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Palynomorphs of the Normapolles group and related plant mesofossils from the Iharkút vertebrate site, Bakony Mountains (Hungary)

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Palynological and paleobotanical investigation of bonebeds and other strata of the Csehbánya Formation from the vertebrate locality at Iharkút (Bakony Mts, Hungary) reveals well-preserved Santonian palynological assemblages dominated by the Normapolles group, with a minor component consisting of other angiosperm pollen, some gymnosperm pollen, and spores. Eleven species of Normapolles-type pollen grains belonging to seven genera and fruit remains of a new taxon, *Sphaeracostata barbackae* gen. et sp. nov., are described. The new species is very abundant in the material, represented by ca. 1000 specimens. The genus *Caryanthus* Friis and an unnamed form previously reported from Hařteg by Lindfors et al. (2010) are also present.

Plants producing Normapolles-type pollen grains diversified during the Late Cretaceous, with a bloom in the Santonian. The palynostratigraphy of the Upper Cretaceous terrestrial sediments in the studied region is based on Normapolles-related species. The studied assemblage is assigned to the *Oculopollis zaklinskaiae-Tetracolporopollenites (Brecolpites) globosus* Zone (or Zone C) indicating a late Santonian age. Comparison of the Iharkút palynoflora with other known Upper Cretaceous palynofloras of Central Europe shows diachronous occurrence of Normapolles taxa at different geographic localities and warrants further investigation.

The ecological requirements of the amphibian fauna reflect azonal conditions controlled by the availability of water, which is in agreement with the inferred ecological conditions based on the paleobotanical investigations. The fauna is of entirely non-marine character, further supported by isotope studies, in line with our data showing that the palynological samples contain no marine forms.

Key words: palynomorphs, mesofossils, Normapolles, Santonian, Iharkút, Hungary

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Introduction

Numerous well-preserved plant remains have been discovered in Upper Cretaceous fluvial sedimentary rocks (Csehbánya Formation) at the Iharkút vertebrate locality (Bakony Mts, Hungary) (Fig. 1). The palynoflora of Iharkút is an angiosperm-dominated assemblage, which provides a unique insight into the Normapolles group, because the palynomorphs appear together with plant mesofossils and macro remains. Normapolles-related pollen grains are important elements of the Late Cretaceous and Paleogene palynofloras. They are mainly abundant within the Normapolles floristic province (eastern North America, Europe and Asia) (Batten 1981, 1982; Batten and Christopher 1981; Zaklinskaya 1981; Schönenberger et al. 2001). The Normapolles group first appeared in the middle Cenomanian and diversified rapidly, reaching its highest diversity during the Late Cretaceous, and became extinct by the end of the Eocene (Góczán et al. 1967; Pacltová 1981; Friis 1983; Sims et al. 1999).

The possible botanical affinities of the Normapolles genera are still being discussed, but several suggestions have been put forward. It has been proposed that some of the genera are related to the modern Juglandales (Juglandaceae, Rhoipteleaceae); others may be related to the Betulales, Urticales, Casuarinales, Myricales, Myrtales, Sapindales and Santalales (Kruttsch 1959; Góczán et al. 1967; Zaklinskaya 1967, 1981; Stanley and Kedves 1975; Friis 1983; Friis 1984; Skarby 1986; Crane et al. 1996; Takahasi 1997; Sims et al. 1999; Schönenberger et al. 2001; Friis et al. 2003; Friis et al. 2006).

The presence of the different Normapolles taxa in the assemblages, with their high diversity and rapid evolution during the Late Cretaceous, makes this group stratigraphically important. In the Central European-Carpathian region, Góczán (1963, 1964) and Góczán and Siegl-Farkas (1990) proposed a palynological zonation, which was later integrated with the Tethyan nannoplankton zones by Siegl-Farkas and Wägrich (1996). The palynoflora of the Csehbánya Formation is known from borehole material (Góczán 1964; Góczán and Siegl-Farkas 1990; Siegl-Farkas 1993; Lantos et al. 1996) but the palynological assemblages and the plant mesofossils from the Iharkút site have not been previously investigated.

Angiosperm fruits and seeds from the Hungarian Upper Cretaceous have not been comprehensively studied so far. Some drill core samples were examined by Knobloch and Mai (1986) and by Rákosi (1991) who reported mainly Magnoliaceae carpolites and lacustrine plant macrospores. The megaspores of the Ajka Coal Formation were studied by Rákosi and Barbacka (1999–2000).

The purpose of this study is to describe the Normapolles-related pollen taxa and to compare them with the angiosperm mesofossils from the same interval, and to compare our material to that of the Knobloch Collection. We also attempt to contribute to the paleoenvironmental reconstruction of this important vertebrate locality and, based on the palynomorphs, provide a more precise stratigraphic age of the bonebed.

Geologic setting

The vertebrate locality is exposed at the abandoned Iharkút open-pit bauxite mine near the villages of Bakonyjákó and Németsbánya, in the northern part of the Bakony Mountains, in western Hungary (Fig. 1). The Csehbánya Formation (Jocha-Edelényi in Császár 1997) is a floodplain and channel deposit composed of variegated clay, silt with interbedded grey and brown sand, and sandstone beds (Bodrogi et al. 1988; Jocha-Edelényi 1988). The formation has an average thickness of 50 m at Iharkút. In the upper part of the section an approximately 2 m-thick layer yielded most of the vertebrate fossils (marked as Bed 6 in Fig. 1). The bone-yielding beds consist of sand, silt, and clay pebbles with fragmentary bones (Tuba et al. 2006; Ósi and Mindszenty 2009).

Fig. 1
Sketch map of the studied locality at Iharkút



A large number of vertebrate remains were collected during the last 10 years, including thousands of fish (Makádi et al. 2006; Ósi et al. 2012), frogs and other amphibians (Szentesi and Venczel 2010, 2012), turtles (Ósi et al. 2012; Rabi et al. 2011), lepidosaurs (Makádi 2006; Ósi et al. 2012), crocodiles (Ósi and Rabi 2006; Ósi et al. 2007), birds (Ósi 2008; Dyke and Ósi, in press) together with a range of bones and teeth fragments. Significantly, new dinosaur species – *Hungarosaurus*

tormai (Ősi 2005), *Ajkaceratops kozmai* (Ősi et al. 2010) – and a new pterosaur (*Bakonydraco galaczi*; Ősi et al. 2005) were also described from the locality. Isotope geochemical and osteology investigation of the fossils suggests a freshwater habitat for the fauna (Kocsis et al. 2009; Makádi et al. 2012).

Materials and methods

Palynomorphs

Fifteen samples from 11 layers were analyzed in this study (Fig. 2). Processing of palynological samples was carried out at the Pollen Laboratory of the Hungarian Geological Institute in Budapest. The palynological processing involved washing of samples, acid treatment with 36% HCl and 40% HF. A ZnCl₂ solution of 2.2 g/cm³ density was used for gravity separation. Only one sample needed oxidation with KOH (30%). The residues were mounted in glycerin jelly. In total 28 palynological slides were prepared. The slides were investigated using

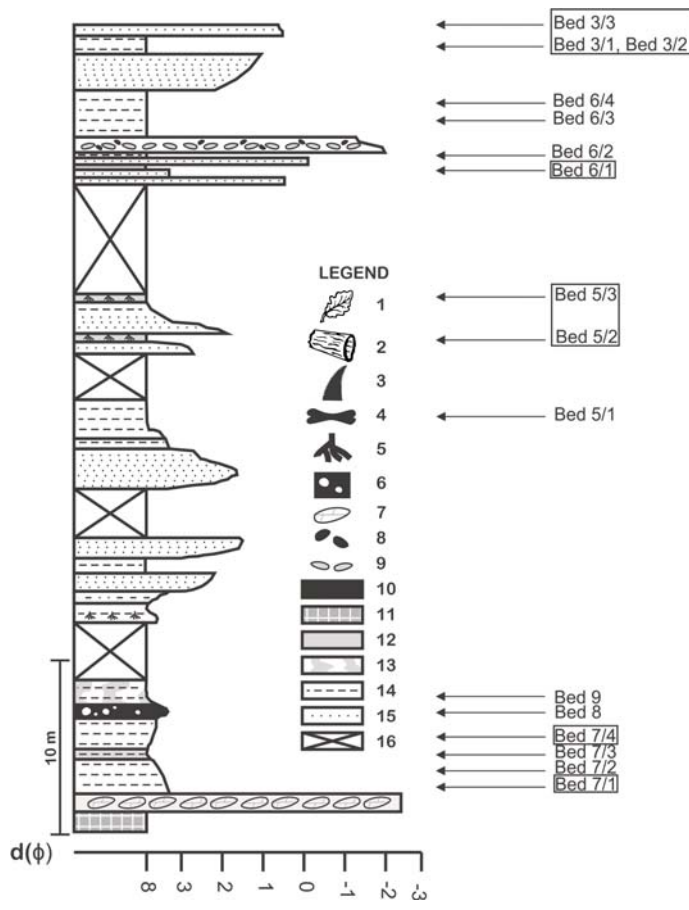


Fig. 2
Stratigraphic column of the Iharkút section with palynological sampling levels. Grain size is given in Krumbain Phi (ϕ) logarithmic scale, which transforms the particle diameter in millimetres by taking their negative logarithm in base 2. Legend: 1. plant macrofossils (mainly leaves); 2. tree trunks and branch fossils; 3. teeth; 4. bones and partial skeleton; 5. root traces; 6. amber; 7. breccia; 8. fibrous coal; 9. mud clasts; 10. coal; 11. bauxite; 12. grey clay; 13. variegated clay; 14. clay; 15. sandstone; 16. covered part of section

a Nikon Eclipse E600 transmitted-light microscope. Light microscope images were taken using a 40× objective and a 100× oil objective, equipped with a QImaging MicroPublisher 3.3 RTV camera. Scanning electron microscopy was carried out at the Department of Plant Anatomy, Eötvös Loránd University, using a Hitachi S-2360N microscope and at the Department of Botany, Hungarian Natural History Museum, using a S-2660N microscope. The palynological samples were mounted on aluminium stubs and sputter coated with Au-Pd using a Polaron SC7520 Mini Sputter Coater. The diversity and the absolute abundance of different palynomorph types were determined by counting 100 specimens in each slide, when it was possible. Stratigraphic diagrams were plotted using C2 software, version 1.5 (Juggins 2007).

