| NATIONAL MUSEUM

PLANT MESOFOSSILS FROM THE LATE CRETACEOUS KLIKOV FORMATION, THE CZECH REPUBLIC

ZUZANA HEŘMANOVÁ[1,*], JIŘÍ KVAČEK[1], ELSE MARIE FRIIS[2,3]

[1] National Museum, Václavské náměstí 68, 110 00 Praha 1, the Czech Republic; e-mail: zuzka.hermanova@gmail.com, jiri.kvacek@nm.cz.
[2] Department of Geoscience, University of Aarhus, Høegh-Guldbergs Gade 2, DK-8000 Aarhus C, Denmark; e-mail: else.marie.friis@geo.au.dk.
[3] Swedish Museum of Natural History, Box 50007, SE-104 05 Stockholm, Sweden.
*corresponding author

Abstract: Late Cretaceous mesofossils are described from the Zliv-Řídká Blana locality in the South Bohemian Basins, the Czech Republic. Angiosperm remains dominate the fossil assemblage both in terms of taxonomic diversity and quantitatively, with about 65 different species based on about 1,000 specimens of flowers, fruits and seeds. There are surprisingly few non-angiosperm species in the flora, with only four specimens assigned to bryophytes, ferns and conifers. There are no megaspores of Selaginellales or Salviniales, which are otherwise common in many Cretaceous mesofossil floras. Among angiosperms, flowers and fruits assigned to the Normapolles group (Fagales) and to the Ericales are particularly prominent. In systematic composition as well as general organization and size of the angiosperm reproductive organs, the Zliv-Řídká Blana mesofossil flora is comparable to other Late Cretaceous mesofossil floras collected from various regions of Laurasia. In addition to the plant remains, the fossil assemblage also includes insect eggs and coprolites.

Key words: angiosperms, fossil fruits, fossil seeds, fossil flowers, Late Cretaceous, mesofossils, Klikov Formation

Introduction

Well-preserved plant mesofossils described from Cretaceous sediments from many parts of the world, particularly since the 1980s, have contributed significantly to our understanding of angiosperm radiation and rise to dominance during the Cretaceous period (e.g., Friis et al. 2011). The first Cretaceous mesofossil assemblage was reported from the Late Cretaceous of the Aachen area at the Dutch-German border (Vangerow 1954). Subsequently, many Late Cretaceous mesofossil assemblages have been reported from Central Europe, mostly from the Czech Republic and Germany (Knobloch and Mai 1983, 1984, 1986, Knobloch 1984, 1985). The Czech mesofossils were prepared and studied by Dr. Erwín Knobloch while he was working at the Czech Geological Survey, CGS, Prague (earlier Ústřední ústav geologický, ÚÚG). Much of the material was obtained from drillings in the Czech Cretaceous Basin, South Bohemia Basins, and from the Carpathian Flysch deposits of Moravia, and has provided invaluable information on the floristic composition of Late Cretaceous vegetation across the basins. The richest assemblages of plant mesofossils from the region are from the fluvio-lacustrine sediments of the Klikov Formation

(late Turonian-Santonian) of the South Bohemian Basins. The Klikov mesofossil assemblages are rich in small fruits and seeds of angiosperms, many of which are related to Fagales (Normapolles complex) (Heřmanová et al. 2011, 2016) and to Ericales (Knobloch and Mai 1986). In addition to mesofossils, the Klikov Formation has also yielded important plant megafossil floras comprising diverse angiosperm leaves preserved as compressions and impressions (e.g., Ettingshausen 1852, Němejc and Kvaček 1975, Váchová and Kvaček 2009) as well as rich palynofloras (Pacltová 1961, 1981). The marked presence of flowers and fruits assigned to the Normapolles complex (Fagales) in the Klikov mesofossil assemblages is also reflected in the palynological spectra that are sometimes dominated by Normapolles-type pollen (Pacltová 1961, 1981), and perhaps in the megafossil floras, from which some leaves are assigned to two species of *Quercophyllum* Fontaine, a fossil genus that may represent Fagales (Knobloch 1964).

The Zliv-Řídká Blana locality is one of the localities in the Klikov Formation that has yielded meso- and megafossils, as well as palynomorphs. Early reports on mesofossils from this locality by Knobloch (1964) and Knobloch and Mai (1983, 1984, 1986) were based on limited collections, and

included 11 taxa. A more detailed study of the Zliv-Řídká Blana mesofossil flora has now been initiated, based on new collections. Revisions and new descriptions of selected flowers and fruits assigned to the Normapolles complex (Heřmanová et al. 2011, 2016, 2017, Heřmanová and Kvaček 2012) and new analyses of the leaf fossils (Váchová and Kvaček 2009) are already published.

This study presents a new analysis of the mesofossil flora from the Zliv-Řídká Blana locality, recording 69 taxa of fossil plants. Angiosperm remains dominate the fossil assemblage in terms of taxonomic diversity and quantity, with about 65 different species based on about 1,000 specimens of flowers, fruits and seeds. In addition to plant remains, the Zliv-Řídká Blana mesofossil flora also includes insect eggs and coprolites (Colin et al. 2011). The floristic signal from the mesofossils is compared to other mesofossil taphocenoses, to the leaf fossil floras and palynomorphs from the same basins.

Material and methods

The plant mesofossils studied here were extracted from sediment samples collected in 2007 by Zuzana Heřmanová and Jiří Kvaček from the Late Cretaceous Klikov Formation exposed in the Zliv-Řídká Blana locality (49.0790333N, 14.3838644E) near the town of Zliv in the cadaster (land registry) of the Zahájí village located in the Budějovice Basin (the Czech Republic). The Budějovice Basin and the Třeboň Basin form the South Bohemian Basins and occupy an area of about 2,300 km^2 (Text-fig. 1). The two basins are elongated depressions developed on the Moldanubian crystalline bedrock of the Bohemian Massif and separated

Text-fig. 1. Geological map of South Bohemian Basins.

by the Lišov Horst. Sedimentation in the basins began in the Late Cretaceous and continued sporadically until the Pliocene (Slánská 1974). The Klikov Formation, with an average thickness of 100–150 m, constitutes the most widely distributed stratigraphic unit in both the Budějovice and Třeboň basins (Slánská 1974). Sediments of the Klikov Formation consist of three types of deposits forming asymmetrical cycles: A) light grey or yellow conglomeratic, coarse- to medium-grain sandstone beds; B) generally fine-grained red beds; C) grey mudstone beds (Slánská 1976). The Klikov Formation is dated as late Turonian-Santonian, based on palynology and geological correlation (Pacltová 1981, Knobloch 1985). However, the irregular depositional cycles impede precise correlation between individual boreholes and exposures in the Klikov Formation (Knobloch 1985). For more details of the locality, see also Němejc and Kvaček (1975).

The Zliv-Řídká Blana locality is a clay pit in the Klikov Formation, exposing a lower horizon of grey fossiliferous mudstone that yielded the plant mesofossils described here, a middle horizon of red beds and an upper horizon of yellow conglomeratic and coarse grain sandstone. Early accounts on the geology and plant fossils from the locality were published by Němejc (1956, 1957, 1961), Malecha et al. (1962), Knobloch (1964), Němejc and Kvaček (1975) and Pacltová (1961). Studies on the plant mesofossils from the Zliv-Řídká Blana locality were first published by Knobloch (1964), who referred to the locality as "Tonsteinbau-Na Blanech" or "Zahájí-Na Blanech". Subsequently, more detailed mesofossil studies were focused on megaspores (Knobloch 1984) and on seeds and fruits (Knobloch and Mai 1983, 1984, 1986).

The plant mesofossils described here were extracted from the mudstone by bulk maceration using sodium bicarbonate, followed by washing in water over a 90 μm sieve. After sieving, the organic residue was treated with hydrofluoric acid, hydrochloric acid, rinsed in water and dried in air. The fossils are charcoalified or lignitised, and usually three-dimensionally preserved. Sorting and preliminary studies were carried out using an Olympus SZX binocular microscope. Specimens for SEM were mounted on aluminium stubs using nail polish, coated with gold and studied using Hitachi S-4300, JEOL JSM 6380 or Hitachi S3700 field emission scanning electron microscopes. Selected specimens were studied using X-ray microtomography using a Bruker SkyScan 1172 tomograph, housed in the National Museum, Prague. Settings used were 250 μA and 40 kV, without a filter. N-Recon Software was used for 3D reconstructions and virtual sections. Specimens were studied uncoated before SEM, or after SEM without removing the gold coating. Data obtained from the SkyScan 1172 scans were analysed and manipulated using Avizo 9.4 software for three-dimensional visualization.

