanová et al., 2017)

**Remarks.** The genus represents small flowers and fruits. The flowers are bisexual, bisymmetrical and have an inferior ovary with a hypanthium. The tepals are attached on top of the hypanthium. The genus has four tepals, in two decussate pairs. The androecium consists of four stamens. The gynoecium is bicarpellate, with a unilocular ovary and two styles. Fruits are nuts with a single erect seed. Non-mapollis pollen grains of *Plicapollis*-type were found on the surface of the fruit (Heřmanová et al., 2017).

*Zliviifructus vachae* Heřmanová, Dašková et J. Kvaček, 2017  
Figure 6A-I



**FIGURE 5.** *Caryanthus triasseris* (A) ribbed fruit round in outline, no. K2901 (B) apical part of fruit, no. K2901 (C) detail of epidermis, no. K2901 (D) ribbed fruit elliptical in outline, no. K2907 (E) apical part of fruit, no. K2907 (F) detail of epidermis, no. K2907. Scale bar for all images 0.1 mm. All specimens from Rakowice Małe locality.

v2017 *Zlivifructus vachae* Heřmanová, Dašková et J. Kvaček; (Z. Heřmanová et al., 2017) p. 181, pl. 1, figs. 1-9, pl. 2, figs. 1-7, pl. 3, figs. 1-2.

**Holotype.** Selected and illustrated by Heřmanová et al. (2017), pl. 1, fig. 1, stored in the National Museum Prague No. NMP F4557, Late Cretaceous, Upper Turonian–Santonian, Třebeč TSv-5 borehole 106.5–107 m, Czech Republic.

**Description.** Two specimens from Rakowice Małe locality are round fruits, flattened to some degree. One almost completely flat (Figure 6A); the other more ovoid (Figure 6D). Lengths 1 and 0.9 mm; breadths 1.1 and 0.7 mm. Apical part of fruits convex, basal parts show scar where fruits were attached to infructescence (Figure 6B, E). Persistent perianth fused basally, forming hypanthium, which covers two-thirds of fruit. Lateral faces of the fruit show three indistinct ribs extending from base of fruit to margin of hypanthium. Androecium consists of four stamens (Figure 6D), but only basal parts of stamens are preserved. Distinct compact

outer layers of the fruit wall consist of small cells. The middle layer has larger cells (Figure 6G-I). Surface covered with irregular thick-walled cells (Figure 6F).

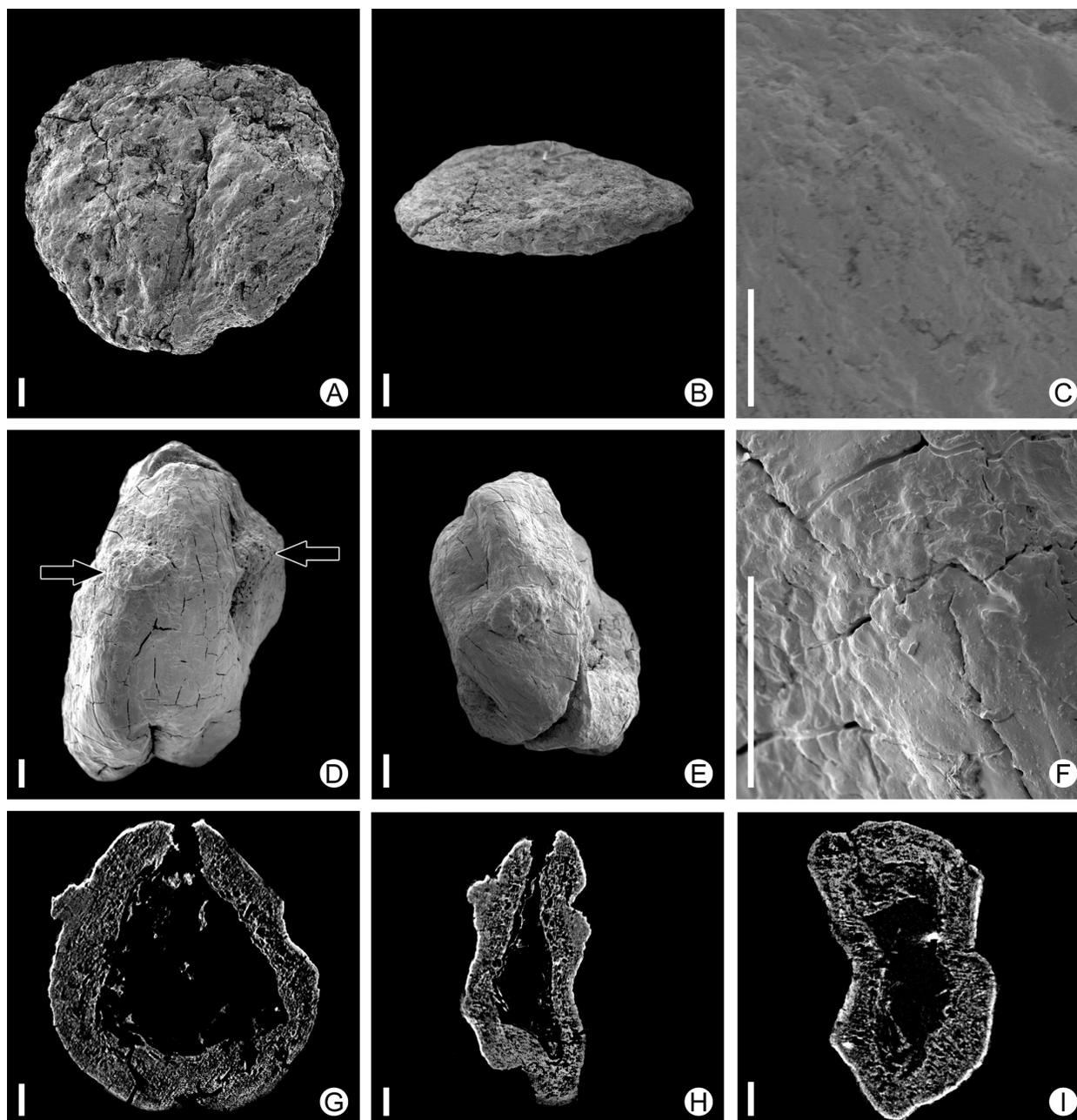
**Remarks.** The present material seems to match the main diagnostic characters of the type, but it is poorly preserved. Tepals are absent in both specimens, but we interpret the preserved scars as resulting from detachment of tepals. We assume tepals attached on top of the hypanthium. Scars are immediately adjacent to each other, with indistinct boundaries and the scars form a roughly regular ring.