The palynological samples are deposited in the collection of the Hungarian Natural History Museum.

Mesofossils

The fluvial clay, sand and bone-bed layers of the Csehbánya Formation yielded a diverse assemblage of small, three-dimensionally preserved angiosperm reproductive structures, including fruits and seeds. The studied mesofossils were extracted from the sediments by sieving. The dry sediment was washed at the site using 2.00 mm, 1.00 mm and 0.32 mm mesh sizes.

The bonebed (Bed 6 in Fig. 2) is the level sampled with highest resolution as it is the host rock of the vertebrate remains. The plant remains were recovered during the search for microvertebrates.

The seeds encountered in our study are black and coalified. SiO₂ grains often adhere to the surface of the seeds but were removed with 40% HF. The specimens are stored in Eppendorf tubes. The unfilled specimens enabled the study of the inner structure of the seeds and fruits. Additionally, SEM studies were carried out on distinct specimens. For the mesofossil determination the material of the Knobloch Collection was used for comparison.

To study the internal structure, the fruits were oriented and placed on two-sided adhesive tape. Subsequently, a 0.5 cm-high plastic tube section was placed on the fruit. This tube was filled with a 2:1 araldite two-component epoxy-type glue mixture, dried for 24 hours, and finally polished with size 320 and size 1000 polishing powder until the middle section was reached. The section was studied using a Carl Zeiss Jena 477460 microscope. Photographs were taken with an Olympus E-500 DSLR camera.

A multivariate data analytical method, nonmetric multidimensional scaling (NMDS), was carried out on 40 whole *Sphaeracostata* specimens to evaluate whether the genus is represented by one or more species in our material. Dimensions, the number, trend, and surface of the ribs, reticulation of the surface, and cellular structures were entered into the data matrix. For analysis of such a mixed scale-type dataset the NMDS with Gower's formulae is the most suitable method (Podani 2001).

Normapolles-related microfossils and mesofossils

Systematic palynology

The palynological assemblage is well preserved, dominated by Normapolles. Other groups such as non-Normapolles angiosperms, gymnosperms (conifers, cycads, Bennettitales), ferns and mosses formed only minor constituents of the assemblages. This study focuses on the Normapolles group. Here we describe eleven species belonging to seven genera. No marine palynomorph could be identified. In this chapter the description of the Normapolles-related key pollen taxa with their known stratigraphic range is provided. Coordinate readings from the Nikon Eclipse E600 microscope of a few examples of the studied specimens are given.

Genus *Oculopollis* Pflug 1953

Oculopollis zaklinskaiae Góczán 1964

Plate 1, figures a–b.

1964. *Oculopollis zaklinskaiae* n. sp. Góczán – p. 246. pl. VI. figs 6a–b.
1976. *Oculopollis zaklinskaiae* Góczán; Andrusov and Snopková – p. 239. pl. III. fig. 3.
1981. *Bohemiapollis* sp. Pacltová – p. 196. pl. X. figs 1-1c.
1988. *Oculopollis zaklinskaiae* Góczán; Siegl-Farkas – p. 205. pl. VII. fig. 3.
1990. *Oculopollis* sp. D Góczán and Siegl-Farkas – p. 367. pl. I. fig. 3.
1990. *Oculopollis* sp. B Góczán and Siegl-Farkas – p. 367. pl. I. fig. 14.
1990. *Oculopollis zaklinskaiae* Góczán; Góczán and Siegl-Farkas – p. 369. pl. III. fig. 2.
1999. *Oculopollis orbicularis* Góczán; Hradecká et al. – p. 515. pl. 10. fig. 27.
1999. *Oculopollis zaklinskaiae* Góczán; Hradecká et al. – p. 515. pl. 10. figs 21–23, fig. 25.

Samples and microscope coordinates: Bed 8: 95/34; 94.5/34.5; 95/39; 95/45; 96/40.5; 98.5/39; 99/31.5; 99.5/48.5; 100.5/; 103/49; 103/41; 110/43.5; 111/37; 114/39. Bed 5/1: 40/92.5; 92/23; 93/34

Material: Well-preserved, yellowish to light brown-colored pollen grains with different grades of coalification.

Dimensions: 15–20 μm in diameter, excluding the length of oculi (based on 17 specimens).

Description: The pollen grain is triporate. The equatorial outline is triangular. The corpus is spheroidal to subspheroidal. The exine consists of two wall layers. No interloclum is visible between the wall layers. The nexine is much thinner than the sexine and their combined thickness is ca. 2–3 μm . The surface of the exine is smooth to verrucate in light microscope. The three protruding oculi are equally developed on both surfaces (on the proximal and distal side). The oculi are oval; they extend up to the center of the corpus. Size of the oculi is variable (5–15 μm). Vestibulum is broad. The endanulus can be split up along the endopore.

Remarks: The Iharkút specimens above show slightly more variety in size compared to the original description but we consider them to fall within

Oculopollis zaklinskaiae based on the germinals (oculi, anulus, oculi extend to center) and outline. The size is a less characteristic diagnostic feature of this species. Góczán (1964) described only large forms (size between 42–53 μm) as *O. zaklinskaiae*, but all of the observed specimens are slightly smaller than the holotype (53 μm in diameter). The biggest forms in the samples are characterized by large oculi (size range is 13–15 μm) and larger corpus diameter (over 20 μm). Small forms with characteristic protruding oculi occur as well. These specimens could be described as *O. orbicularis* based on the size, but the patterns of oculi, endanulus and outline differentiate them from *O. orbicularis* or other *Oculopollis* species.

Pacltová (1981) provided a photograph of a large, smooth-walled pollen grain, with large protruding oculi extending up to centre of the corpus. She described this form as *Bohemiapollis* sp., although according to Góczán (1964) this form is *Oculopollis zaklinskaiae*.

Pavlishina (1999) described *O. zaklinskaiae* from the lower Santonian of northern Bulgaria. On the illustration the protruding, large oculi that extend to the center of the corpus are not observable. Portniagina (1971) and Andrusov and Snopková (1976) mentioned this species from the Carpathians. The comparison is difficult in these cases because of the different microscope settings. Pavlishina et al. (2004) mentioned *O. sp. B* Góczán and Siegl-Farkas from the lower part of the upper Santonian from the Gosau Basin, but no systematic description or illustrations were presented. In the present work *O. sp. B* documented in Góczán and Siegl-Farkas (1990, p. 367 pl. I. fig. 14) is related to the species *O. zaklinskaiae* based on comparisons with those described in Góczán and Siegl-Farkas (1990).

Stratigraphic distribution: Lower Santonian of northern Bulgaria (Pavlishina 1999); lower Santonian of the Northern Calcareous Alps (Hradecká et al. 1999); Santonian of southern Bohemia (Pacltová 1977, 1981); upper Santonian of the Transdanubian Range (Góczán 1964; Siegl-Farkas 1987, 1993, 1999); Santonian – lower Campanian of the Carpathians (Andrusov and Snopková 1976), lower Campanian of the Klippenbelt in the Carpathians (Portniagina 1971).

Oculopollis orbicularis Góczán 1964
Plate 1, figure c, Plate 2, figure a–c

1964. *Oculopollis orbicularis* n. sp. Góczán – p. 246. pl. VI. figs 1–5.

1976. *Oculopollis orbicularis* Góczán; Andrusov and Snopková – p. 235. pl. I. fig. 4.

1999. *Oculopollis orbicularis* Góczán; Siegl-Farkas – p. 185. pl. III. fig. 2.

Samples and microscope coordinates: Bed 8: 100/44. Bed 5/1: 91.5/23; 91.5/27; 92/39; 101/36.5; 104.5/35; 107/44; 110/42.5. Bed 9: 96/41.5. SEM tracer/1.

Material: Well to moderately preserved. yellowish to light brown-colored pollen grains with different grades of coalification.

Dimensions: 10–15 μm in diameter excluding the length of oculi (based on 10 specimens).

Description: The pollen grain is triporate. The equatorial outline is triangular. The corpus is spheroidal. Size of the pollen grains is generally small (diameter ~20–25 μm including the length of the oculi). The exine is multilayered; interloculum is not clearly visible. Surface of the exine is granulate. The oculi are developed both on the proximal and distal side of the pollen grain. They never extend up to center of the corpus and over the equatorial outline. Their length is c. 5 μm .

Remarks: *Oculopollis orbicularis* is generally smaller than *O. zaklinskaiae* in all investigated samples and differs further in orientation and size of oculi. Oculi of *O. orbicularis* never extend up to the center and the surface of these specimens is always strongly sculptured. Surface of *O. orbicularis* is granulate, contrary to *O. zaklinskaiae* which is smooth to verrucate. Interloculum can be observed in *O. orbicularis* contrary to *O. zaklinskaiae*.

Stratigraphic distribution: Upper Santonian–Campanian of the Transdanubian Range, Hungary (Góczán 1964; Siegl-Farkas 1987, 1993, 1999); northeastern Spain, southern France (Médus 1972); lower Santonian–lower Campanian of northern Bulgaria (Pavlishina 1999), Santonian of the Northern Calcareous Alps (Hradecká et al. 1999; Pavlishina et al. 2004), Santonian–lower Campanian of Romania (Mogoş 1992); lower Campanian of the Klippenbelt in the Carpathians (Portniagina 1971).

Oculopollis parvoculus Góczán 1964

Plate 1, figure d

1964. *Oculopollis parvoculus* n. sp. Góczán – p. 246. pl. VI. fig. 9a–c.

1999. *Oculopollis parvoculus* Góczán; Siegl-Farkas – p. 186. pl. IV. fig. 8.

Samples and microscope coordinates: Bed 8: 94.5/42; 99/47. Bed 5/1: 109/44; 93/35; 108.5/36. Bed 9:109/53

Material: Well-preserved, yellowish, greenish to light brown-colored pollen grains with low grade of coalification.