Internal structures of specimens (nos NM-F 3620, NM-F 3621, NM-F 3780, NM-F 3781, NM-F 3782, NM-F 3783) were studied using attenuation-based synchrotron-radiation x-ray tomographic microscopy (SRXTM), performed at the TOMCAT beamline of the Swiss Light Source of the Paul Scherrer Institut, Switzerland. Raw data from the SRXTM analyses are housed in the Swedish Museum of Natural History. An even black background for the figures was made using Adobe Photoshop CS5. All specimens are housed in the National Museum, Prague.
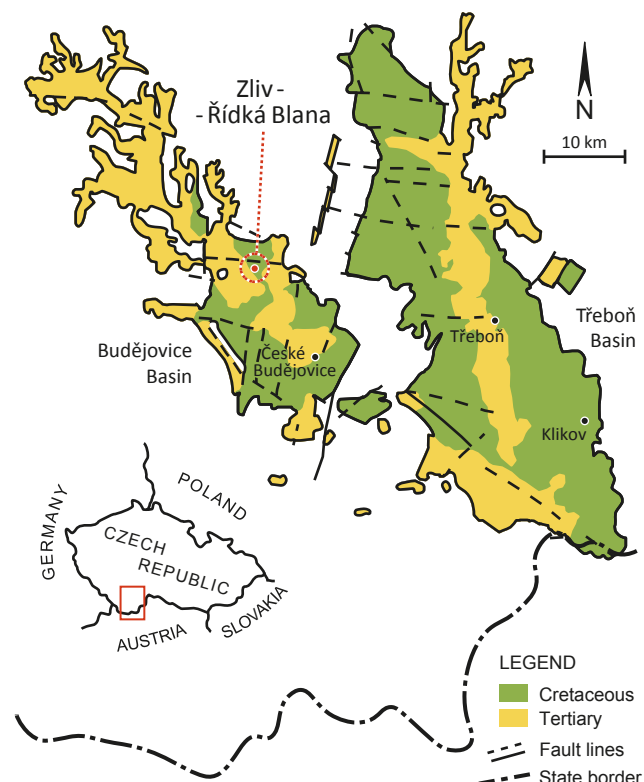
Text-fig. 2. Scanning electron micrographs of non-angiosperm remains (a–d) and insect remains (e–f) from Zliv-Řídká Blana locality. a: *Eopolytrichium* sp. small leafy shoot, no. NM-F 3631; b: Taxon 1, single tip of a young fern frond with circinate vernation, no. NM-F 4130; c: Taxon 2, fern with simple leaves and circinate vernation, no. NM-F 3459; d: *Pagiophyllum* sp., small needle-like leaf, no. NM-F 4132; e: *Microcarpolithes hexagonalis*, a faecal pellet/coprolite with subcylindrical shape, no. NM-F 4520; f: *Palaeoaldrovanda splendens*, pieces of compact walls formed by rectangular cells, no. NM-F 3237.

Results

Non-angiosperms

Bryophytes

Eopolytrichum sp. (Text-fig. 2a) comprises a single charcoalified fragment of a bryophyte gametophyte. The specimen is a small leafy shoot, about 3.1 mm long and 0.5 mm broad, with leaves spirally arranged along a slender axis. Each leaf has a broad, membranous basis that tapers into a long narrow blade. The abaxial surface of the leaf is characterised by rectangular cells with raised anticlinal cell walls. No stomata were observed on the leaves. In most cases, only the abaxial surfaces of the leaves are visible, but in one place, the adaxial surface of a leaf blade is exposed showing distinct, longitudinal aligned lamellae. The features are clearly those of a polytrichaceous bryophyte gametophyte. A similar fragment of a leafy polytrichaceous gametophyte was described from the Late Cretaceous of Georgia, USA, as *Eopolytrichum antiquum* Konopka, Herend., G.L.Merr. et P.R.Crane, together with associated sporophyte capsules (Konopka et al. 1997).

Pteridophytes

Ferns are represented in the Zliv-Řídká Blana mesofossil flora by a single tip of a young frond with distinct pinnate organisation and circinate vernation (Text-fig. 2b). There are also several enrolled blades that may represent ferns with simple leaves and circinate vernation (Text-fig. 2c). However, none of the fragments has sufficient details preserved for a more precise systematic assessment, and there are no remains of more mature fronds or fern sporangia among the mesofossils.

Conifers

Pagiophyllum sp. (Text-fig. 2d) is a small, needle-like leaf with obovate to elliptical lamina contracting to a short petiole. The presumed adaxial cuticle is thick, shiny without stomata, while the presumed abaxial cuticle has two bands of poorly preserved stomata on either side of the mid-rib, indicating the presence of a mesophytic to xerophytic conifer in the Zliv-Řídká Blana vegetation. Critical details for a secure systematic placement are lacking, but it is included here to document the full spectrum of plant fossils recovered in the mesofossil flora.

Angiosperms

Angiosperms are diverse in the Zliv-Řídká Blana mesofossil flora, with about 65 species identified from flowers, fruits and seeds (see Appendix). All fossils are very small, with fruits and seeds ranging from about 0.5 mm to 3.2 mm in length, with arithmetic mean of fruit width 1.27 mm and arithmetic mean of fruit length 2.7 mm. Some of the taxa have been described in detail in previous studies (see references below), while systematic analyses of other taxa are in progress. The following account is intended to provide documentation of the diversity in general terms of organisation and broad systematic affinities to understand the Zliv-Řídká Blana vegetation in the context of other Late Cretaceous floras.
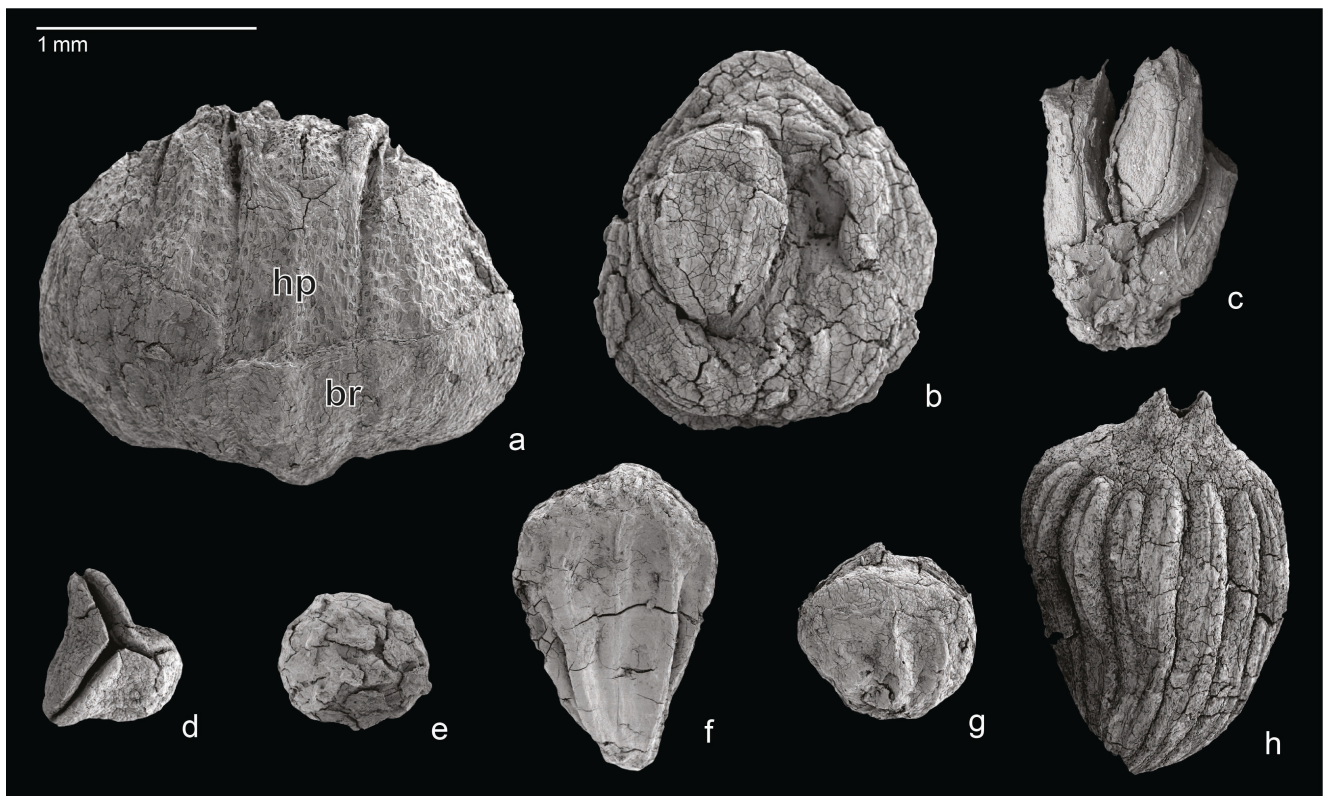
Text-fig. 3. Scanning electron micrographs of Normapolles flowers/fruits from Zliv-Řídká Blana locality. a: *Budvaricarpus serialis*, aggregation of laterally fused fruits supported by a common bract (br – bract, hp – hypanthium), no. NM-F 3160; b: *Budvaricarpus* sp., aggregation of laterally fused fruits supported by several bracts, no. NM-F 3619; c: *Caryanthus trebecnsis*, reproductive unit consists of three bisexual, epigynous flowers/young fruits, no. NM-F 3286; d: *Dahlergeniantus* sp., hypogynous flower with radial symmetry, no. NM-F 4495; e: *Calathiocarpus* sp., epigynous flower with radial symmetry, no. NM-F 4631; f: *Caryanthus* sp. 1, ribbed fruit–nut of deltoid shape, no. NM-F 3208; g: *Zlivifructus vachae*, bisymmetrical flower with four tepals and four stamens, no. NM-F 3172; h: Taxon 3, ribbed fruit of Normapolles affinity, no. NM-F 3724.