**Range.** Late Coniacian or early Santonian age.

**Occurrence.** Rakowice Małe locality.

**Material studied.** K2905, K2903; the material is housed in the National Museum Prague.

*Zlivifructus microtriasseris* (Knobloch et Mai)  
Heřmanová, J. Kvaček et Halamski 2019  
Figure 7A-C

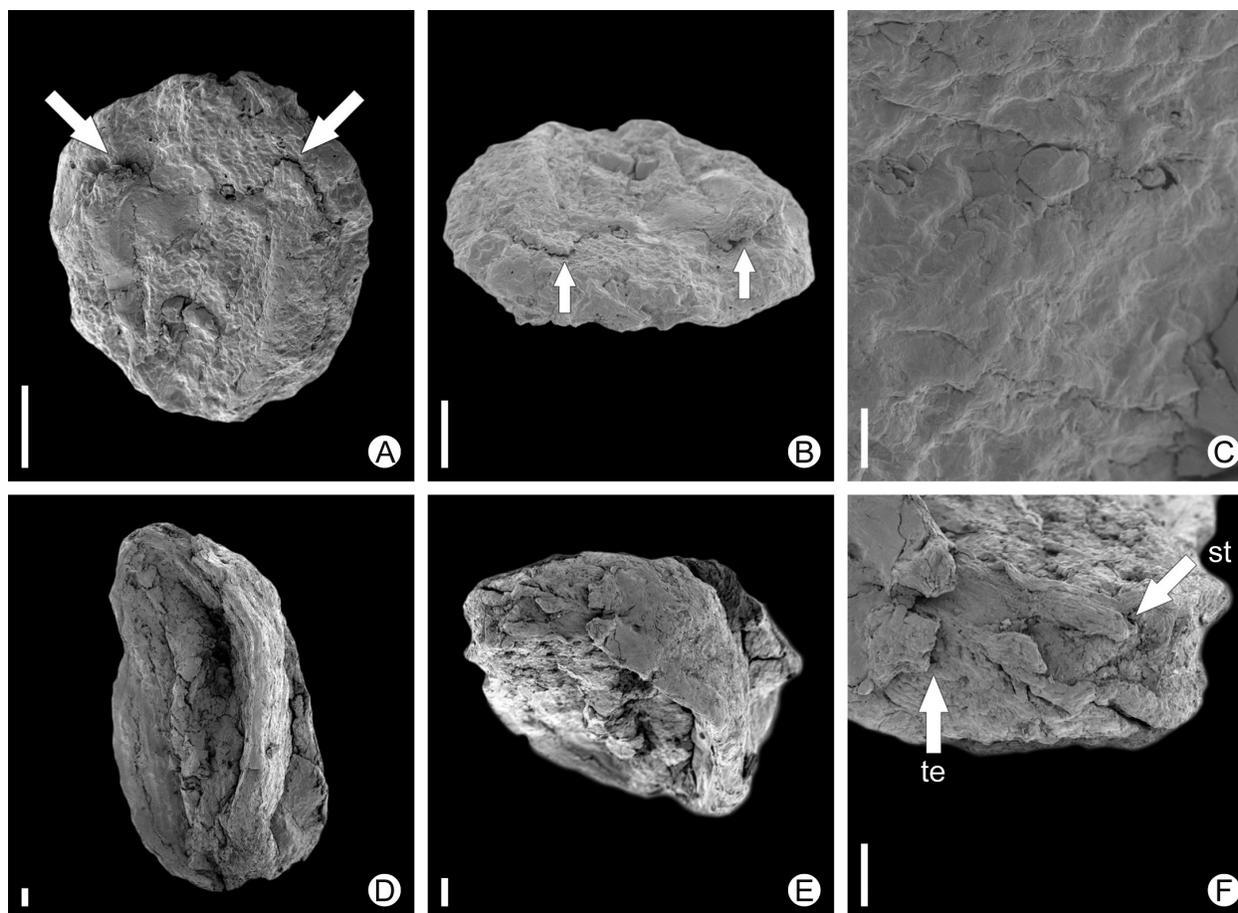


**FIGURE 6.** *Zlivifructus vachae* (A) fruit, round in outline, no. K2903 (B) apical part of fruit, no. K2903 (C) detail of epidermis, no. K2903 (D) fruit, basal parts of stamens arrowed, no. K2905 (E) apical part of fruit, no. K2905 (F) detail of epidermis, no. K2905 (G) X-ray image, longitudinal/adaxial-abaxial section of fruit, no. K2905 (H) X-ray image, longitudinal/lateral section of fruit, no. K2905 (I) X-ray image, transversal section of fruit, no. K2905. Scale bar for all images 0.1 mm. All specimens from Rakowice Małe locality.

- v1983 *Caryanthus microtriasseris* Knobloch et Mai;  
(Knobloch and Mai, 1983) p. 308-309, pl.8, fig.  
9.
- v1986 *Caryanthus microtriasseris* Knobloch et Mai;  
(Knobloch and Mai, 1986) p. 76, pl. 5, figs. 5-6,  
pl. 55, fig. 3.
- v2006 *Caryanthus microtriasseris* Knobloch et Mai;  
(Friis et al., 2006) p. 113.

- v2016 *Caryanthus microtriasseris* Knobloch et Mai;  
(Heřmanová et al., 2016) p. 40, pl. 5, figs. 1-3.
- v2019 *Zlivifructus microtriasseris* (Knobloch et Mai)  
Heřmanová, J. Kvaček, Halamski in  
(Heřmanová et al., 2019), p. 90, p. 11, figs. 1-9.

**Holotype.** No. NMP F3872, selected and illustrated by Knobloch and Mai (1983); pl. 8 fig. 9, stored in the National Museum Prague, Late Creta-



**FIGURE 7.** Fruits of Normapolles (A) *Zlivifructus microtriasseris* small fruit, basal parts of stamens arrowed, no. K 1290 (B) *Zlivifructus microtriasseris* apical part of fruit, basal parts of stamens arrowed, no. K 1290 (C) *Zlivifructus microtriasseris* detail of epidermis, no. K 1290 (D) Normapolles aff., deformed fruit, no. K2904 (E) Normapolles aff., apical part of the fruit, no. K2904 (F) Normapolles aff., apical part of the fruit, basal parts of stamens arrowed (st), basal parts of two very narrow tepals arrowed (te), no. K2904. Scale bar for all images 0.1 mm. All specimens from Rakowice Małe locality.

ceous, Upper Turonian–Santonian, Záblatí bore-hole 65/21, 34.0–35.0, Czech Republic.