Dimensions: 10–15 μm in diameter excluding the length of oculi (based on six specimens).

Description: The pollen grain is triporate. The equatorial outline is triangular with convex sides. The inner outline is club-shaped. The exine has two layers; their combined thickness is about 2–3 μm . The surface of corpus is punctate. The oculi are visible on both surfaces, but they are short and not well developed. The atrium is broad. Size of the grains is variable (diameter 25–40 μm including the length of the oculi).

Remarks: *Oculopollis parvoculus* is a transitional form between species of *Oculopollis* and *Trudopollis* (Góczán 1964). The germinal area of *Trudopollis* is less developed than that of *O. parvoculus*; surface ornamentation, inner contour and equatorial outline of the two forms can be very similar. Oculi of *O. parvoculus* are faintly developed. Interloculum can be observed both in *O. orbicularis* and in *O. parvoculus*.

Stratigraphic distribution: Lower part of upper Santonian of the Gosau Basin, Austria (Siegl-Farkas 1994); Santonian–lower Campanian of the Carpathians (Andrusov and Snopková 1976); upper Santonian of the Transdanubian Range, Hungary (Góczán 1964; Siegl-Farkas 1987, 1993, 1999).

Laudaypollis Góczán 1964
Laudaypollis clarus Góczán 1964
Plate 1, figure f

1964. *Laudaypollis clarus* n. sp. Góczán – p. 257. pl. IX. figs 17a–c.
1967. *Laudaypollis clarus* Góczán; Góczán et al. – p. 548. pl. IX. figs 1–5.
1988. *Laudaypollis clarus* Góczán; Siegl-Farkas – p. 203. pl. VI. figs 10–11.
1990. *Laudaypollis* sp. Góczán and Siegl-Farkas – p. 367. pl. I. figs 15–16.

Samples and microscope coordinates: Bed 5/1: 99/25; 110.5/26.5. Bed 6/3: 95/22.5

Material: Well-preserved, yellowish-light green-colored pollen grains.

Dimensions: Length is ~20 µm (based on two specimens).

Description: The pollen grain is diporate. The equatorial outline is bipolar, ellipsoidal. The exine is thin, less than 1 µm in thickness, and the surface is punctate.

Remarks: Only two specimens were identified in the studied samples. They differ from other Normapolles genera in having two germinals, and in their bipolar, ellipsoidal shape.

Stratigraphic distribution: Santonian (Transdanubian Range, Hungary, Góczán 1964; Siegl-Farkas 1999); early Santonian of the Northern Calcareous Alps (Siegl-Farkas 1994).

Complexiopollis Krutzsch 1959
Complexiopollis complicatus Góczán 1964
Plate 1, figure g, Plate 2, figure e–f

1964. *Complexiopollis complicatus* n. sp. Góczán – p. 244. pl. V. figs 8–9d.
1981. *Complexiopollis* sp. Pačtová – p. 188. pl. III. fig. 2.
1988. *Complexiopollis complicatus* Góczán; Siegl-Farkas – p. 199. pl. IV. figs 4–10.
1990. *Complexiopollis complicatus* Góczán; Góczán and Siegl-Farkas – p. 367. pl. I. figs 4–6, 11.

Samples and microscope coordinates: Bed 8: 94.5/39; 95/33.5; 101/34.5. Bed 5/1: 95/49; 96/49.5; 97/41; 101/41, SEM tracer 1.

Material: Well to moderately preserved, yellowish to brown pollen grains, in some cases extremely folded.

Dimensions: 10–20 µm in diameter (based on seven specimens).

Description: The pollen grain is triporate. The equatorial outline is triangular with convex to extremely concave sides. The corpus is spheroidal. The germinals are elongated and longer than the corpus diameter. The exine is multilayered. The surface of the exine is smooth to finely ornamented. Secondary folds on the

proximal side of the pollen grain are common. The endanulus can be split up along the endopore, forming a fissure.

Remarks: They differ from the other Normapolles genera in having elongated germinals, a smoother surface and secondary exine folds. No oculi or plicae are present. *C. labilis* is generally larger and its sides are extremely concave. The diameter of corpus is much smaller than the length of the germinals.

Stratigraphic distribution: Santonian of the Transdanubian Range, Hungary (Góczán 1964; Siegl-Farkas 1987, 1993, 1999).

Complexiopollis labilis (Góczán 1964)

Góczán and Krutzsch 1967 n. comb. in Góczán et al. 1967

Plate 1, figure h

1964. *Latipollis labilis* n. sp. Góczán – p. 244. pl. V. fig. 7.

Samples and microscope coordinates: Bed 5/1: 98/40, 95/32.5, 94.5/29.5

Material: Well to moderately preserved, yellowish to brown pollen grains, in some cases extremely folded.

Dimensions: 20–25 μm in diameter (based on three specimens).

Description: The pollen grain is triporate. The equatorial outline is triangular with extremely concave sides. Fragile forms with elongated and narrow germinals. The surface of the exine is smooth to finely ornamented. Secondary folds on the proximal side of the pollen grain are common. The endanulus can be split up along the endopore, forming a fissure.

Remarks: It differs from *Complexiopollis complicatus* in having a larger size and extremely concave sides and long, narrow germinals.

Stratigraphic distribution: Santonian of the Transdanubian Range, Hungary (Góczán 1964; Siegl-Farkas 1987, 1993, 1999).

Hungaropollis Góczán 1964

Hungaropollis krutzschi Góczán 1964

Plate 1, figure e

1964. *Hungaropollis krutzschi* n. sp. Góczán – p. 251. pl. VIII. figs 4–5.

1967. *Hungaropollis krutzschi* Góczán; Góczán et al. – p. 546. pl. VII. figs 7–16.

1988. *Hungaropollis krutzschi* Góczán; Siegl-Farkas – p. 207. pl. VIII. figs 5–6.

1983. *Hungaropollis krutzschi* Góczán; Kedves and Diniz – p. 345. pl. 2. figs 1–3.

1988. *Hungaropollis* sp. Siegl-Farkas – p. 207. pl. VIII. figs 7–8.

2002. *Hungaropollis krutzschi* Góczán; Siegl-Farkas and Haas – p. 170. pl. II. fig. 26.

Samples and microscope coordinates: Bed 8: 95/375; 99/48.5; 100/44. Bed 5/1: 94/29.5; 111/35; 104/26.5; Bed 9: 109/37

Material: Well-preserved, yellowish to light brown-colored pollen grains.

Dimensions: 40–50 μm in diameter (based on seven specimens).

Description: The pollen grain is triporate. The equatorial outline is triangular with convex sides and rounded angles. The inner contour is triangular with extremely rounded angles to circular. Exine is multilayered. The sexine is very thick, the nexine is thinner; it consists of three layers. Their combined thickness can reach 6–8 μm (up to 10 μm in the germinal region). The vestibulum is narrow. The surface of the exine is strongly sculptured in the central region of the proximal side. The ornamentation is verrucate. On the distal side no characteristic sculpture is visible.

Remarks: Only a few specimens of this genus occurred in the studied samples. They differ from other Normapolles genera in their large size, characteristic outline and ornamentation. No oculi, plicae or secondary folds are present. *Hungaropollis krutzschi* and other species of the genus are well known from the Upper Cretaceous of Hungary (Góczán 1964; Góczán et al. 1967; Góczán and Siegl-Farkas 1985, 1990, 1991; Kedves and Diniz 1983; Siegl-Farkas 1988; Siegl-Farkas and Haas 2002). The comparison with those pollen grains is not possible as they were not illustrated by Mogoş (1992).

Stratigraphic distribution: Upper Santonian of the Transdanubian Range, Hungary (Góczán 1964; Siegl-Farkas 1988, 1993, 1999), Santonian–lower Campanian of the Borod Basin, Romania (Mogoş 1992).

Schulzipollis Góczán 1967 in Góczán et al. 1967

Schulzipollis pannonicus n. sp. Góczán 1967 in Góczán et al. 1967

Plate 1, figure i

1967. *Schulzipollis pannonicus* n. sp. Góczán; Góczán et al. – p. 555. pl. XVI. figs 1–12.

1988. *Schulzipollis pannonicus* Góczán; Siegl-Farkas – p. 203. pl. VI. figs 6–7.

1990. *Schulzipollis pannonicus* Góczán; Góczán and Siegl-Farkas – p. 367. pl. I. figs 17–19.

1999. *Schulzipollis pannonicus* Góczán; Hradecká et al. – p. 515. pl. 10. figs 16–20.

Samples and microscope coordinates: Bed 5/1: 110/36.5; 98/40

Material: Well-preserved, yellow-green-colored pollen grains with low grade of coalification.

Dimensions: 20–25 μm in diameter (based on two specimens).

Description: The pollen grain is triporate. The equatorial outline is triangular with convex sides and slightly rounded angles. The exine consists of two wall layers. Interoculum is present. The surface of the exine is ornamented on both sides with granulae in varying intensity. On the proximal side a Y-shaped plica connects the three germinals over the corpus. In the germinal area there is a poorly developed annulus.

Remarks: *Schulzipollis* is a monospecific genus. Only two specimens were identified in the investigated samples. *S. pannonicus* differs from other Normapolles types in having plicae and an ornamented surface.

Stratigraphic distribution: Santonian of the Transdanubian Range, Hungary (Góczán et al. 1967); lower Santonian of the Northern Calcareous Alps (Hradecká et al. 1999; Siegl-Farkas 1994).

Verroculopollis Kedves and Diniz 1983

Verroculopollis sp.

Plate 1, figure j

Samples and microscope coordinates: Bed 5/1: 93/24.5; 101/40.5

Material: Moderately preserved, brown-colored pollen grains.

Dimensions: ~40 μm in diameter including the length of the oculi (based on two specimens).

Description: The pollen grain is triporate. The equatorial outline is triangular with convex sides. The corpus is spheroidal to subspheroidal. The exine consists of two wall layers. No interloculum is visible between the wall layers. The nexine is much thinner than the sexine; their combined thickness is about 5 μm in the extragerminal region. The surface of the exine is strongly verrucate. Vestibulum is broad. The three oculi are protruding, but their length is reduced. Oculi are developed on both proximal and distal side of the pollen grain. The rims of the oculi are undulating. The oculi are oval; they do not extend up to the centre of the corpus. Size of the oculi is 15 μm .