The Normapolles complex (Fagales)

So far, 12 species in five genera have been recognised, including *Budvaricarpus serialis* Erw.Knobloch et Mai, *Budvaricarpus* sp., *Calathiocarpus* sp., *Caryanthus trebecensis* Erw.Knobloch et Mai, *Caryanthus triasseris* (Erw.Knobloch) Erw.Knobloch et Mai, *Caryanthus* sp. 1, *Caryanthus* sp. 2, *Caryanthus* sp. 3, *Dahlgrenianthus* sp., *Zlivifructus microtriasseris* (Erw.Knobloch et Mai) Heřmanová, J.Kvaček et Halamski and *Zlivifructus vachae* Heřmanová, Dašková et J.Kvaček. Further, one fruit assignable to the Normapolles complex is not assigned to any specific genus (Taxon 3; Text-fig. 3h). Several of the Zliv-Řídká Blana Normapolles fruits have been described in detail elsewhere (Heřmanová et al. 2011, 2016, 2017, Heřmanová and Kvaček 2012), so here we provide only a short overview of the general features of the fossils.

Inflorescence fragments are known for *Budvaricarpus serialis* (Text-fig. 3a) and *Caryanthus trebecensis* (Text-fig. 3c). In *Budvaricarpus serialis*, each reproductive unit is an aggregation of laterally fused fruits supported by a common bract. Typically, the unit consists of three fruits, but specimens with four fruits are also present. In *Caryanthus trebecensis*, each reproductive unit consists of three bisexual, epigynous flowers/fruits. Each flower/fruit is supported by several bracts, but the number of bracts is not fully established.

Fossils in the Zliv-Řídká Blana mesofossil flora assigned to the Normapolles complex are mostly small flowers or young fruits, often with remains of tepals and stamens preserved, and sometimes with adhering pollen. The flowers are epigynous in all species except for *Dahlgrenianthus* sp. (Text-fig. 3d), which has hypogynous flowers, and all species have bisexual flowers, except for the lateral flowers of *Budvaricarpus* Erw.Knobloch et Mai, which are unisexual. Symmetry of the fruits is radial in species of *Calathiocarpus* sp. (Text-fig. 3e) and *Dahlgrenianthus* sp., while bisymmetrical in species of *Budvaricarpus*, *Caryanthus* E.M.Friis (Text-fig. 3f) and *Zlivifructus* Heřmanová, Dašková et J.Kvaček (Text-fig. 3g). The bisymmetrical flowers have four tepals, four (*Zlivifructus*) or six (*Budvaricarpus* and *Caryanthus*) stamens and two carpels. Pollen associated with species of all three genera with bisymmetrical flowers/fruits is of the *Plicapollis* Pflug type, and the three genera are clearly closely related. *Calathiocarpus* sp. and *Dahlgrenianthus* sp. have five tepals, five stamens and three carpels. No pollen was observed associated with *Calathiocarpus* sp. and *Dahlgrenianthus* sp. from the Zliv-Řídká Blana flora. But in other mesofossil floras, *Calathiocarpus* Erw.Knobloch et Mai is known to be associated with pollen of *Trudopollis* Pflug type, and *Dahlgrenianthus* E.M.Friis, K.R.Pedersen et Schönenb. with pollen of *Minorpollis* Krutzsch type (Friis et al. 2006).

The outer surfaces of the flowers/fruits are covered by short, stiff, and unicellular trichomes that are usually broken, leaving distinct hollow trichome bases. *Caryanthus*

sp. 1 (Text-fig. 3f) is distinguished from other species of the Zliv-Řídká Blana flora by its peltate hairs.

Capsular fruits and seeds of ericalean affinity

Capsular fruits and isolated seeds closely similar to fruits and seeds of extant Ericales are abundant and diverse in the Zliv-Řídká Blana mesofossil flora, including fruits closely similar to *Epacridicarpum cretaceum* (W.W.Jung) Erw.Knobloch et Mai and *Pentaphylax protogaea* Erw.Knobloch et Mai (see Appendix), and seeds assignable to *Eurya* Thunb. and *Protovisnea* Erw.Knobloch et Mai. Most of the capsular fruits in the Zliv-Řídká Blana mesofossil flora are preserved
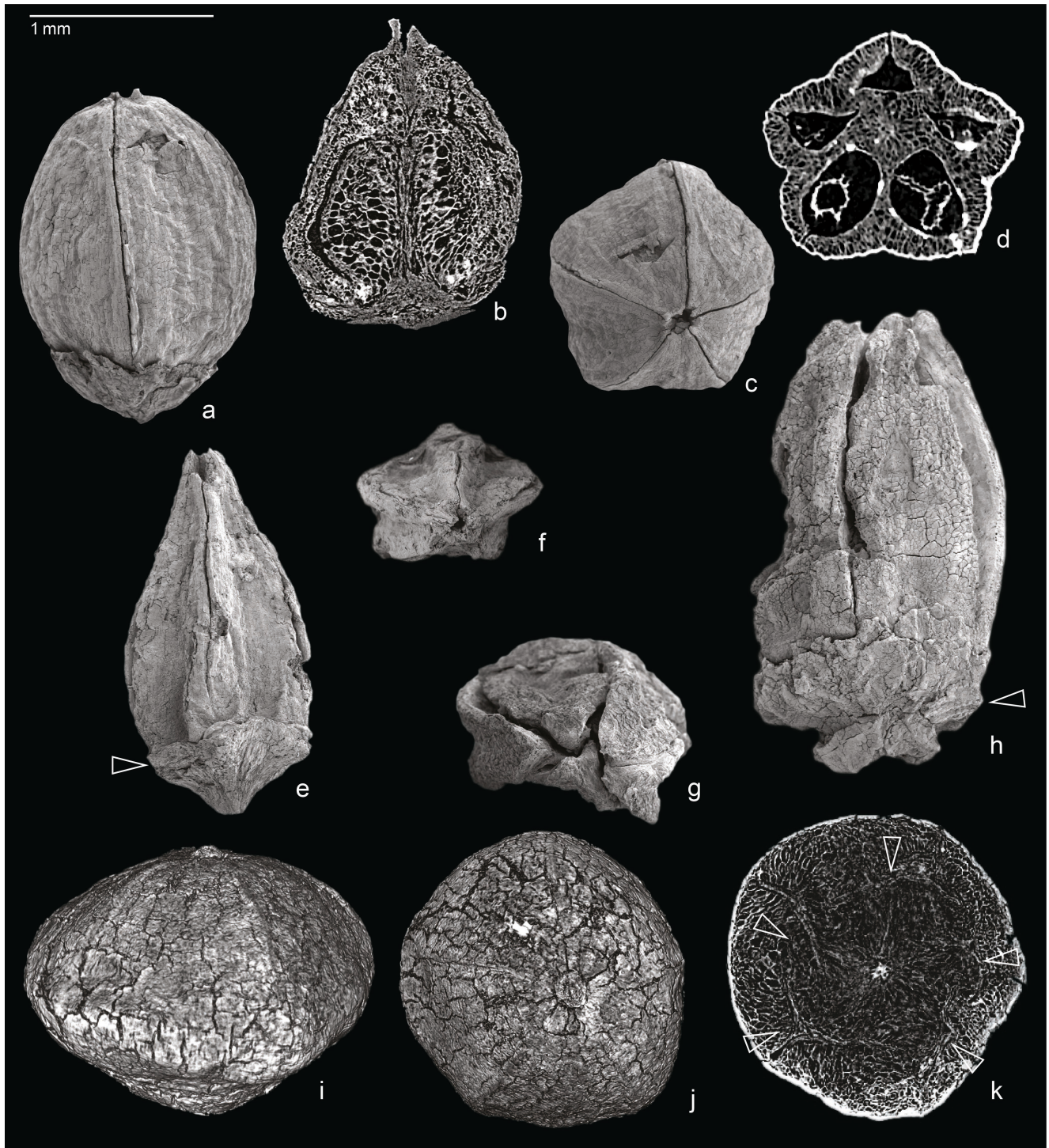
Text-fig. 4. Scanning electron micrographs (a, c, e–k) and X-ray microtomographic orthoslices (b, d) of capsular fruits compose of five carpels from Zliv-Řídká Blana locality. a–d: Taxon 4, a – fruit elliptical in shape, no. NM-F 3188, b – young fruit with reminisce of free styles at top and showing central placentation of seeds, no. NM-F 3188, c – pentacarpellate capsules in apical view, no. NM-F 3188, d – fruit with five locules, no. NM-F 3235; e, f: Taxon 6, e – elongated fruit in lateral view, the persistent perianth at the base of the fruit (arrowhead), no. NM-F 3194, f – fruit in apical view, no. NM-F 3194; g, h: Taxon 5, g – elongated fruit in lateral view, no. NM-F 3193, h – fruit showing remains of a persistent calyx in the basal part (arrowhead), no. NM-F 3193; i–k: Taxon 7, i – pentacarpellate capsules of broadly elliptical shape, no. NM-F 4091, j – fruit, apical view, no. NM-F 4091, k – fruit with five seeds (arrowheads) ellipsoidal or triangular in outline and with a thick seed coat, no. NM-F 4091.
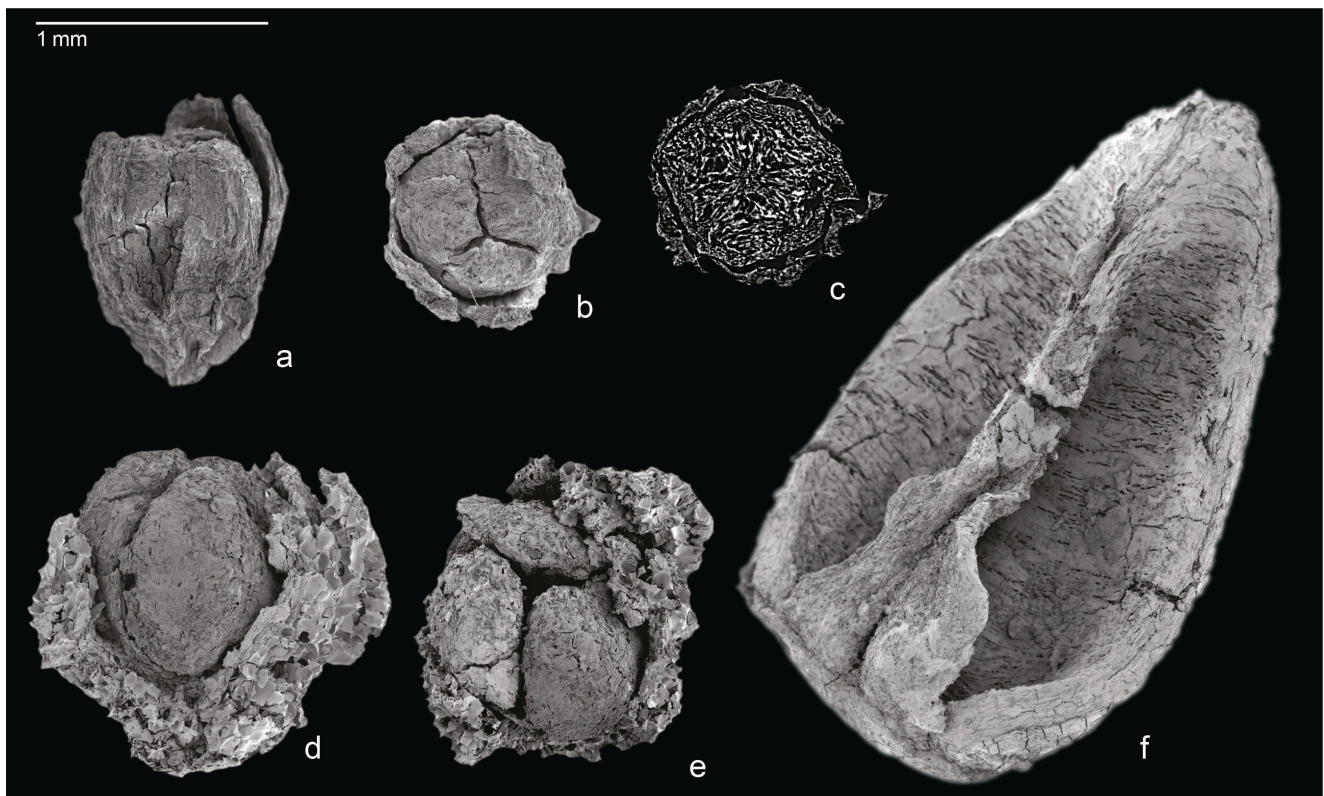
Text-fig. 5. Scanning electron micrographs (a, b, d–f) and X-ray microtomographic orthoslices (c) of capsular fruits composed of three carpels fruits and fragment of a capsular fruit from Zliv-Řídká Blana locality. a–c: Taxon 12, a – capsules of broadly elliptical shape, no. NM-F3302, b – tricarpellate capsules in apical view, no. NM-F 3302, c – tricarpellate capsules with pentamerous calyx, no. NM-F3302; d, e: Taxon 13, d – tricarpellate capsules of broadly elliptical shape, no. NM-F 4501, e – tricarpellate capsules in apical view, no. NM-F 4501; f: Taxon 11, fragment of a capsular fruit, no. NM-F 4622.