**Description.** The single specimen from Rakowice Małe locality is a small, flat fruit, round in outline (Figure 7A). Length 0.4 mm; breadth 0.4 mm. Apical part of the fruit concave (Figure 7B), basal part convex. Persistent perianth fused basally, forming hypanthium, which extends more than two thirds of the fruit. Tepals not preserved; but scars indicating their insertion present. Lateral attachment scars of tepals and medial attachment scars immediately adjacent to each other, with indistinct boundaries forming a ring. Androecium consists of four stamens (Figure 7B), but only basal parts of stamens are preserved. Lateral faces of the fruit show two parallel ribs running from base of fruit to margin of hypanthium.

**Remarks.** This specimen was revised in Heřmanová et al. (2019). Flowers and fruits of *Zlivifructus microtriasseris*, originally described as *Caryanthus microtriasseris* from the North Sudetic Basin and South Bohemian Basins (late Turonian - Santonian) were reinterpreted. *Zlivifructus microtriasseris* differs from species assigned to genus *Caryanthus* Friis (1983) in the presence of four stamen scars, and in having two lateral ribs in the face of the fruit (Heřmanová et al., 2019).

**Range.** Late Coniacian or early Santonian age.

**Occurrence.** Rakowice Małe locality.

**Material studied.** K 1290; the material is housed in the National Museum Prague.

Family unknown  
Fruit of Normapolles affinity  
Figure 7D-F

**Description.** One specimen from Rakowice Małe locality is a slightly deformed fruit, elliptic in outline (Figure 7D). Length 2.1 mm; breadth 1.0 mm. Apical part of fruit slightly pointed. Perianth persistent, fused basally, forming hypanthium, which extends for almost entire length of fruit. Tepals attached on top of hypanthium. Basal parts of two, very narrow tepals are preserved (Figure 7F). Lateral faces of fruit strongly deformed, epidermis largely destroyed.