Remarks: The main feature of this genus is the undulating outline of the oculi and the strongly verrucate to rugulate surface. The genus *Verroculopollis* includes three species: *V. pflugii*, *V. tschudyi* and *V. skarbyae*. Both *V. pflugii* and *V. tschudyi* have long, well-developed, protruding oculi. *V. skarbyae* has similar characteristics to the studied specimens with reduced oculi; however, the ornamentation of the two forms differ. The size of sculptural elements of *V. skarbyae* is larger compared to our specimens. Based exclusively on ornamentation, the studied specimens are more similar to *V. pflugii*; however, the germinal area differs significantly. We have not been able to determine our specimens at the species level and thus leave it in open nomenclature.

Stratigraphic distribution: Upper Santonian of the Transdanubian Range, Hungary (Kedves and Diniz 1983).

Krutzschipollis Góczán 1967 in Góczán et al. 1967

Krutzschipollis crassus (Góczán 1964) Góczán 1967 n. comb. in Góczán et al. 1967

Plate 1, figure l

1964. *Extratripoporopollenites crassus* n. sp. Góczán – p. 251. pl. VIII. figs 1–2.

1986. *Krutzschipollis crassus* (Góczán) Góczán; Siegl-Farkas – p. 449. pl. VI. figs 7–8.

1999. *Krutzschipollis crassus* (Góczán) Góczán; Pavlishina – p. 201. pl. I. figs 17–19.

2002. *Krutzschipollis crassus* (Góczán) Góczán; Siegl-Farkas and Haas – p. 171. pl. III. fig. 19.

Samples and microscope coordinates: Bed 7/2: 108/25.5; 106/44, Bed 5/1: 108/25.5

Material: Well-preserved, brown-colored pollen grains.

Dimensions: 30–40 μm in diameter (based on three specimens).

Description: The pollen grain is triporate. The equatorial outline is triangular with convex sides. The inner contour is circular. The exine is thick consisting of two wall layers of equal thickness. The exine is thickened in the germinal area to form oculus-like elements.

No interloculum is present. The surface of the exine is verrucate-rugulate. The outer part of the germinal area is slightly elongated. The annulus is well developed. The atrium is broad.

Remarks: The surface of *Krutzschipollis spatiosus* is more heavily ornamented than *K. crassus* (Góczán et al. 1967). The oculi of *Oculopollis* species are more developed. The surface ornamentation is coarser compared to *Hungaropollis* and the germinal area is different from that of *Krutzschipollis*. *Longanulipollis* differs from *Krutzschipollis* in having more elongated germinals, club-shaped inner contour and its surface ornamentation can be smoother (Góczán et al. 1967).

Stratigraphic distribution: Upper Santonian–Campanian of the Transdanubian Range, Hungary (Góczán 1964; Siegl-Farkas 1988, 1993, 1999); first occurrence is in the Lower Santonian of northern Bulgaria (Pavlishina 1999).

Krutzschipollis spatiosus Góczán 1967 in Góczán et al. 1967

Plate 1, figure k

1967. *Krutzschipollis spatiosus* Góczán; Góczán et al. – p. 547. pl. VIII. figs 16–19.

1990. *Krutzschipollis spatiosus* Góczán; Góczán and Siegl-Farkas – p. 372. pl. V. figs 1–2.

1996. *Krutzschipollis* cf. *spatiosus* Lantos et al. – p. 115. pl. 5. fig. 5.

1999. *Krutzschipollis spatiosus* Góczán; Pavlishina – p. 201. pl. I. fig. 16.

Samples and microscope coordinates: Bed 5/1: 96/24.5

Material: Moderately preserved, yellowish to brown pollen grains with different grades of coalification.

Dimensions: 30–40 μm (based on one specimen).

Description: The pollen grain is triporate. The equatorial outline is triangular with convex sides. The inner contour is circular. The exine is thick and consists of two wall layers of equal thickness except in the germinal area where outer wall layer is thickened. No interloculum is present. The surface of the exine is strongly ornamented with 2–6 μm long scarps.

Remarks: The surface of *Krutzschipollis spatiosus* is more densely ornamented compared to *K. crassus*. They are the largest representatives of the genus (Góczán et al. 1967).

Stratigraphic distribution: Lower Campanian of the Transdanubian Range, Hungary (Góczán 1964; Siegl-Farkas 1993, 1999); first occurrence in the middle Santonian of northern Bulgaria (Pavlishina 1999).

Systematics of plant mesofossils

On the basis of a rich assemblage of small, three dimensionally-preserved fossil angiosperm reproductive structures, two morphotypes of fruits with Normapolles affinity are described herein.

Order and family: *Incertae sedis*

Genus *Sphaeracostata* Bodor et Baranyi, gen. nov.

Type species: *Sphaeracostata barbackae* Bodor et Baranyi, sp. nov.

Etymology: From the two most important morphological characters of the genus. *Sphaera* (Latin) refers to the spherical shape; *costata* (Latin) refers to the surface ribs.

Generic diagnosis: Fruit is small, spherical to ovoid, displays radial outer symmetry, possesses one seed. Surface is ribbed, base of the style has two or four branches. Inner section divided into three by the cotyledons. The cotyledons of the embryo are folded in the seed. Fruit wall is at least two-layered. Rounded, puffed cells on the pericarp. Surface cells are angular, ordered in rows.

Sphaeracostata barbackae Bodor et Baranyi, sp. nov.

Plate 3, figures a–h

Holotype: 2011.180

Other specimens examined: 2011.181–2011.184; 2011.191

Repository: Hungarian Natural History Museum, Department of Botany, Budapest.

Material: Well-preserved, coalified, three-dimensionally preserved fossils from sieved organic residue. Occur in variegated clay, silt, marl, grey and brown sand, and sandstone beds. The greatest number of fruits were found in the bonebed.

Type locality: Csehbánya Formation; Hungary; abandoned Iharkút open pit bauxite mine.

Stratigraphic horizon: Bed 6, a bonebed in the Santonian fluvial sequence.

Etymology: In honor of paleobotanist Dr. M. Barbacka.

Specific diagnosis: Small, spherical to ovoid fruits. The fruit is a nut. Style appears as small suture at the apical part, branching into two or four. Ovary is sickle-shaped. Rounded and puffed cells, 8–12 μm in diameter, form the pericarp. Conspicuous longitudinal ridges appear on the fruit surface. The fruit wall is approximately 10–50 μm thick, with 5–8 μm , angular surface cells, standing in parallel rows to the ribs. Cotyledons are folded.

Dimensions: Breadth: 0.9–1.2 mm (arithmetic mean 1.00 mm); length: 0.8–1.3 mm (arithmetic mean 1.08 mm); 100 complete fruits were measured.

Description: The fruit is approximately 1 mm wide and 1 mm long, rounded, longitudinally ridged on the entire surface (Plate 3, figures b, c, d, f). The number of the ribs varies between 8 and 30. Attachment scar at the base is not visible (Plate 3, figure b). In transverse section the fruits are round or ovate. The fruit wall is up to 50 μm thickness (Fig. 3). The inner structure is always divided by an endopleura; the thickness of the endopleura is usually half of the fruit wall (Plate 3, figures g, h). These pleuras most likely represent the two cotyledons. The fruits show two types of morphology depending on the shape of cells on their surface. The cells of the first type are elongated and angular (Plate 3, fig. f). The other type

is characterized by rounded cellular structures (Plate 3, fig. c). The angular cells are presumably the inner cells of the fruit coat. The rounded cells could be the outer cells of the fruit coat. Uncertainty remains due to the state of preservation.

Remarks: The existence of different morphotypes was explored using a multivariate statistical method, nonmetric multidimensional scaling (NMDS). The analysis was carried out on 40 complete specimens, and a distinction of two morphotypes was possible based on the following characters: dimension, number and trend of ribs, surface of ribs, reticulation of the surface, and cellular structures. However, the taxonomic significance of these two morphotypes is questionable. The possibility remains that they represent different developmental stages or different preservation. The low importance of the above-mentioned characters in the taxonomy of extant taxa suggests that these two morphotypes likely belong to the same species.

The possible affinities of *Sphaeracostata* were evaluated. The morphological similarities with the outer surface of *Spirellea* Knobloch and Mai may suggest a phylogenetic relationship (Knobloch 1977), but the detailed study of the inner structure (Fig. 3 and Plate 3, figs g, h) show important differences. The *Spirellea* specimens are all charcoaled, small ovoid in shape; their size is usually between 0.5 and 2 mm and they are covered by longitudinal ribs occasionally anastomosing or intermittent to pearl-structure, and the inner part is never divided.

Microcarpolithes striatus Vangerow 1954 has a similar outer surface structure and ornamentation to *Sphaeracostata*; the inner structure, however, is not known, and it is a synonym of *Spirellea multistriata* Knobloch and Mai 1986. The lectotype of *Spirellea multistriata* was re-examined and an undivided inner structure was discovered that excluded a relationship to *Sphaeracostata*.

Microcarpolithes costatus also shows similarity to *Sphaeracostata* in its ribbed outer surface (Plate 3, figs b-d, f), but it differs from our new species in always having 8 ribs dividing the fruit (Knobloch 1964). The holotype of *Microcarpolithes costatus* was re-examined, but the specimen had deteriorated, rendering a re-examination impossible.

Sphaeracostata shows similarities to Normapolles; thus a comparison with mesofossils belonging to the Normapolles group was necessary. *Manningia* Friis 1983 is triangular in cross-section, a feature never seen in the studied material. *Manningia* commonly has a persistent style, with a different shape and aspect ratio of the whole fruit compared to *Sphaeracostata*. In the case of *Manningia*, the style could reach one third of the total length; in *Sphaeracostata* this ratio is not more than one tenth (Plate 3, fig. a). In *Manningia* the surface is characterized by 10 longitudinal ribs. The number of ribs of *Sphaeracostata* shows a higher variability, from 8 to 30 (arithmetic mean 14.8, counted on 100 complete specimen). *Manningia* nuts always contain one seed (Friis 1983), and the folded cotyledons have never been examined. These differences are significant enough to warrant placement into separate genera.