in an early stage of maturity, and typically are closed. Critical internal features such as placentation and ovule/seed orientation are therefore known only for abraded specimens and specimens studied using X-ray microtomography. Detailed comparison with previously described fruits is not always straightforward. The general organization of the fruits and the presence of distinct ericalean seeds suggests that at least some of the fruits are of ericalean affinity, but the assignment is tentative here, and the fruits are merely referred to as Taxon 4 – Taxon 16.

All the capsular fruits are derived from hypogynous flowers (Text-figs 4a–k, 5a–f), indicated by remains of a persistent calyx below many of the fruits (Text-figs 4a, e, h, 5a, d). When known, the calyx is pentamerous and the calyx lobes are typically thick or very thick (Text-fig. 4h). In all taxa, petals appear to be shed, and none of the specimens shows remains of the androecium.

Seven of the capsular fruits are pentacarpellate, with five locules and an elongate elliptical to ovoid shape (Text-fig. 4a–k). Four are tricarpellate, with three locules and a broad elliptical shape (Text-fig. 5a–e). Further, a fragment of a capsular fruit indicates the presence of an additional pentacarpellate species (Text-fig. 5f). Five free styles are present at top of the fruits of Taxon 4. In other taxa, the styles are abraded. A few specimens show initial loculicidal dehiscence, but most specimens are closed. For specimens with known internal features, placentation is central, as seen in Taxon 4 (Text-fig. 4b). The number of ovules/seeds varies from one to several per carpel. Seeds in Taxon 7 (Text-fig.

4k) are ellipsoidal or triangular in outline with a thick seed coat, while others have a thinner seed coat and a reticulate surface. The outer fruit wall in all taxa is covered by numerous trichomes that are typically broken, leaving only the rounded trichome bases on the surface.

The five different kinds of ericalean seeds are clearly assignable to the Pentaphylacaceae family, and three of them are assigned to extant *Eurya*. Two other species are assigned to the extinct genus *Protovisnea*, which is closely similar to extant *Visnea* L.F. Both *Protovisnea* and *Visnea* have campylotropous seeds. Seeds of *Protovisnea* (Text-fig. 6a, b) are rounded to angular in shape, with the narrow elongate seed cavity flanked by two bulging regions of larger cells. The outer cells of the seed coat are characterised by polygonal facets that are smaller over the seed cavity and larger over the lateral bulging regions. Seeds of *Eurya crassitesta* Erw.Knobloch (Text-fig. 6c, d) are almost circular in outline, with cells around the curved raphe forming a narrow horseshoe-shaped condyle. The outer cells of the seed coat are palisade-shaped, with finely pitted cell walls and a deep cell lumina that narrows towards the inside.

Fruits of uncertain affinity

In addition to the fruits and seeds of fagalean and ericalean affinities described above, the Zliv-Řídká Blana mesofossil flora includes thirteen other taxa of fruits that are currently of uncertain systematic affinity (see Appendix). Two of them (*Trebecenia sarcocalycalis* Erw.Knobloch et
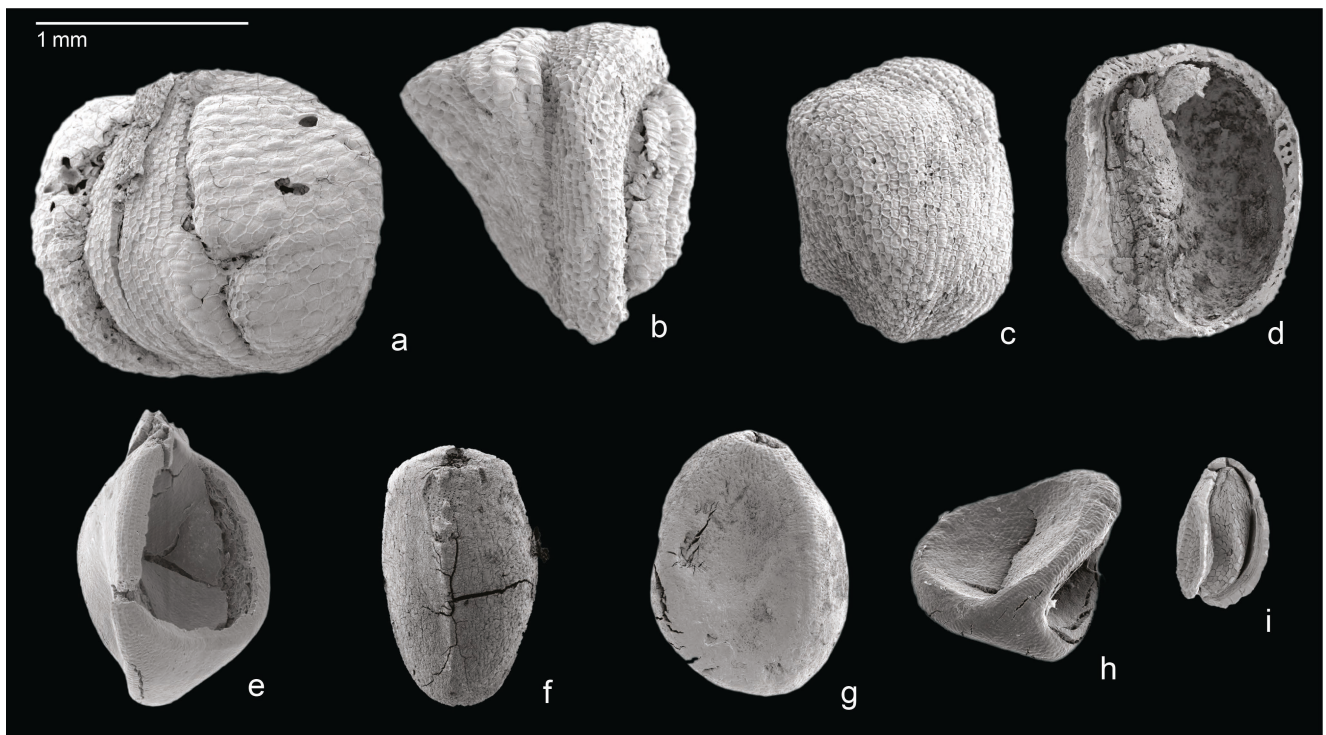
Text-fig. 6. Scanning electron micrographs of seeds of ericalean affinity (a–d) and seeds of uncertain affinity (e–i) from Zliv-Řídká Blana locality. **a:** *Protovisnea* sp. 1, rounded seed with the narrow elongate seed cavity flanked by two bulging regions of larger cells, no. NM-F 3177; **b:** *Protovisnea* sp. 2, angular seed with the narrow elongate seed cavity flanked by two bulging regions of larger cells, no. NM-F 3179; **c, d:** *Eurya crassitesta*, one seed split into two parts, no. NM-F 3211, c – surface cells of the seed coat are palisade, d – cross-section of the seed; **e:** Nympheaceae sp. 1, seed, no. NM-F 3636; **f:** Nympheaceae sp. 2, seed, no. NM-F 4634; **g:** *Klikovispermum* sp.1, seeds with irregular outline and smooth outer surface, no. NM-F 3203; **h:** *Klikovispermum malechii*, seed with an orange-segment shape, no. NM-F 3299; **i:** Taxon 35, seed, no. NM-F 3236.