**Remarks.** The number of stamens is not clear, so it is difficult to decide to which genus the specimen belongs, but probably to *Caryanthus* or *Calatiocarplus*.

**Range.** Late Coniacian or early Santonian age.

**Occurrence.** Rakowice Małe locality.

**Material studied.** K2904; the material is housed in the National Museum Prague.

Pistillate flower of Normapolles affinity  
Figures 8A, 9A-C

**Description.** Specimen No. K2951 from Żeliszów shows a unit of flowers on a common short twig (Figures 8A, 9A), subtended by a common bract. The unit consists of three epigynous flowers, each subtended by a bract (Figure 9B). Length of flowers - 1.7-2.0 mm; breadth 0.9-1.2 mm. Each flower is extremely flattened consisting of five tepals (Figure 9C) that are fused basally; their free parts are triangular, 0.4 x 0.5 mm in size. The gynoecium is very flattened and of unknown structure (Figure 9A, C).

**Remarks.** The studied fragment of an inflorescence and its general construction argues for its systematic affinity to plants of the Normapolles Complex. However, more and better preserved material is necessary for closer comparison with other genera of the Complex.

**Range.** Late Coniacian or early Santonian age.

**Occurrence.** Żeliszów locality.

**Material studied.** K2951; The material is housed in the National Museum Prague.

Staminate flower of Normapolles affinity  
Figure 8B-F

**Description.** The homogenous material consisting of three studied specimens from Żeliszów shows compound units, very probably fragments of larger inflorescences. The best preserved unit (Figure 8B) consists of three flowers, subtended by a massive bract. Length of each flower is 2.1-2.4 mm (Figure 8D). Each of the three flowers subtended by a small bract each consists of five oblanceolate (0.5–0.7 mm x 2.1–2.4 mm) that are fused in their very basal parts (Figure 8D, E). The androecium of

the flowers consists of several, probably five stamens. The stamens are preserved as basal parts of filaments. Each filament is covered by dense indumentum consisting of long unicellular trichomes. Trichomes occur also on external surfaces of tepals (Figure 8F), but in lower density. A loose fragment of an anther adhering to an inner part of one tepal in one flower (Figure 8B) shows pollen of *Oculipollis* type (Figure 8C).

**Remarks.** Absence of the gynoecium in the studied flowers suggests their possible dioecious character. Free oblanceolate tepals fused only in basal parts and flowers arranged in compound inflorescences recall in some way the genus *Endressianthus* Friis et al., described from the Campanian–Maastrichtian of Portugal (Friis et al., 2003). However, the studied material differs from *Endressianthus* in having longer tepals and bearing a different pollen type found in situ.

**Range.** Late Coniacian or early Santonian age.

**Occurrence.** Żeliszów locality.

**Material studied.** K 2949, K2950, K 2952, K 2961; the material is housed in the National Museum Prague.

Kingdom OPISTHOKONTA Cavalier-Smith, 1987  
Subkingdom ANIMALIA Linné, 1758  
Phylum ARTHROPODA von Siebold, 1848  
Class INSECTA Linné, 1758  
Insect coprolite  
Figure 10A-C

**Description and remarks.** The single specimen from Rakowice Małe is of ellipsoid shape (Figure 10A) and hexagonal in transverse section (Figure 10B). Length 0.7 mm; breadth 0.4 mm. Surface of the fossil is smooth. No inner structures documented from this fossil (Figure 10C). Fossil faecal pellets, also called coprolites, are associated with many Cretaceous mesofloras (Colin et al., 2011; Knobloch, 1971, 1977; Vangerow, 1954). Affinity of fossil insect coprolites traditionally assigned to *Microcarpolithes hexagonalis* Vangerow to recent *Kaloterms* (Isoptera) has been suggested by Colin et al. (2011).