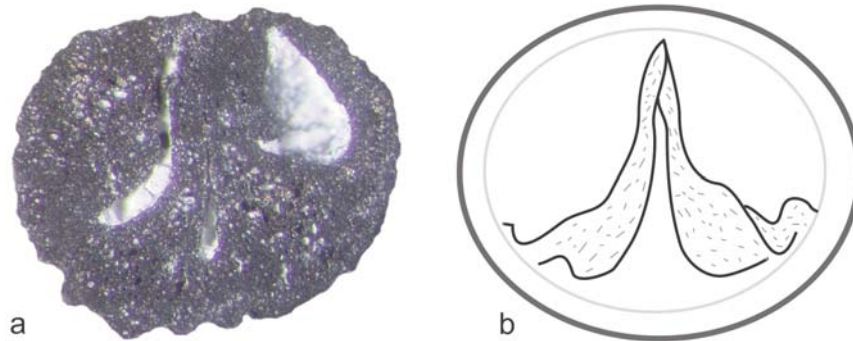


Fig. 3

- a) Photomicrograph of the cross-section of *Sphaeracostata barbackae* sp. nov.
 b) Schematic drawing of the inner section of *Sphaeracostata barbackae* sp. nov.

The organization and structure of *Calathiocarpus* Knobloch et Mai is similar to that of *Manningia*. *Calathiocarpus* also differs in its inner structure from *Sphaeracostata*, as *Calathiocarpus* is never divided, whereas *Sphaeracostata* is always divided. The ribs of *Calathiocarpus* occasionally diverge; this feature has never been observed on the almost 1000 specimens of *Sphaeracostata*.

Antiquacarya fruits display three scars and shows actinomorphic symmetry with triangular cross section. The nuts contain only one seed (Friis 1984); the cotyledons have never been observed in this genus, which rules out the possibility of it belonging to the same genus as *Sphaeracostata*.

The above comparison to other fossil fruits clearly necessitates the erection of a new genus and species. The proposed relationship to the Normapolles group is based on the actinomorphic outer symmetry of the fruits, which is rather common in this group (Friis 1984). The folded cotyledons (Fig. 3) are characteristic of the Fagales (Karsten 1891). The divided appearance of the nuts is another typical feature in Fagales (Schimper 1908). Without establishing whether our form is gynous (hypo-, peri-, or epigynous), the taxonomical affinity could not be established more precisely. The Normapolles group is obviously not monophyletic; both epigynous and hypogynous floral organisation also occurs within it (Friis et al. 2006). The floral structures described in the Normapolles group also show several synapomorph characters with the Fagales (Friis et al. 2006). The fagalean affinity of *Sphaeracostata*, together with the dominance of Normapolles pollen grains in the Iharkút material, suggest the Normapolles affinity of the new genus.

Order and family: *Incertae sedis*
cf. *Caryanthus* Friis 1983
Plate 4, figs g, h

Material: 43 specimens of poorly preserved, charcoallified, fragmented, abraded, three-dimensionally preserved fruits.

Dimensions: 0.8–1.6 mm in length and 0.5–1.5 mm in breadth.

Description: Fruits are asymmetrical or bilateral. The poor preservation makes it difficult to distinguish the main taxonomical characters. The fruits have an apical split (Plate 4, figure h). The shape of the fruits is elongated or lanceolate (Plate 4, fig. g). The fruits are one-loculed. Bract is small or not detectable. Bracteoles cannot be seen in the Iharkút material. The wall structure and the testa are not noticeable. The floral part is not preserved. The lateral face of fruit is convex to concave with irregular ridges (Plate 4, fig. g). The surface is often gently and sparsely papillated. The size of papillae is less than 10 μm . On the damaged surface small (approx. 5 μm in diameter), angular, cell-like structures are observable (Plate 4, fig. h).

Remarks: The average size of the fruits is 1.3 mm. Some characters (one-loculed, elongate or lanceolate fruits with an apical split) indicate their relationship with the genus *Caryanthus* Friis.

On the studied specimens the edge of the discus is missing, as in *Caryanthus multiasseris* Knobloch 1986. But they also show similarities in the number and trend of the vascular bundles to some specimens of *Caryanthus trebecensis* Knobloch and Mai 1983. The size of the Iharkút specimens varies between the size of *C. triaseris* and *C. multiasseris*. In every case the bundles appear as ridges; they never exceed 50 μm in thickness, commonly approximately 20 μm . There is a tip on some specimens, but not as big as in *C. triaseris* (Friis 1983; Knobloch and Mai 1983; Knobloch 1985; Knobloch and Mai 1986). It never exceeds 10% of the fruit length. The specimens show three varieties of ornamentation. There are 8 specimens with no vascular bundles. Another 27 specimens display three distinct vascular bundles on both sides. The middle bundle does not reach the margin as in *C. triaseris* (Friis 1983; Knobloch and Mai 1983; Knobloch and Mai 1986). The third variety has at least three bundles, but their trend is irregular (Plate 4, fig. g), sinuous, and their number is difficult to establish as in *C. multiasseris* (Knobloch and Mai 1986). The poor preservation of the specimens does not allow a more precise identification.

Discussion

This work focuses on the Normapolles-related plant fossils that dominate the studied material, in which we identified three fruit taxa and 20 pollen taxa.

All studied samples yielded similar palynological assemblages, differing only in the abundance of different palynomorph groups (Fig. 4). Samples Bed 5/1 and Bed 8 are characterized by the highest species diversity, which is primarily the

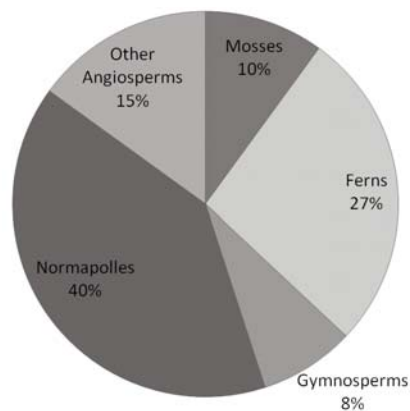


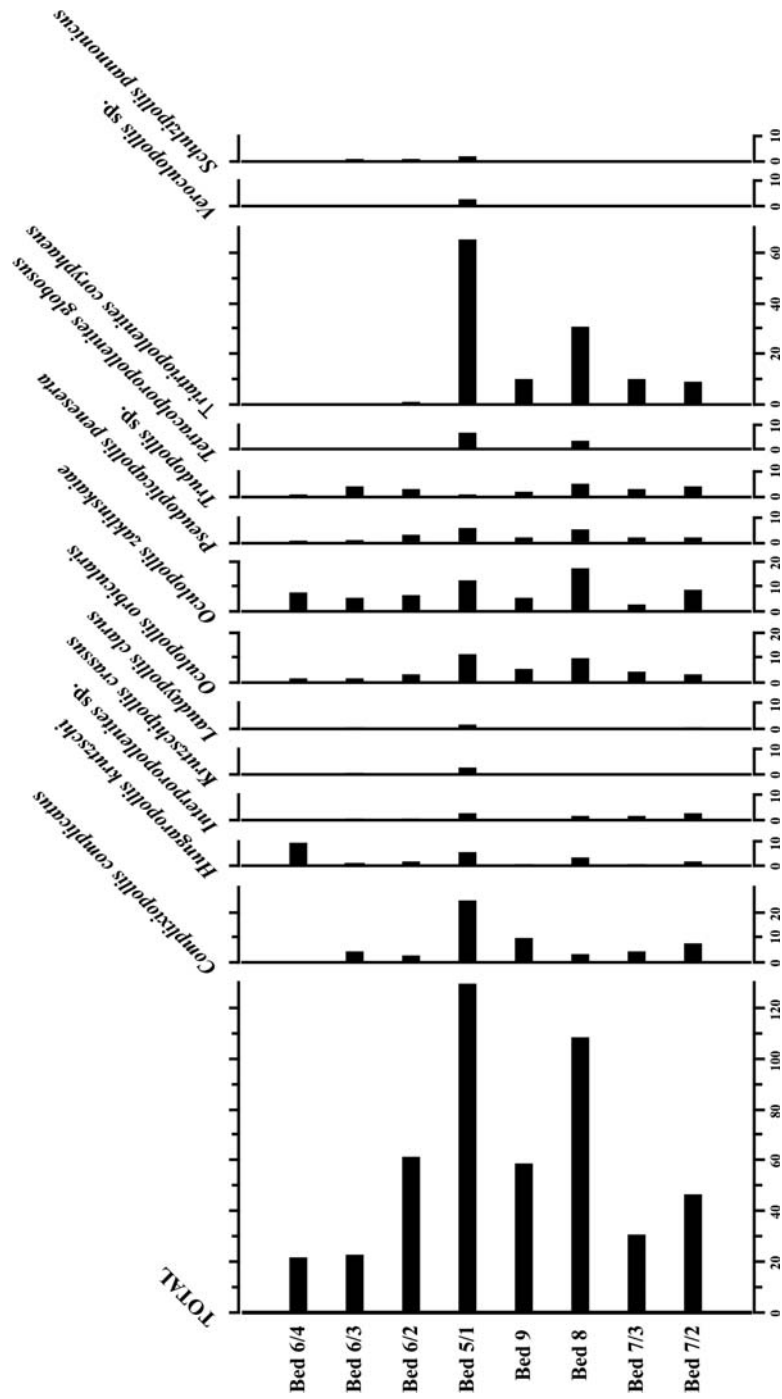
Fig. 4
Distribution of different sporomorph groups of the Iharkút assemblage

result of the very high abundance of pollen and spores in these two samples (Fig. 5). In all investigated samples the species of the genus *Oculopollis* dominate, particularly *O. zaklinskaiae* and *O. orbicularis*. In sample Bed 5/1 the relative abundance of *Triatriopollenites coryphaeus* (of Postnormapolles affinity) reaches 60% in the palynological assemblage. *Tetracolporopollenites (Brecolpites) globosus* (Plate 2, fig. d) also shows a high abundance in these two samples. In the uppermost layers the percentage of the species of *Hungaropollis* slightly increases, and the percentage of *Complexiopollis* decreases. *Laudaypollis clarus* and *Schulzipollis pannonicus* are extremely rare. *Trudopollis*, *Interporopollenites* and *Pseudoplicapollis peneserta* are common elements of the palynological assemblage. *Krutzschipollis crassus* and *Verroculopollis* sp. occur rarely.