MAI and cf. *Sabia menispermoides* ERW.KNOBLOCH et MAI) are assigned to species previously described by Knobloch and Mai (1983, 1986), while eleven are unassigned and referred to as Taxon 17 – Taxon 26 and Taxon 28.

Fruits of *Trebecenia sarcocalycalis* (Text-fig. 7a–c) are almost circular in transverse section, formed from a syncarpous and tricarpellate, superior gynoecium with three free styles at the top. The fruits are supported by a pentamerous and persistent calyx. Sepals are very thick and coriaceous, extending well beyond the apex of the fruit. X-ray microtomography documents that the fruits are trilocular. There is no indication of sutures on the fruit surface, and the fruits may be indehiscent nuts or drupes. However, because they are probably preserved in a young developmental stage, the possibility that the mature fruits were capsules cannot be ruled out. *Trebecenia sarcocalycalis* was first described by Knobloch and Mai (1986) from the Klikov Formation, based on a single specimen. It was compared to fruits of extant Saxifragales and Cunoniales (now Oxalidales), but the systematic position of this taxon remains to be established.

Two fruits here assigned to Taxon 17 (Text-fig. 7d) and Taxon 28 are broadly ovoid to ellipsoid in outline, with slightly sunken stylar region. The fruits are dehiscent capsules, with two apparent equal valves opening along the larger circumference.

Another very distinct and common fossil in the Zliv-Řídká Blana mesofossil flora, here referred to as Taxon 19, is represented by about 350 specimens, typically preserved as charcoalifications. The fruits are single-seeded, almost spherical, with a thick fruit wall mainly composed of large isodiametric and thick-walled cells covered by a thin outer layer of smaller, thin-walled cells (Text-fig. 7f). In well-preserved specimens, the apical part of the fruits is slightly pointed with an apparently bifid stigmatic region. The fruits are bisymmetrical, in some specimens with a narrow furrow extending all around the fruit. Another species of Taxon 19 are slightly opened along the furrow, and the fruit is interpreted as a one-seeded pod that may be comparable to the very thick-walled pods of *Hakea* SCHRAD. et J.C.WENDL. and several other serotinous fruits of extant Proteaceae. The fruit surface is almost smooth to rugulate, with large isodiametric cells (125 × 125 μm) of the outer fruit wall exposed in abraded specimens (Text-fig. 7e). The single seed is small and bitegmic. A more detailed investigation of this fossil is in progress, but the systematic position of the fossil is currently unknown.

Two other unassigned fruits are syncarpous, multicarpellate and apparently capsular. One has seven carpels (Taxon 22; Text-fig. 7h) and the other has ten carpels (Taxon 20; Text-fig. 7g).

There are also several endocarps with a thick fruit wall of small isodiametric cells and an irregularly sculptured surface of deep furrows and depressions, indicating the presence of drupaceous fruits (Text-fig. 7i–k). These drupaceous fruits include cf. *Sabia menispermoides*, which has a laterally flattened and almost half-moon shape, with shallow cavities forming an irregularly sculptured surface
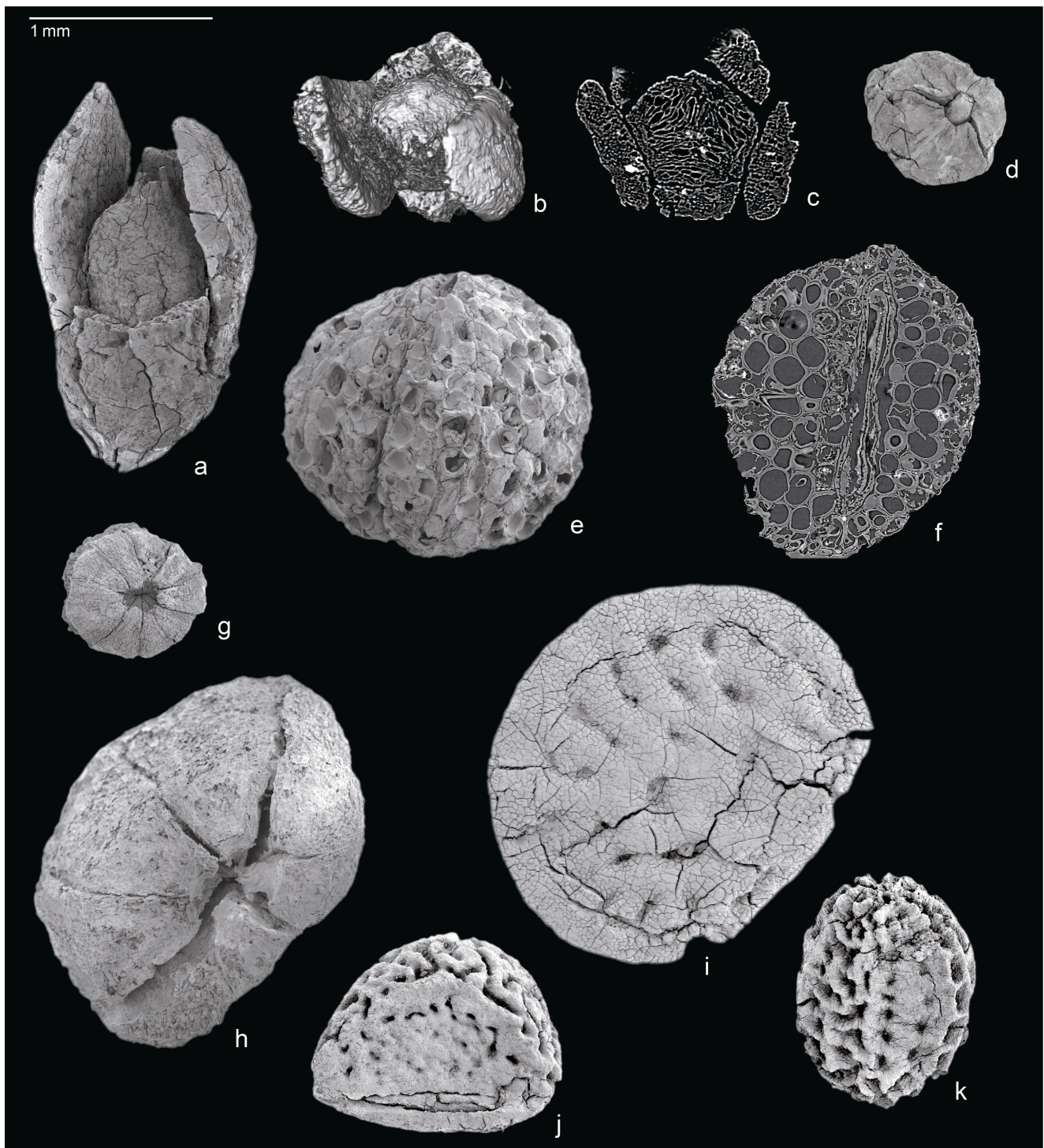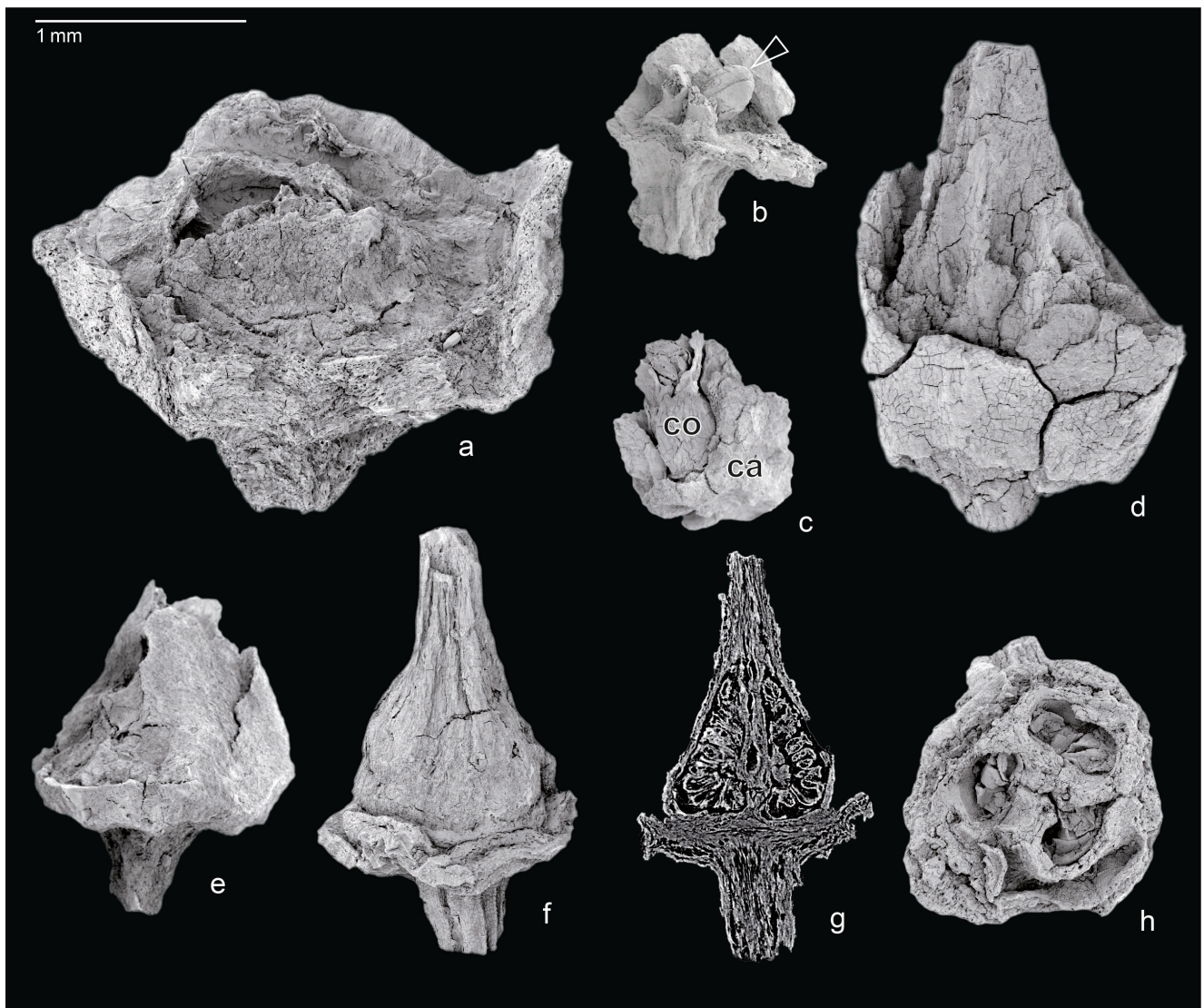
Text-fig. 7. Scanning electron micrographs (a, b, d, e, g–k), X-ray microtomographic orthoslices (c) and synchrotron radiation X-ray tomographic microscopy orthoslices (f) of fruits and endocarps of uncertain affinity from Zliv-Řídká Blana locality. a–c: *Trebecenia sarcocalis*, a – tricarpellate fruit, no. NM-F 3637, b – fruits supported by pentamerous and persistent calyx, no. NM-F 3637, c – fruit almost circular in transverse section, no. NM-F 3637; d: Taxon 17, small fruit with slightly sunken stylar region, no. NM-F 3201; e: Taxon 19, spherical fruit, the fruit wall composed of large isodiametric, thick walled cells, no. NM-F 3181; f: Taxon 19, single-seeded fruit, no. NM-F 3621; g: Taxon 20, syncarpous, multicarpellate fruit of ten carpels, no. NM-F 3200; h: Taxon 22, syncarpous, multicarpellate fruit of seven carpels, no. NM-F 3159; i: cf. *Sabia menispermoides*, endocarp of drupaceous fruits, no. NM-F 4624; j: Taxon 25, endocarp triangular in cross-section, no. NM-F 3218; k: Taxon 24, endocarp spherical in cross-section with a distinctly ribbed and foveolate surface, no. NM-F 3217.