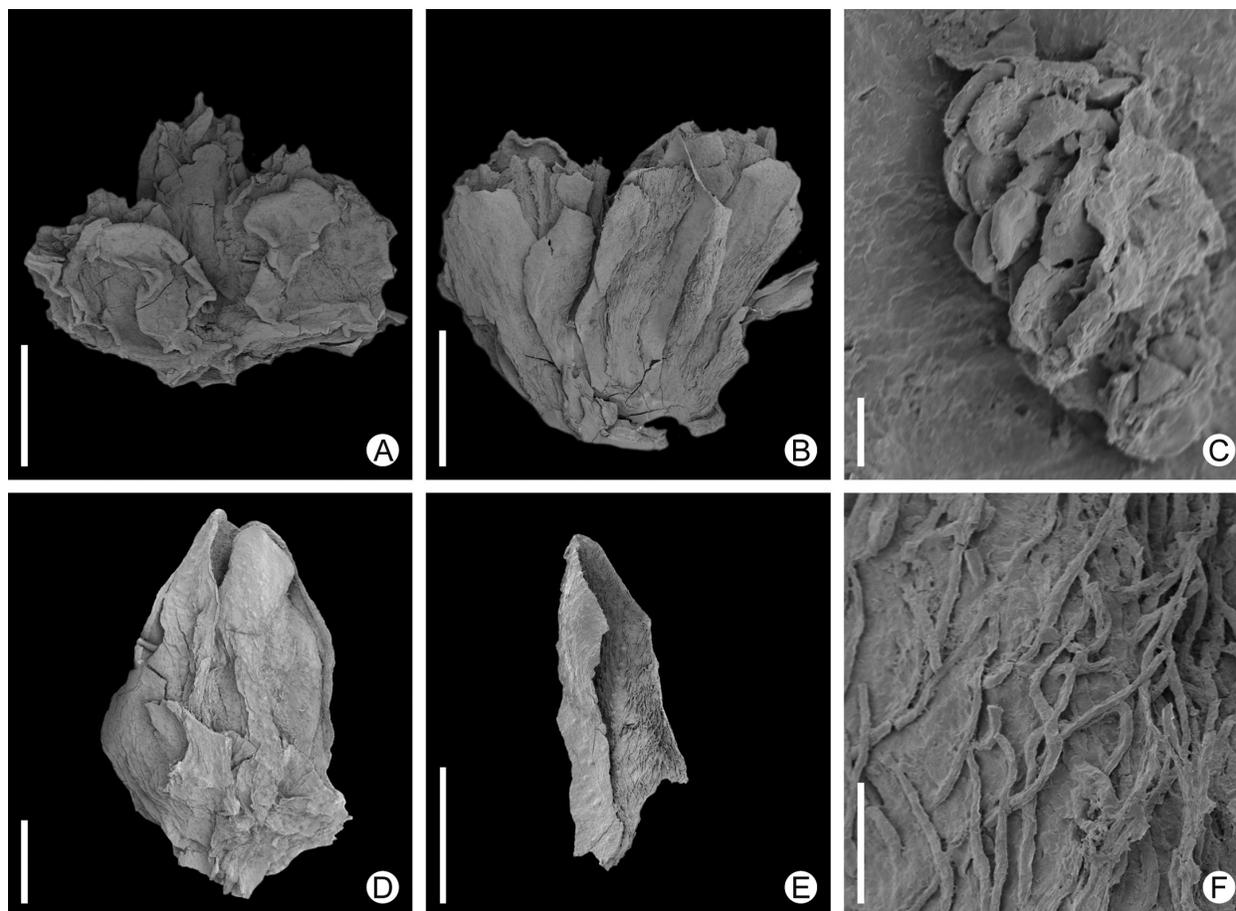
**Range.** Late Coniacian or early Santonian age.

**Occurrence.** Rakowice Małe locality.

**Material studied.** K2768; the material is housed in the National Museum Prague.

Kingdom, Phylum/Division, Class INCERTAE  
SEDIS  
Genus COSTATHECA Hall, 1967

**Type species.** *Chrysotheca diskoensis* Miner, 1935, p. 590, pl. 18, figs. 1-10 = *Costathea diskoensis* (Miner) Hall, 1967, p. 1298, figs. 1-3.



**FIGURE 8.** Inflorescence of Normapolles Complex (A) inflorescence formed by three pistillate flowers, no. K2951, scale bar 1 mm (B) inflorescence formed by three staminate flowers, no. K2950, scale bar 1 mm (C) detail showing pollen, no. K2950, scale bar 100  $\mu$ m; (D) isolated staminate flower showing basal parts of five tepals (terminal part of one tepal removed), no. K2961, scale bar 0.5 mm (E) removed tepal from the specimen figured on image 8D, no. K2961 scale bar 0.5 mm (F) detail of indumentum from the specimen figured on image 8D, no. K2961 scale bar 50  $\mu$ m. All specimens from  $\dot{Z}$ eliszów locality.

**Remarks.** The studied material shows typical parallel ribs and transversely orientated wrinkles - characters typical for the genus *Costatheca* (Batten and Zavattieri, 1996, 1995; Knobloch, 1981).

*Costatheca striata* (Dijkstra 1949) Hall, 1967  
Figure 10D, E

- 1949 *Chrysotheca striata* Dijkstra, p. 26, pl. 2, fig. 7.  
1967 *Costatheca striata* (Dijkstra) Hall, p. 1298  
1983 *Costatheca striata* (Dijkstra) Hall, Binda and Nambudiri, p. 2721, figs. 10, 12 (emended diagnosis).