Spores also appear in the samples, as well as few gymnosperms (Fig. 5) and dispersed cuticles of angiosperms and of Bennettitalean affinity. Angiosperm pollen grains show a much higher abundance compared to spores; however, the diversity of spore genera is comparable to that of the angiosperms. Gymnosperms (*Araucaraicites australis* Cookson 1947, *Inaperturopollenites* sp., *Cycadopites* sp.) are rare constituents of the palynological assemblage. In many cases the gymnosperms are reworked from older sediments (e.g. *Ovalipollis* sp.). No marine palynomorphs occur in the studied samples.

The studied Normapolles-related fruits are dominant in the mesofossil assemblage, representing almost 70% of the studied seeds and fruits. A new taxon is described from the mesofossil material. *Sphaeracostata* is represented by almost 1000 specimens. The *Sphaeracostata* fruits are most common in the bonebed-type layers. The other layers (Bed 7 and 8, Fig. 1) are characterized by the dominance or co-dominance of Magnoliaceae-type seeds. In addition to the fossils described here, the Iharkút material includes Sabiaceae-related fossils as well as not yet classified forms (Bodor et al. 2012).

Fig. 5
Abundance distribution of selected Normapolles and other angiosperm pollen from Iharkút. Variations in relative abundance are given in percentages



Systematic assignment

The microflora is in general similar to other Late Cretaceous floras of the region, with predominance of the Normapolles group. The comparison is difficult because of the inconsistency in the systematics of a few Normapolles genera, especially in the case of the genus *Oculopollis*. As a consequence, the age-diagnostic species *Oculopollis zaklinskaiae* is mentioned only by relatively few authors (Góczán 1964; Siegl-Farkas 1988, 1993; Góczán and Siegl-Farkas 1990; Hradecká et al. 1999; Pavlishina 1999; Pavlishina et al. 2004).

The systematic assignment of *Sphaeracostata* places it within the Normapolles group. The folded cotyledon, the divided inner structure and the persistent but small stylus together suggest a possible relationship to Fagales. This morphology, according to Friis et al. (2006), suggests that a the high percentage of Normapolles plants has a fagalean affinity. Apart from the new species, *Caryanthus* is a well-known genus of unquestionable Normapolles affinity at the European Upper Cretaceous localities. This relationship is beyond dispute. The fossil fruit described from Haĕteg as "Taxon 1" (Lindfors et al. 2010) was also found at Iharkút (Plate 4, figs a–f), derived from an inferior ovary. Unfortunately, the maturation stage of the fruits identified in the Iharkút material does not allow to decide whether it was uni- or bisexual (Plate 4, figs a–c, f). The relation of this form to Normapolles was first suggested by Lindfors et al. (2010). This fruit is ellipsoidal (Plate 2, figs b, c, f), with forking ridges and an undivided inner structure (Plate 4, figs d, e).

Normapolles pollen grains have not been found *in situ*. Flowers are not common at the locality and *in situ* pollens are rarer in fruits. In some published cases the parent plant of some Normapolles-related pollen forms is known (Tschudi 1975; Batten and Christopher 1981; Friis 1983; Crane et al. 1989; Sims et al. 1999; Friis et al. 1999; Friis et al. 2006). From the Iharkút material, the pollen *Plicapollis* is known to represent the parent plant *Caryanthus* (Tschudi 1975; Friis 1983; Friis et al. 2009). The high percentage of *Plicapollis* is in contrast with the low abundance of *Caryanthus* in the mesofossil material. The parent plants of the dominant palynomorphs *Oculopollis* spp. are not yet known.

Palynostratigraphy

Based on the investigations of Góczán (1964), Góczán and Siegl-Farkas (1990) and Siegl-Farkas and Wagreeich (1996) the palynological assemblage of the locality belongs to the *Oculopollis zaklinskaiae*–*Tetracolporopollenites (Brecolpites) globosus* Dominance Zone, indicating a late Santonian age of the bonebeds.

The correlation with other European palynostratigraphic schemes is not straightforward, due of the differences between the stratigraphic ranges of the dominant taxa (Fig. 6). The age-diagnostic *Oculopollis* group is dominant in the Santonian in Europe (Góczán 1964; Góczán et al. 1967; Portnigina 1971; Médus 1972; Andrusov and Snopková 1976; Siegl-Farkas 1988, 1993, 1999; Góczán and

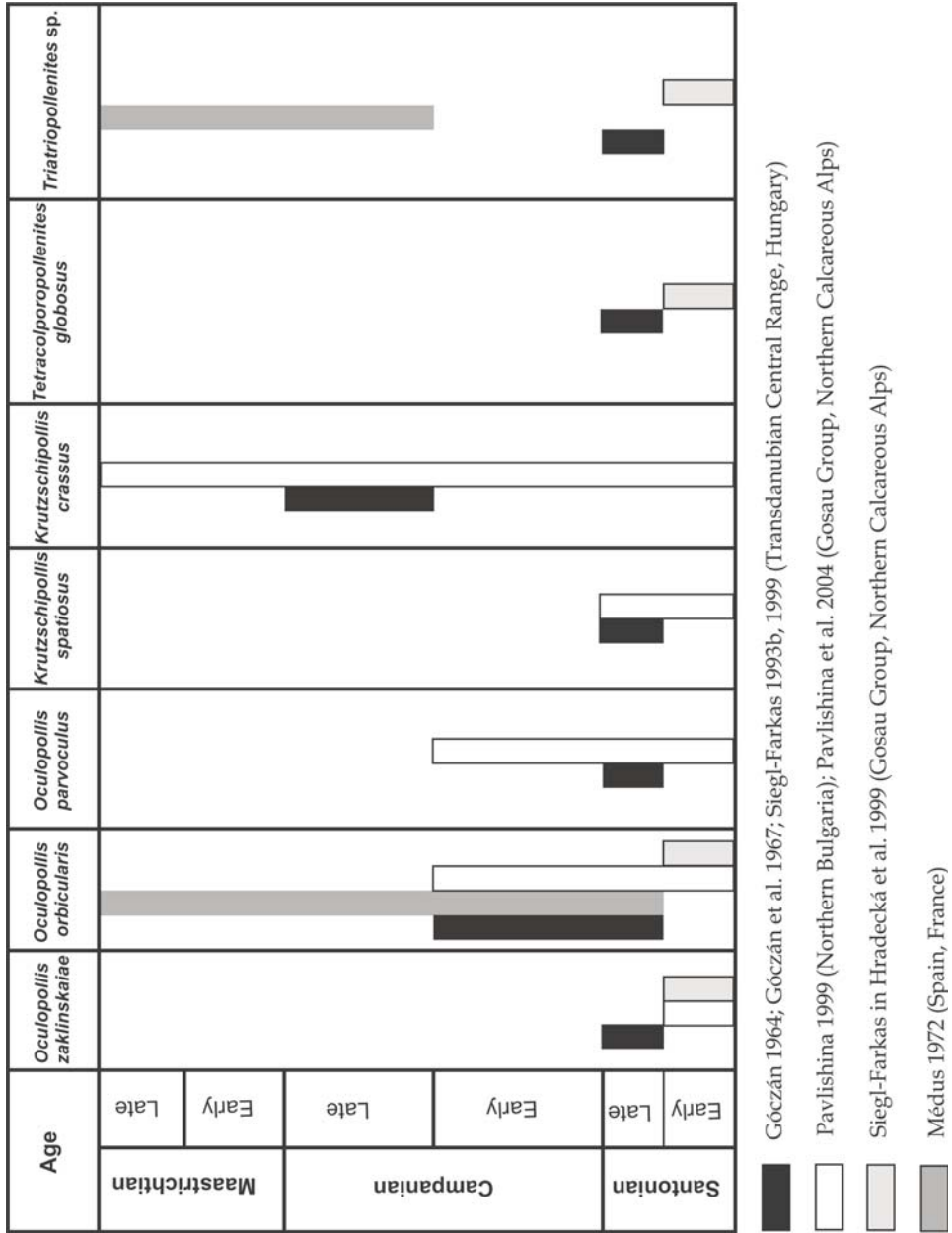
Siegl-Farkas 1990; Mogoş 1992; Siegl-Farkas and Wagnreich 1996; Hradecká et al. 1999; Pavlishina 1999; Siegl-Farkas and Haas 2002; Pavlishina et al. 2004).

The dominance of *Oculopollis zaklinskaiae* was documented from lower Santonian strata in the lower Gosau Subgroup in Austria (Siegl-Farkas in Hradecká et al. 1999) and from Northern Bulgaria (Pavlishina 1999). However, according to the standard palynological zonation of Góczán (1964) and Siegl-Farkas (1999), this species clearly indicates a late Santonian age.

Oculopollis orbicularis and *O. parvoculus* are common in late Santonian and early Campanian palynofloras described from Hungary (Góczán 1964; Siegl-Farkas 1988; Góczán and Siegl-Farkas 1990), Spain, southern France (Médus 1972), Bulgaria (Pavlishina 1999) and the Gosau area in Austria (Siegl-Farkas 1994; Siegl-Farkas in Hradecká et al. 1999; Pavlishina et al. 2004). *Krutzschipollis* and *Hungaropollis* diversify during the Campanian in Hungary (Góczán 1964; Siegl-Farkas 1988, 1993; Siegl-Farkas and Wagnreich 1996). *K. spatiosus*, *K. crassus* and *Hungaropollis krutzschii* dominate the early Campanian palynofloras in the Transdanubian Range (Góczán 1964; Góczán and Siegl-Farkas 1990; Siegl-Farkas 1988, 1993, 1999; Siegl-Farkas and Haas 2002). The Iharkút assemblage is characterized by a few specimens of *Krutzschipollis* cf. *spatiosus* (Siegl-Farkas, pers. com.). *K. spatiosus* first appeared in the middle Santonian (Pavlishina 1999). In northern Bulgaria *K. crassus* dominates the early Santonian palynofloras, together with *Oculopollis zaklinskaiae* (Pavlishina 1999).