(Text-fig. 7i), as well as three unassigned types (Taxon 24 – Taxon 26). One is spherical in cross-section with a distinctly ribbed and foveolate surface (Text-fig. 7k), and one is triangular in cross-section, probably part of a segmented fruit (Text-fig. 7j).

Flowers of uncertain affinity

The Zliv-Řídká Blana mesofossil flora also includes eight different flower types of unknown affinity (see Appendix). They are all typical eudicots with a whorled arrangement of perianth parts and syncarpous ovaries formed from three

Text-fig. 8. Scanning electron micrographs (a–f, h) and X-ray microtomographic orthoslices (g) of flowers from Zliv-Řídká Blana locality. a: Taxon 27, epigynous flower, no. NM-F 4504; b: Taxon 30, epigynous flower, remains of two thick sepals, a massive nectary disk (arrowhead) and two styles, no. NM-F 3199; c: Taxon 29, flower with stamens have long filament, calyx (ca) and corolla (co), no. NM-F 3198; d: Taxon 32, flower, no. NM-F 4503; e–h: Taxon 14, e – hypogenous flower, no. NM-F 3196, f – floral bud with a thick pedicel, no. NM-F 3196, g – flower with gynoecium showing central placentation and several seeds, no. NM-F 3196, h – flower with gynoecium showing several seeds, no. NM-F 4505.

(Taxa 29, 30, 31) or five (Taxa 27 and 32) carpels. They are generally of poor preservation, but clearly represent a diversity of forms. Currently, none of the flowers has been assigned to a family or order. Two of the flower types, taxa 27 (Text-fig. 8a) and 30 (Text-fig. 8b) are epigynous. All other flower types are hypogynous. The flowers have a pentamerous perianth arranged in one or two whorls. Taxon 29 (Text-fig. 8c) has a perianth differentiated into calyx and corolla. The imbricated sepals are prominent and woody, while the petals are thin. The flower assigned to Taxon 29 (Text-fig. 8c) is clearly bisexual and has stamens with long filaments. However, no pollen grains have been observed. The flower assigned to Taxon 30 (Text-fig. 8b) is abraded, but shows remains of two thick sepals, a massive nectary disk and two styles. Taxon 14 (Text-fig. 8e–h) is a hypogynous flower, preserved in pre-anthetic stage, with a thick pedicel, a pentamerous perianth, imbricate sepals and tricarpellate gynoecium tricarpellate (Text-fig. 8h) and central placentation (Text-fig. 8g).

Seeds of uncertain affinity

In addition to the ericalean seeds of *Protovisnea* and *Eurya*, the Zliv-Řídká Blana mesofossil flora also comprises 16 other kinds of isolated seeds (see Appendix). All are anatropous and most of them have a hard seed coat. Two types are probably related to the Nymphaeaceae, Taxon Nymphaeaceae sp. 1 (Text-fig. 6e) and Taxon Nymphaeaceae sp. 2 (Text-fig. 6f). They are characterised by their sclerified exotestal seed coat and jigsaw-like surface pattern formed from the outlines of the undulate anticlinal walls of the outer palisade-shaped cells.

Seven different kinds of seeds are assigned to the genus *Klikovispermum* Erw.Knobloch et Mai (Text-fig. 6g, h). This genus, as used by Knobloch and Mai (1983, 1986), is heterogeneous, including a variety of probably unrelated seeds with irregular and angular outline and a smooth, shiny outer surface. One of the *Klikovispermum* seed types with an orange-segment shape (Text-fig. 6h) conforms with seeds described as *Klikovispermum malechii* (Erw.Knobloch)

ERW.KNOBLOCH et MAI from the Klikov Formation (Knobloch and Mai 1986).

Insect remains

Two different kinds of fossils interpreted as remains of insects are associated with the plant fragments, and similar to fossils described previously as fruits or seeds. *Microcarpolithes hexagonalis* VANGEROW, 1954 (Text-fig. 2e) includes fossils with a characteristic subcylindrical shape and hexagonal transverse section. They are about 0.8 mm long, 0.4 mm broad, and solid. The species was first thought to be small fruits (Vangerow 1954), but now interpreted as faecal pellets/coprolites (Knobloch 1977, Colin et al. 2011). The fossil assigned to *Palaeoaldrovanda splendens* KNOBLOCH et MAI, 1984 (Text-fig. 2f) is a small compact fragment resembling a fragment of a seed coat with a shiny outer surface, sometimes with an imprint of rectangular cells. Based on comparison with eggs of extant insects, *Palaeoaldrovanda splendens* is now thought to be insect remains (Heřmanová and Kvaček 2010), rather than seeds related to *Aldrovanda vesiculosa* L. as originally suggested by Knobloch and Mai (1984).

Discussion

Systematic composition and diversity of the Zliv-Řídká Blana mesofossil flora

Currently 69 plant species, together with two different kinds of insect remains, have been recognised from the new mesofossil flora from the Zliv-Řídká Blana locality. The flora was extracted from a single horizon in the Klikov Formation and provides a representative subset of the total mesofossil diversity reported previously from this formation. Based on numerous samples from drillings and various exposures in the Klikov Formation, Knobloch and Mai (1986) reported about 100 different species of angiosperm reproductive structures. The number of taxa in the Zliv-Řídká Blana mesofossil flora may increase somewhat when more material is sorted and more detailed examinations have been carried out using non-destructive methods such as SRMXT and micro-CT. For instance, most of the capsular fruits are closed, and there is generally little information on placentation and number of ovules/seeds important for distinguishing superficially similar fruits (e.g., Knobloch and Mai 1986). There are also a few fruits with partly abraded surfaces and uncharacteristic external morphology, which may come from more than one taxon. However, the number of species is in conformity with several other mesofossil floras with angiosperm fossils from the Cretaceous (e.g., Eriksson et al. 2000), although there are also Cretaceous mesofossil floras that are considerably more diverse (e.g., Friis et al. 2011).