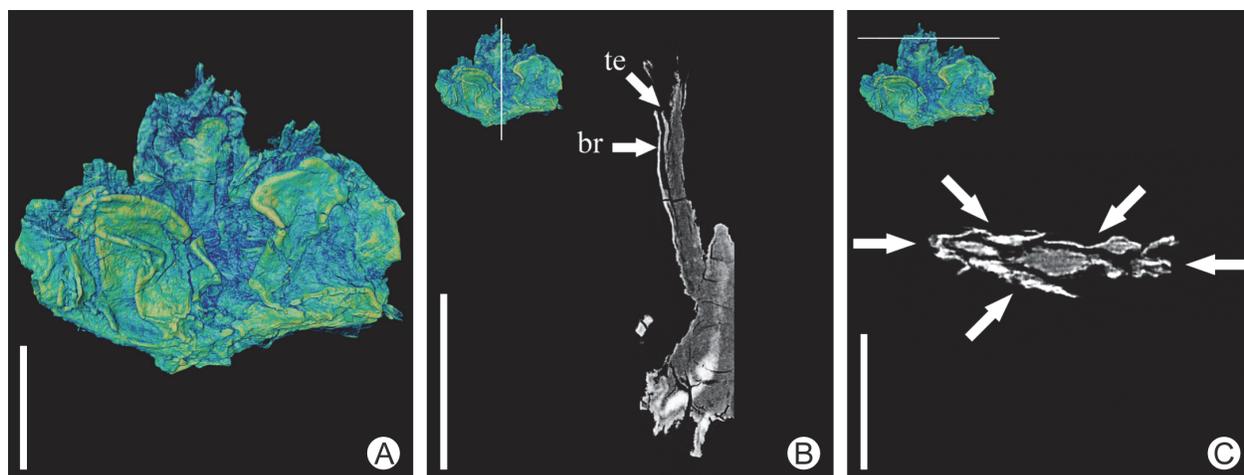
For a more extensive synonymy see (Batten and Zavattieri, 1996, 1995).

**Lectotype.** Sample/slide 738-9. Maurits State Mine selected by Batten (1988, pl. 19, fig. 30).

**Description.** Elongate bodies, 2.2–2.5 mm long and 0.6–0.8 mm broad (Figure 10D, E); ends slightly S-shape curved. A more complete speci-

men shows a scar (Figure 10E) that may represent the structure termed “operculum” by Batten and Zavattieri (1995). About ten ribs running parallel to the longitudinal axis, and less pronounced perpendicular structures resembling striation caused by thickly cutinised cells.

**Remarks.** According to Knobloch (1981), *C. diskoensis* shows a large variability in terms of size, shape and number of ribs. This opinion was questioned by Batten (1988), who studied the type material from Greenland, and who distinguished the specimens grouped by Knobloch into a separate species of *Costatheca*. Following Batten (1988), we assigned the studied material to *C. striata* (Dijkstra) Hall from the Santonian of Limburg (Dijkstra, 1949). *C. striata* was described from the Santonian of Limburg. This species differs from most species of *Costatheca* in having perpendicular striations. *C. lata* (Vangerov) Hall from the San-



**FIGURE 9.** Flower of *Normapolles* affinity; X-ray pictures; specimen no. K2951. (A) inflorescence of three flowers; scale bar 1 mm. (B) Cross section through one flower, showing bract (br) and tepal (te) and documenting the epigynous nature of the flower; scale bar 1 mm. (C) Perianth of each flower consisting of five tepals (arrowed); scale bar 1 mm. Locality Żeliszów.

tonian of Aachen (Vangerow, 1954) differs from *C. striata* in having relatively low length/width ratio (Kovach and Dilcher, 1988). It is not clear what *Costatheca* represents. It could be an insect egg as suggested by Tiffney (1983) and Batten and Zavattieri (1995), whereas Binda and Nambudiri (1983) assumed that *Costatheca* could be related to the seeds of angiosperms of the Butomaceae family.

**Range.** Late Coniacian or early Santonian age.

**Occurrence.** Żeliszów locality.

**Material studied.** K 3010, K 3011; the material is housed in the National Museum Prague.

## DISCUSSION

Generally, Late Cretaceous mesofossil floras from central Europe are dominated by fruits of the *Normapolles* complex (Table 1). However, both localities studied herein show relatively low diversity of reproductive structures compared with other European Late Cretaceous assemblages (Knobloch and Mai, 1986). With a total of 11 taxa from Rakowice Małe and seven from Żeliszów, these assemblages belong to the smallest mesofloras in Central Europe.