Triatriopollenites coryphaeus, a species with *Postnormapolles* affinity, occurs in the early Campanian assemblages of Spain and France (Médus 1972). In contrast, in Hungary it occurs in the Santonian according to Góczán (1964) and Siegl-Farkas and Wagnreich (1996), and it predominates in upper Santonian sediments in the Transdanubian Range.

This inconsistency between the ranges of the Normapolles taxa in different geographic areas makes them less valuable for biostratigraphy (Fig. 6). The known range of *Oculopollis zaklinskaiae* was previously restricted to the late Santonian but is here extended to the early Santonian–early Campanian. Likewise, the range of *Krutzschipollis crassus*, previously considered late Santonian–Campanian, is extended to the early Santonian–Campanian interval. A possible explanation is that in the study areas the paleoenvironmental changes were not synchronous, and the Normapolles-bearing plants were able to migrate to meet their ecological requirements. This was already suggested by Siegl-Farkas (1996): “the dominance zones may indicate paleoenvironments rather than ages”. It is possible that similar paleoenvironments supporting a distinct type of vegetation and palynoflora developed during different times in the Central European area. Another possible explanation is the archipelago effect, proposed for continental vertebrates (Pereda-Suberbiola 2009). This effect can also control distinct vegetation distribution patterns, reflected by distinct palynofloras in the hypothesized archipelago of the Tethyan Realm. Some degree of endemism is suggested by the characteristic predominance of the species *O. zaklinskaiae*, and the dominance of



the genus *Hungaropollis*. *Laudaypollis* and *Schulzipollis* occur solely in the investigated region and in the Gosau Basin, located close to the Iharkút archipelago according to the paleogeographic reconstruction of Csontos and Vörös (2004). A complete isolation of the pollen assemblages is precluded by transport by wind, fluvial processes and currents. Wind transport is proposed to account for the mass occurrence of Normapolles taxa in the Upper Cretaceous sediments (Friis et al. 2006). Pollen assemblages reflect the regional vegetation, but each locality, e.g. each island, is characterized by specific pollen abundances.

In younger marine Upper Cretaceous sediments, the pollen zonation could be of significant biostratigraphic value (Jochá-Edelényi 1988; Lantos et al. 1996), as it is combined with biostratigraphy based on marine microfossils such as nannoplankton, plankton foraminifera and dinoflagellates (Siegl-Farkas 1997). Further work is needed to improve the zonation by correlating the terrestrial and marine records.

Paleoecological reconstruction based on Normapolles-related plant remains

The plant material described herein is incomplete and cannot be regarded as a representative assemblage. The Normapolles group is extinct and the ecological requirements of their parent plants are not known. However, the morphology of the newly described *Sphaeracostata* support the fagalean affinity of the majority of the Normapolles-related plants, supporting the observations of Friis et al. (2003, 2006). The dominance of these plants suggests arboraceous vegetation.

Biofacies and lithofacies indicate deposition in a fluvial environment, also suggested by the channel fill deposits in which vertebrate megafossils are abundant (Tuba et al. 2006; Ósi and Mindszenty 2009). Paleosoil horizons further support a non-marine paleoenvironment. The differences indicate that slight but clearly identifiable paleoecological differences may exist between the sampled stratigraphic levels.

Sample Bed 8 contains abundant plant debris, resin fragments and large dispersed cuticle fragments which indicate sedimentation in a low-energy environment, probably on a flood plain or near an abandoned channel.

These environmental conditions are supported by the vertebrate paleontological data from the locality. Fluvial habitats and wet conditions were necessary for the amphibians from Iharkút. Using the methods of Böhme et al. (2006) to infer frog habitats, Szentesi and Venczel (2012) assigned *Bakonybatrachus fedori* to a periaquatic group whereas *Hungarobatrachus* represents a semiaquatic and woodland group (Szentesi pers. comm.). The most common lizards of the

← Fig. 6

Ranges of selected pollen taxa from the Transdanubian Range (Iharkút included) (Góczán 1964; Góczán et al. 1967; Siegl-Farkas 1993b, 1999), southern France and northeastern Spain (Médus 1972), northern Bulgaria (Pavlishina 1999), and the Northern Calcareous Alps (Hradecká et al. 1999; Pavlishina 2004)

locality are the scincomorphs (Makádi 2006). Some well-preserved specimens belong to *Bicuspidon*. Most skinks are members of the heliophile ecophysiological group and some of them belong to the subterranean arboreal group (Böhme et al. 2006). Crocodiles belong to the obligate aquatic ecophysiological group, and their modern representatives live in subtropical and tropical climate. Turtles are also very common at the fossil site (Rabi et al. 2011); they belong to the periaquatic, semiaquatic and obligate aquatic groups (Böhme et al. 2006). Closer environmental determination has not yet been possible. The environmental requirements of the other vertebrate groups known from the locality are not well known (Ósi et al. 2012). In summary, the vertebrate-based paleoecological inferences are in accordance with the paleobotanical evidence. The Normapolles-related plants appear to be members of arboreal vegetation, but the presence of other seeds, fruits and palynomorphs at the locality suggest that the forest was not completely closed. The heliophile skinks were able to live in these glades. Abundance of water for animals of high water demand was provided by a nearby fluvial system.

Conclusions

The palynoflora and mesoflora of Iharkút provide information on the age and composition of the vegetation of this rich and diverse vertebrate locality. Palynostratigraphy allows assigning the bonebed to the *Oculopollis zaklinskaiae*–*Tetracolporopollenites (Brecolpites) globosus* Dominance Zone of the standard palynological zonation of Góczán (1964) and Góczán and Siegl-Farkas (1990), indicating a Santonian age. Based on the new data, including the dominant Normapolles species, the precise age is probably early-middle Santonian, on the basis of the occurrence of *Oculopollis zaklinskaiae* and *Tetracolporopollenites (Brecolpites) globosus* in lower Santonian sediments of the Gosau Basin (Austria). These results provide an improved stratigraphical resolution for the sampled interval.

Our study of the Iharkút mesofossils have led to the erection of a new angiosperm fruit genus and species, based on almost 1000 specimens. With remarkable preservation of the inner structure, the morphology of the newly described genus supports the fagalean affinity of similar Normapolles-related fossils. The fagalean affinity of these plants indicates an aboraceous vegetation at the Iharkút site.

The paleogeographic reconstruction of the Late Cretaceous archipelago of this region suggests that local environmental variations may have controlled the differences between palynological assemblages, highlighting the significance of the mesofossils for vegetation reconstruction.

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Plate 1

Scale in fig. a applies to all.

- a: *Oculopollis zaklinskaiae* Góczán 1964, Bed 5/1, [40/92,5]
- b: *Oculopollis zaklinskaiae* Góczán 1964, Bed 5/1, [92/23]
- c–d: *Oculopollis orbicularis* Góczán 1964, Bed 5/1, [91,5/23]
- e: *Hungaropollis krutzschi* Góczán 1964, Bed 9, [109/37]
- f: *Laudaypollis clarus* Góczán 1964, Bed 5/1, [99/25]
- g: *Complexiopollis complicatus* Góczán 1964, Bed 5/1, [95/49]
- h: *Complexiopollis labilis* (Góczán 1964) Góczán and Krutzsch, 1967, Bed 5/1, [98/40]
- i: *Schulzipollis pannonicus* Góczán 1967, Bed 5/1, [110/36,5]
- j: *Verroclopollis* sp., Bed 5/1, [93/24,5]
- k: *Krutzschipollis spatiosus* Góczán 1967 in Góczán et al., 1967, Bed 5/1, [96/24,5]
- l: *Krutzschipollis crassus* (Góczán 1964) Góczán, 1967, Bed 5/1, [108/25,5]

Plate 2

- a, b, c: *Oculopollis orbicularis* Góczán 1964, SEM/1
- d: *Tetracolporopollenites (Brecolpites) globosus* Góczán, 1964, SEM/1.
- e, f: *Complexiopollis complicatus* Góczán 1964, SEM/1.

Plate 3

Sphaeracostata barbackae sp. nov.

- a: Micropilar region
- b, c, d, f: Plan view of entire fruit
- e, g, h: Inner wall structure

Plate 4

a–f: Unnamed form, "Taxon 1" of Lindfors et al. (2010)

- a: Micropilar region.
- b, c, f: plan view.
- d: Inner structure.
- e: Inner wall structure.
- g: cf. *Caryanthus*, plan view
- h: Apical split of cf. *Caryanthus*