The majority of mesofossils from the Zliv-Řídká Blana mesofossil flora can be assigned to angiosperms, while non-angiosperms are rare. The only non-angiospermous plant fossils are a single fragment of a bryophyte gametophyte, a few leaf fragments with circinate vernation that may all represent ferns, and a single conifer needle.

Angiosperm remains from the Zliv-Řídká Blana mesofossil flora are mainly fruits and seeds. Flowers are rare, but several fruits have scars or remnants of floral parts preserved, allowing reconstruction of the original floral organisation for some of the fossils. Fossils assignable to the Normapolles complex (Fagales) and of possible ericalean affinity dominate the mesofossil flora. The Normapolles complex, first defined by their characteristic triaperturate pollen, is a group of extinct angiosperms that are common and widespread in Late Cretaceous and early Tertiary floras within the so-called Normapolles Province (Góczán et al. 1967, Batten and Christopher 1981, Pacltová 1981, Knobloch and Mai 1983, Friis and Crane 1989, Sims et al. 1999, Schönenberger et al. 2001, Friis et al. 2006, Heřmanová et al. 2011, 2017, Polette and Batten 2017). The discovery of Normapolles pollen in situ in fossil floral structures or closely associated with floral structures has demonstrated that these fossils are related to extant members of the higher Fagales (e.g., Friis 1983, Friis et al. 2006). Normapolles pollen have long been known as a predominant element of the Late Cretaceous palynofloras of the Czech Republic (Pacltová 1981), and mesofossils assignable to the Normapolles complex are also an important constituent of the Zliv-Řídká Blana mesofossil flora, with more than half of the specimens assignable to this complex, comprising 620 specimens in five genera and twelve species. Fossils included in this complex are flowers or fruits with epigynous or partial epigynous organisation. The gynoecium is formed from two or three carpels and the fruits are nuts. Species of *Budvaricarpus*, *Caryanthus* and *Zlivifructus* are particularly distinct and common in Zliv-Řídká Blana mesofossil flora. They show close similarity in floral organisation and pollen morphology to flowers of the extant genus *Rhoiptelea* DIELS et HAND.-MAZZ., indicating a position close to the Juglandaceae for these taxa (Heřmanová et al. 2011). This is in line with reports from other Late Cretaceous mesofossil floras from Europe and eastern North America where the Normapolles group is particularly diverse (Friis 1983, Knobloch and Mai 1986, Friis et al. 2011).

Another major group of fossils in the Zliv-Řídká Blana mesofossil flora are capsular fruits of possible ericalean affinity and isolated seeds assignable to Ericales, with a total of about 100 specimens and about 15 species. The number of genera is not fully established. Remains of floral parts show that the fruits were derived from hypogynous flowers, and fruits are three- to five-loculed capsules. The diversity of ericalean taxa in the Zliv-Řídká Blana mesofossil is in line with records from other Late Cretaceous mesofossil floras of Central Europe, where more than 30 different taxa of capsular fruits and seeds of ericalean affinity were described by Knobloch and Mai (1983, 1984, 1986) and assigned to several families of the Ericales, including Actinidiaceae, Clethraceae, Cyrillaceae, Ericaceae, Pentaphylacaceae and Theaceae (see also survey in Friis et al. 2011). However, internal features, including modes of placentation and organisation of ovules/seeds are missing for several of the fossils, and more detailed systematic evaluations are currently not possible. The isolated ericalean seeds are campylotropous, and clearly assignable to species of *Protovisnea* and *Eurya crassitesta* (Pentaphylacaceae).

Flower organisation

The position of the perianth can be established for 31 taxa. 17 have an inferior or partly inferior ovary, and 20
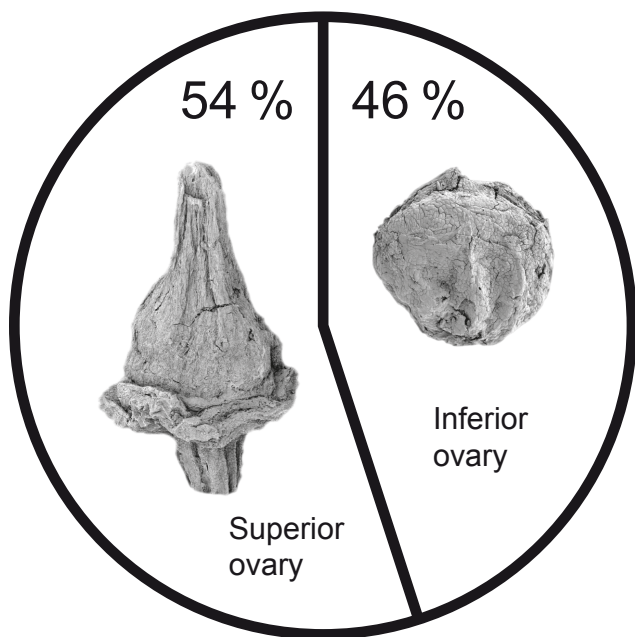
Text-fig. 9. The drawing shows the ratio of epigynous and hypogenous flowers in Zliv-Řídká Blana mesofossil flora. The ovary is inferior, and the flower is epigynous in 17 taxa. The ovary is superior, and the flower is hypogenous in 20 taxa.

have a superior ovary (Text-fig. 9). This is in line with floral organisation in other more or less contemporaneous angiosperm floras (Allon flora, Georgia, USA; Åsen flora, Scania, Sweden; Kamikitaba flora, Japan; Mira and Esquira, Portugal), where flowers with inferior/semi-inferior ovaries constitute 45–50 % of the flowers (Friis et al. 2011).

Most of the fruits encountered in the mesofossil flora can be characterised as indehiscent nuts (12 taxa), dry capsular fruits (17 taxa) or drupes/endocarps (4 taxa) (see Appendix). The nuts mainly represent the Normapolles complex. Most of the capsular fruits are probably ericalean, while the drupes are currently unassigned. Taxon 19 fruit is interpreted as a one-seeded pod comparable to the very thick-walled pods of *Hakea*. The five different kinds of campylotropous seeds are clearly assignable to the Pentaphylacaceae family (*Eurya*, *Protovisnea*). 16 other kinds of isolated seeds are anatropous, and most of them have a hard seed coat. Two types are probably related to the Nymphaeaceae.

Microfossils versus mesofossils from the Klikov Formation

Several palynological studies have been carried out for the Klikov Formation, based mainly on samples from boreholes (Pacltová 1955, 1958a, b, 1961, 1981). In all assemblages, angiosperms are predominant. For instance, in the assemblages from the GB 4 borehole (České Budějovice Basin, South Bohemia) and Pecák 4003 borehole (Třeboň Basin, South Bohemia), angiosperms make up 60 % to 84 % of all sporomorphs. Conifers are not encountered in the mesofossil flora, and conifers are also rare in the dispersed pollen floras from the Klikov Formation, where they are subordinate to bryophytes and pteridosperms in samples from the younger part of the formation, while they are more common in samples from the older part of the formation (Pacltová 1981).

Pollen grains assigned to the Normapolles complex are particularly important in the Klikov Formation. They are diverse in both number of species and number of specimens, and they totally dominate some assemblages. For instance, in the Pecák 4003 borehole sample, Normapolles pollen constitutes 67 % of all palynomorphs (Pacltová 1981). Pollen grains of the genus *Plicapollis*, similar to grains produced by *Budvaricarpus*, *Caryanthus* and *Zlivifructus* were also observed by Pacltová (1961) in great numbers in the Klikov Formation.

Macrofossils versus mesofossils in the Klikov Formation

Fossil leaves from the Klikov Formation include species of *Debeya* MIQ., *Ettingshausenia* STIEHLER, *Araliophyllum* ETTINGSH., *Quercophyllum*, *Proteophyllum* P.A.FRIEDRICH, *Myricophyllum* SAPORTA and *Cocculophyllum* VELEN. (Němejc 1961, Knobloch 1964, Němejc and Kvaček 1975). Systematic affinities have been suggested for only two of these genera: *Cocculophyllum* was assigned to the Laurales (Němejc and Kvaček 1975), and *Ettingshausenia* is of platanoid affinity (Kvaček and Váchová 2006). However, no lauralean or platanoid reproductive structures have been recovered from the mesofossils. The leaf fossils and mesofossils were derived from slightly different facies in the Klikov Formation, and the disparity in composition between the two different kinds of assemblages may reflect local variation of the vegetation. Frequent occurrence of Normapolles pollen and mesofossils may suggest that some of the leaves, like *Quercophyllum*, are representatives of the same fagalean plants, but a definite link between these leaves and the Normapolles complex has not been made.