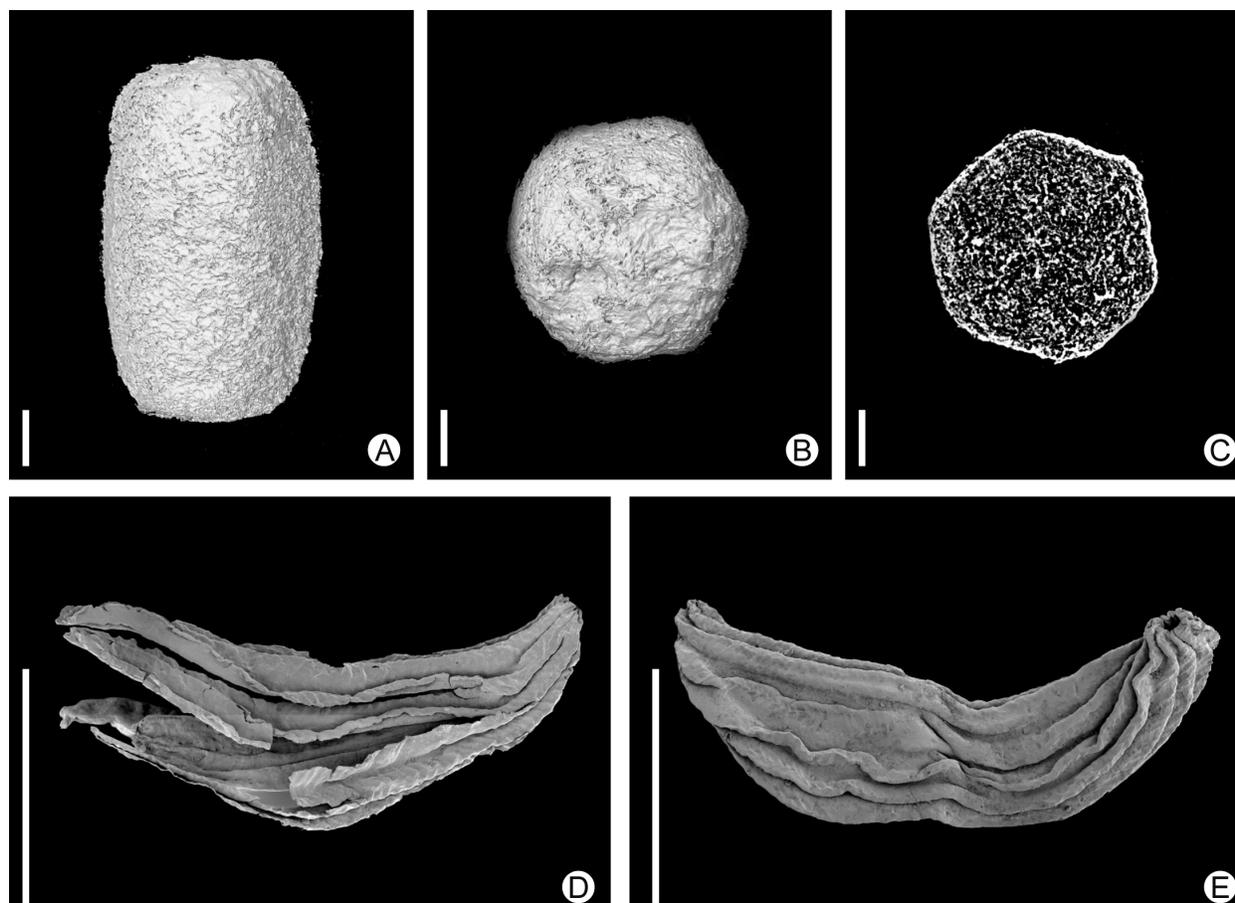
Sixteen taxa of mesofossils are described and figured in this paper: one species of megaspores, two species of conifer twigs, two conifer seeds, eight angiosperm reproductive structures, a single species of *Costatheca* (problematic, probably insect egg), and one type of insect coprolite. Additionally, there are two taxa *Calathiocarpus octocostatus* (Knobloch) Knobloch et Mai and

*Walbeckia guttaeformis* (Knobloch) Knobloch et Mai that should be mentioned: that material was not found in the collections, but was properly described and documented by Knobloch and Mai (1986); we, therefore, consider these two species to be part of the Lower Silesian Late Cretaceous mesoflora. *Calathiocarpus* is assigned to the *Normapolles* complex (Friis et al., 2011). The systematic position of genus *Walbeckia* was briefly discussed by Friis et al. (2006) as follows: the “fossil probably also belongs to *Normapolles* complex of plants based on close morphological and organizational similarity, however, so far no pollen has been observed.” We agree in supposing that this taxon may be related to the *Normapolles* complex.

Sediments of the two localities, Rakowice Małe and Żeliszów, contain different mesofloras, and so represent rather different vegetation types:

- The Rakowice Małe mesoflora has a prevalence of fossil fruits of the *Normapolles* complex, representing alluvial plain and upland vegetation, similarly to the Turonian–Santonian flora from the South Bohemian Basins, described in detail by Knobloch and Mai (1986).
- The Żeliszów mesoflora is rich in conifer remains, representing swamp/wetland vegetation, with *Geinitzia* twigs and *Seletya kristofovichii* seeds, similarly to the Santonian mesoflora of Quedlinburg (Knobloch and Mai, 1986; Kunzmann, 1999).