Plate 1

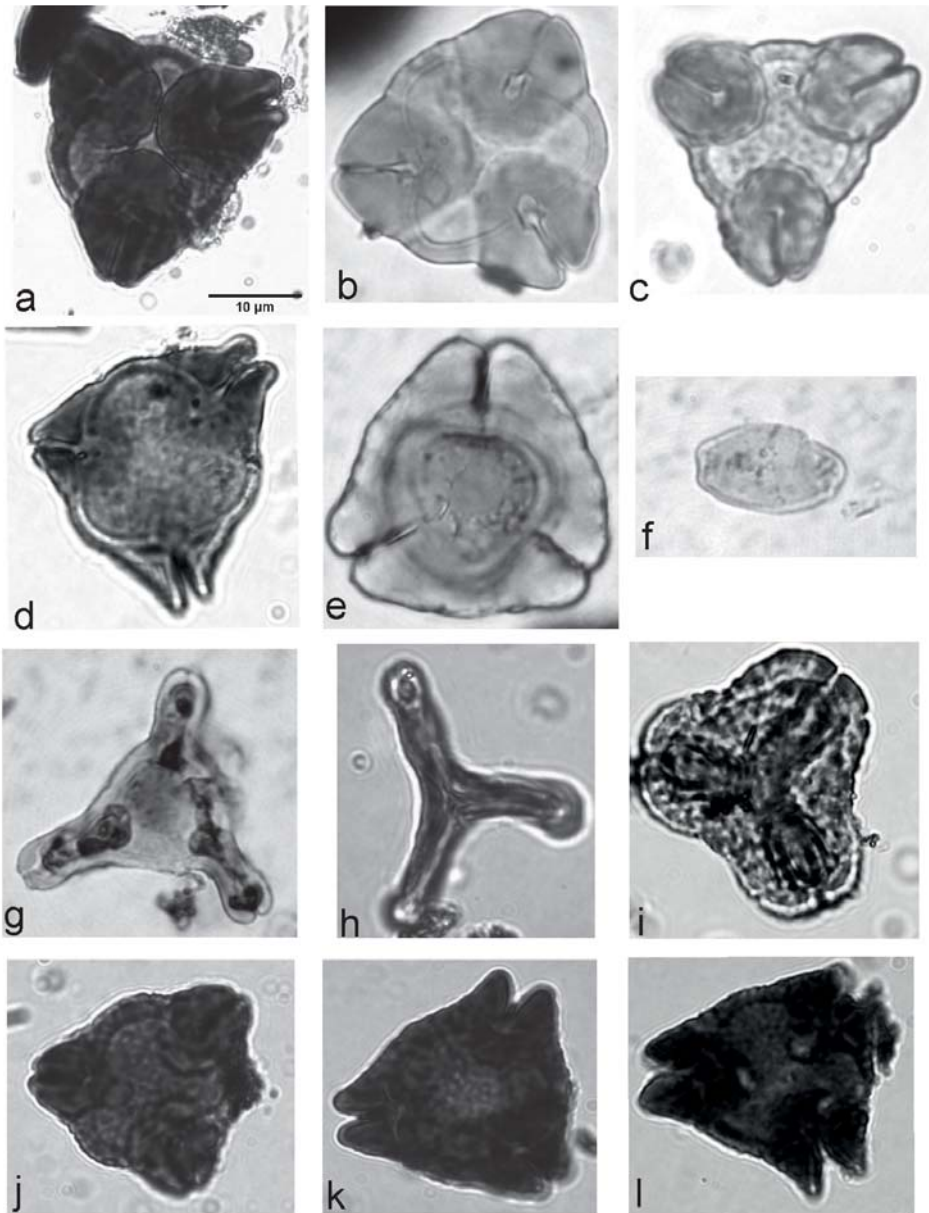


Plate 2

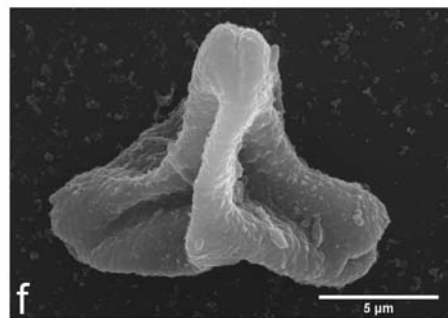
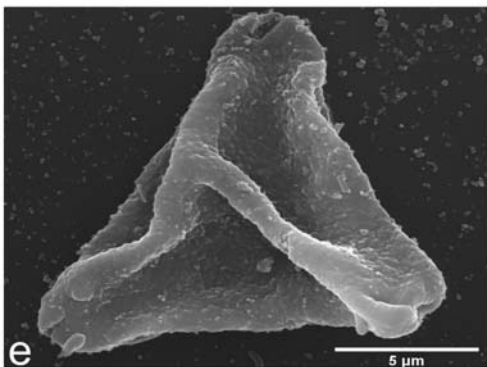
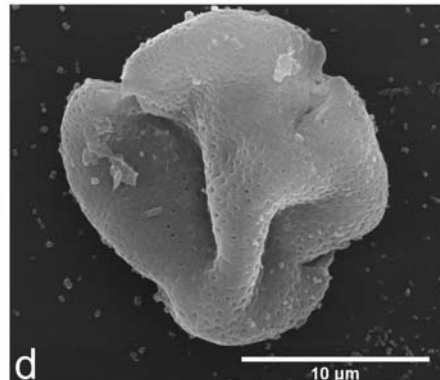
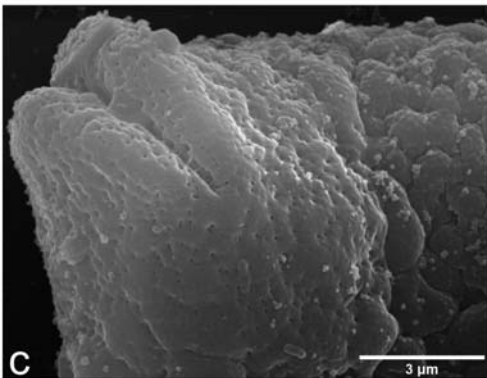
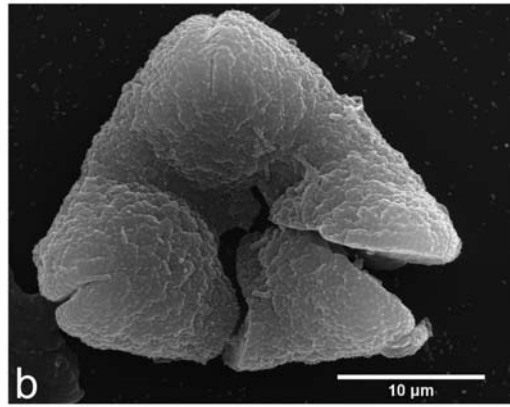
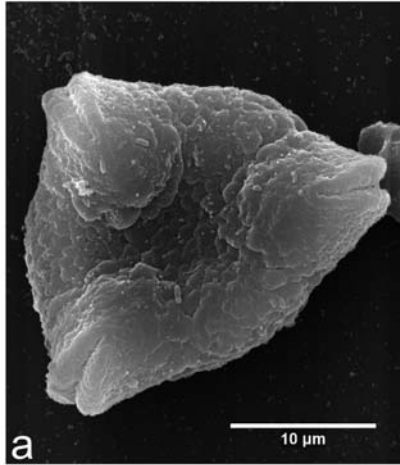


Plate 3

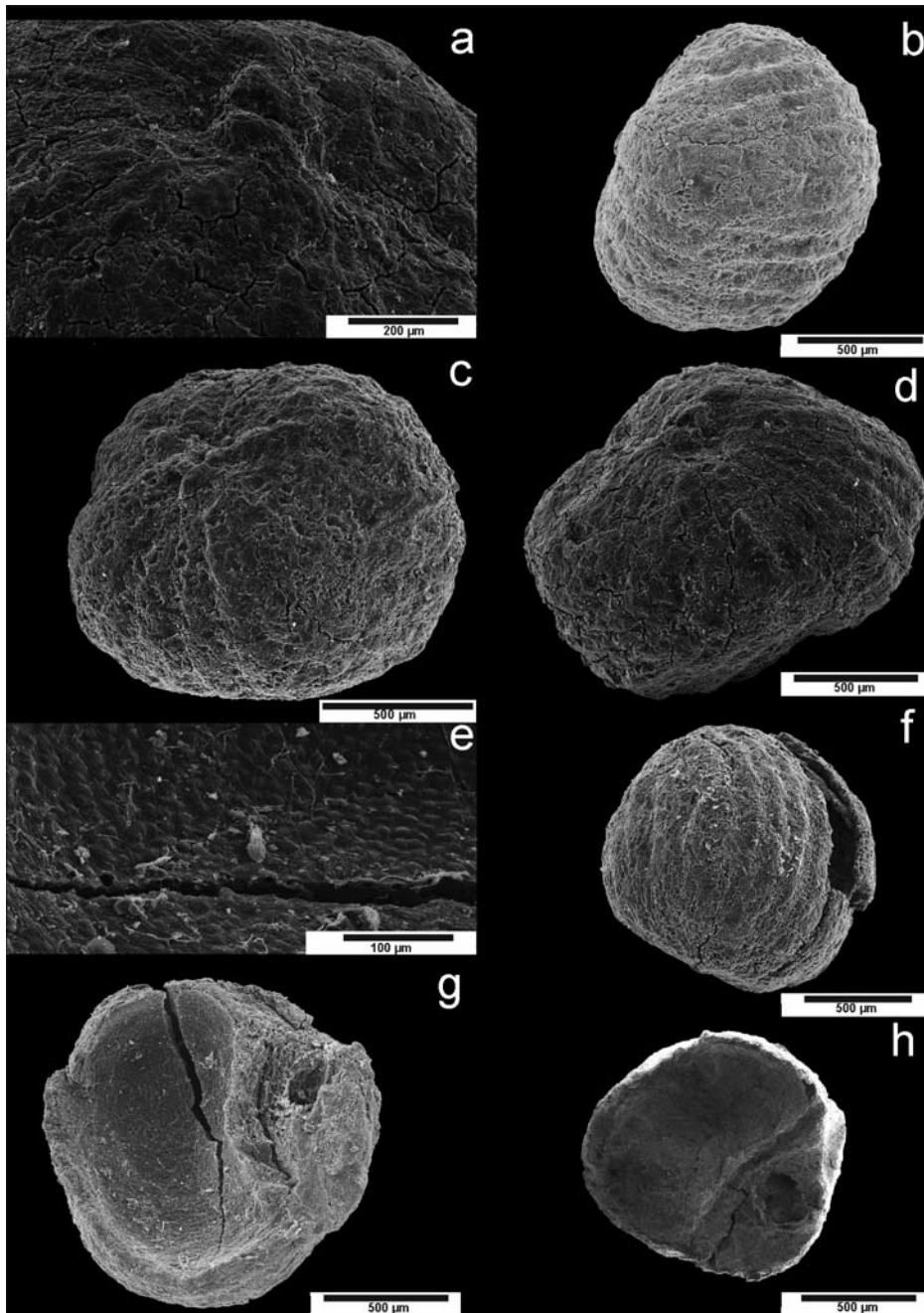


Plate 4