The terrestrial flora, the source of the mesofossils described herein (Rakowice Małe assem-



**FIGURE 10.** Insect remains (A) insect coprolite no. K2768 (A) coprolithes lateral view, no. K2768, scale bar 0.1 mm, Rakowice Małe locality (B) coprolite apical view, hexagonal in outline, no. K2768, scale bar 0.1 mm, Rakowice Małe locality (C) X-ray image, cross section, no. K2768, scale bar 0.1 mm, Rakowice Małe locality. (D) *Costatheca striata* no. K3010 scale bar 1 mm, Żeliszów locality (E) *Costatheca striata* showing “operculum” no. K3011 scale bar 1 mm, Żeliszów locality.

blage as well as Żeliszów mesoflora), grew on the East Sudetic Island, one of those forming the European Archipelago on the seaway between the Northern Ocean and the Tethys in the south (Csiki-Sava et al., 2015; Leszczyński, 2018). The Coniacian–Santonian vegetation of the East Sudetic Island, characterised on the basis of angiosperm-dominated mega- and mesofossil assemblages and of fern-dominated palynoassemblages (Halamski et al., 2020), consisted of several communities, among which back swamps and several variants of riparian forests are of interest herein as possible sources of mesofossils. Important megafossil taxa include the conifer *Geinitzia*, three species of the presumed basal eudicot *Dewalquea*, the fagalean *Dryophyllum*, and platanoids.

Halamski et al. (2020) distinguished eight Late Cretaceous megafossil assemblages in the North Sudetic Basin. The Assemblage 5 corresponds to the upper (coaly) portion of the Nowogrodziec Mb.,

which is the only part of the stratigraphic sequence that yielded any mesoflora. The upper portion of the Nowogrodziec Mb. has also yielded one of the two palynological assemblages studied by Halamski et al. (2020), termed Palynoassemblage A. However, plant megafossils from the Assemblage 5 are interpreted to have originated from a conifer swamp forest. The Normapolles mesofossils were produced by plants growing in communities more alike those recorded as megafossils in the slightly younger Assemblages 6 and 8 (Czerna Fm., unnamed member, lower–middle Santonian). The latter are interpreted as recording variants of riparian forests.

The Rakowice Małe mesoflora is similar to the South Bohemian flora in dominance of Normapolles complex. However, flowers and fruits of Normapolles complex are present in the South Bohemian flora in significantly greater amounts, both in terms of specimens and of taxa and other

**TABLE 1.** List of the taxa found on the localities Rakowice Małe and Żeliszów.

Taxon	Found at locality Rakowice Małe in 1986	Found at locality Rakowice Małe in 2017	Found at locality Żeliszów in 2019
<i>Ricinospora</i> sp.		X	
<i>Cunninghamites</i> cf. <i>squamosus</i>			X
<i>Alapaja</i> sp.			X
<i>Seletya</i> sp.			X
<i>Geinitzia formosa</i> Heer 1871			X
<i>Calathiocarpus octocostatus</i>	X		
<i>Caryanthus communis</i>	X		
<i>Caryanthus trebecensis</i>	X		
<i>Caryanthus triasseris</i>	X		
<i>Caryanthus</i> sp.	X		
<i>Walbeckia guttaeformis</i>	X		
<i>Zlivifructus vachae</i>	X		
<i>Zlivifructus microtriasseris</i>	X		
Fruit of Normapolles affinity	X		
Flower of Normapolles affinity			X
Staminate flower of Normapolles affinity			X
Insect coprolite	X		
<i>Costatheca striata</i>			X

angiosperm groups (platanoids, ericoids) also show high diversity there. The Rakowice Małe mesoflora is also similar to the Aachen Santonian mesoflora, with which it shares three genera: *Caryanthus*, *Calathiocarpus*, and *Walbeckia* (Knobloch and Mai, 1986). It also shares two genera, *Caryanthus* (*C. triasseris*) and *Calathiocarpus*, with the Santonian mesoflora of the German locality Walbeck from the foothills of the Vosges (Vogesen) mountains. There are additional minor findings of reproductive organs from Carpathian flysch sediments in southern Poland (Turonian - Santonian) that also show “Normapolles nuts” similar to those from Rakowice Małe, for example, *Caryanthus communis* and *Caryanthus deltoides* as well as insect eggs *Knoblochia cretacea* from Rabka Zaryte (Heřmanová et al., 2013). However, flysch sediments are sedimentologically different from the sediments bearing the flora of Rakowice Małe.

In the Nowogrodziec Member of the Czerna Formation in Lower Silesia, palynological studies by M. Svobodová and E. Durska in Halamski et al. (2020) showed that the palaeoassemblage was dominated by fern spores and pollen grains of the Normapolles type. Our current study confirms this work by documenting the presence of a certain number of angiosperms of various genera that may have produced such pollen.

## CONCLUSIONS

Eighteen taxa of mesofossils are mentioned in this paper. One species of megaspore, two species of conifer twigs, two conifer seeds, 10 angiosperm reproductive structures related to the Normapolles complex, one species of *Costatheca* (problematic, probably insect egg), and one type of insect coprolite. The material investigated herein comes from two localities, Rakowice Małe and Żeliszów (Lower Silesia). The Rakowice Małe mesoflora has a prevalence of fruit fossils of the Normapolles complex, representing alluvial plain and upland vegetation. The Żeliszów mesoflora is rich in conifer remains, representing swamp/wetland vegetation, with *Geinitzia* twigs and *Seletya kristofovichii* seeds.

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