Palaeoecology of the Klikov Formation

Fluvial sediments are common in the South Bohemian Basins (Slánská 1976). The preservation of plant fossils in the meso- and macrofossil floras suggests that they were subject to only moderate transport before burial, and probably derived from a vegetation growing close to the depositional basin. Sedimentological studies suggest that the mudstone lenses containing the plant fragments were deposited on an alluvial flood plain of a small, braided river (J. Laurin oral communication 2010). The vegetation in close vicinity of the river was probably formed from a gallery forest with platanoids and lauroids growing directly on the alluvial plain, as suggested by the plant megafossils (Němejc and Kvaček 1975, Váchová and Kvaček 2009). Vegetation growing on slopes of the valley adjacent to the gallery forest was probably more open and shrubby, as documented by mesofossils.

Flower and pollen morphology of the Normapolles fossils, together with the abundance of Normapolles pollen in the sediments, indicate wind-pollination for this dominant element of the flora (Friis 1983, Schönenberger et al. 2001, Friis et al. 2003). The close relationship of some of the Normapolles taxa to *Rhoiptelea* might indicate a relatively open vegetation of smaller, wind-pollinated trees. The diverse ericalean component of the flora was probably derived from a shrubby understory, or perhaps a more open heath landscape bordering the forest. The small size of the seeds and fruits is in accordance with that of other Cretaceous floras (Tiffney 1984, Eriksson 2000), and also suggests open vegetation. Both the Normapolles plants and the ericalean plants are thought to have been woody shrubs or small trees.

Palaeoclimatic conditions during the deposition of the Klikov Formation were approximated using Leaf Margin Analysis, Climate Leaf Analysis Multivariate Program (CLAMP) and the Nearest Living Relative on the dicotyledonous leaf remains recovered from the formation (Váchová and Kvaček 2009). All analyses suggest a seasonally dry, paratropical to warm temperate climate, with a mean annual temperature of about 15°C (Váchová and Kvaček 2009). A seasonally dry climate is indicated by the presence of abundant charcoalified fragments of wood and reproductive structures, suggesting frequent wildfires. Periods of warm and dry climate during the deposition of the Klikov Formation is further corroborated by the cyclic occurrence of red beds.

Conclusions

The new mesofossil flora from the Zliv-Řídká Blana locality comprises a diversity of small flowers, fruits and seeds of angiosperms, and scattered fragments of bryophytes and ferns. The Zliv-Řídká Blana mesofossil flora is comparable to other Late Cretaceous mesofossil floras in the small size of all reproductive structures and in the organization of the angiosperm floral structures. The flora documents the presence of a diverse, angiosperm-dominated vegetation in the late Turonian-Santonian of Central Europe. It corroborates previous studies that show a high proportion of taxa related to the wind-pollinated fagalean Normapolles complex, as well as many fossils of probable ericalean affinity in Late Cretaceous floras of Laurasia and other parts of the world. Many proxies, such as the small size of the fruits and seeds, the high proportion of wind-pollinated taxa, data from the associated leaf flora and sedimentology all suggest that the Zliv-Řídká Blana region was covered by a rich, open vegetation growing close to the alluvial plain in a climate with seasonally dry periods.

Acknowledgements

References

Batten, D. J., Christopher, R. A. (1981): Key to recognition of Normapolles and some morphologically similar genera. – Review of Palaeobotany and Palynology, 35: 359–383.
https://doi.org/10.1016/0034-6667(81)90117-2

Colin, J. P., Néraudeau, D., Nel, A., Perrichot, V. (2011): Termite coprolites (Insecta: Isoptera) from the Cretaceous of western France: A palaeoecological insight. – Revue de Micropaléontologie, 54: 129–139.
https://doi.org/10.1016/j.revmic.2011.06.001

Eriksson, O., Friis, E. M., Lofgren, P. (2000): Seed size, fruit size, and dispersal systems in angiosperms from the Early Cretaceous to the Late Tertiary. – American Naturalist, 156: 47–58.
https://doi.org/10.1086/303367

Ettingshausen, C. (1852): Über fossile Pflanzen bei Wittingau in Böhmen. – Jahrbuch der Kaiserlich-Königlichen Geologischen Reichsanstalt, 3(4): 144.

Friis, E. M. (1983): Upper Cretaceous (Senonian) floral structures of juglandalean affinity containing Normapolles pollen. – Review of Palaeobotany and Palynology, 39: 161–188.
https://doi.org/10.1016/0034-6667(83)90015-5

Friis, E. M., Crane, P. R. (1989): Reproductive structures of Cretaceous Hamamelidae. – In: Crane, P. R., Blackmore, S. (eds), Evolution, Systematics, and Fossil History of the Hamamelidae, Vol. 1. Clarendon Press, Oxford, pp. 155–174.

Friis, E. M., Crane, P. R., Pedersen, K. R. (2011): Early Flowers and Angiosperm Evolution. – Cambridge University Press, Cambridge, 585 pp.
https://doi.org/10.1017/CBO9780511980206

Friis, E. M., Pedersen, K. R., Schönenberger, J. (2003): *Endressianthus*, a new Normapolles-producing plant genus of fagalean affinity from the Late Cretaceous of Portugal. – International Journal of Plant Sciences, 164(5 Suppl.): S201–S223.
https://doi.org/10.1086/376875

Friis, E. M., Pedersen, K. R., Schönenberger, J. (2006): Normapolles plants: a prominent component of the Cretaceous rosid diversification. – Plant Systematics and Evolution, 260: 107–140.
https://doi.org/10.1007/s00606-006-0440-y

Góczán, F., Groot, J., Krutzsch, W., Pacltová, B. (1967): Die Gattungen des "Stemma Normapolles Pflug 1953b" (Angiospermae) – Neubeschreibungen und Revision europäischer Formen (Oberkreide bis Eozän). – Paläontologische Abhandlungen, B – Paläobotanik, 2(3): 427–633.

Heřmanová, Z., Dašková, J., Ekrt, B., Kvaček, J. (2017): *Zlivifructus* gen. nov., a new member of the Normapolles complex. – Review of Palaeobotany and Palynology, 246: 177–184.
https://doi.org/10.1016/j.revpalbo.2017.06.012

Heřmanová, Z., Kvaček, J. (2010): Late Cretaceous *Palaeoaldrovanda*, not seeds of a carnivorous plant, but eggs of an insect. – Journal of the National Museum (Prague), Natural History Series, 179: 105–118.

Heřmanová, Z., Kvaček, J. (2012): A new record of the genus *Caryanthus* from the Cretaceous of South Bohemia (Czech Republic). – Acta Musei Nationalis Pragae, Series B – Historia Naturalis, 68: 47–50.

Heřmanová, Z., Kvaček, J., Dašková, J. (2016): *Caryanthus* diversity in the Late Cretaceous. – Review of Palaeobotany and Palynology, 231: 33–47.
https://doi.org/10.1016/j.revpalbo.2016.04.012

Heřmanová, Z., Kvaček, J., Friis, E. M. (2011): *Budvaricarpus serialis* Knobloch & Mai, An Unusual New Member

of the Normapolles Complex from the Late Cretaceous of the Czech Republic. – International Journal of Plant Sciences, 172: 285–293.
https://doi.org/10.1086/657278

Knobloch, E. (1964): Neue Pflanzenfunde aus dem südböhmischen Senon. – Jahrbuch des Staatlichen Museums für Mineralogie und Geologie zu Dresden, 1964: 133–201.

Knobloch, E. (1977): Paläokarpologische Charakteristik der Flyschzone der mährischen Karpaten. – Sborník geologických věd, Paleontologie, 19: 79–135.

Knobloch, E. (1984): Megasporen aus der Kreide von Mitteleuropa. – Sborník geologických věd, Paleontologie, 26: 157–195.

Knobloch, E. (1985): Paläobotanisch-biostratigraphische Charakteristik der Klikov-Schichtenfolge (Oberturon – Santon) in Südböhmen. – Sborník geologických věd, Geologie, 4: 101–145.

Knobloch, E., Mai, D. H. (1983): Carbonized seeds and fruits from the Cretaceous of Bohemia and Moravia and their stratigraphical significance. – In: Brzobohatý, R. (ed.), Miscellanea micropalaeontologica: A memorial volume dedicated to the 18th European colloquy on micropalaeontology (Knihovnička zemního plynu a nafty, no. 4). Moravské naftové doly, Hodonín, pp. 305–332.

Knobloch, E., Mai, D. H. (1984): Neue Gattungen nach Früchten und Samen aus dem Cenoman bis Maastricht (Kreide) von Mitteleeuropa. – Feddes Repertorium, 95: 3–41.
https://doi.org/10.1002/fedr.4910950103

Knobloch, E., Mai, D. H. (1986): Monographie der Früchte und Samen in der Kreide von Mitteleuropa. – Rozpravy Ústředního ústavu geologického, 47: 1–219.

Konopka, A. S., Herendeen, P. S., Smith Merril, G. L., Crane, P. R. (1997): Sporophytes and Gametophytes of Polytrichaceae from the Campanian (Late Cretaceous) of Georgia, U.S.A. – International Journal of Plant Sciences, 158: 489–499.
https://doi.org/10.1086/297459

Kvaček, J., Váchová, Z. (2006): Revision of platanoid foliage from the Cretaceous of the Czech Republic. – Journal of the National Museum, Natural History Series, 175(3-4): 77–89.

Malecha, A., Špinar, Z., Bořková-Gabrielová, N., Mrázek, A., Němejc, F., Pacltová, B., Řeháková, Z., Slánská, J. (1962): Nové dělení a označení stratigrafických jednotek jihočeských pánví [New subdivision and naming of stratigraphic units of South Bohemian Basins]. – Věstník Ústředního ústavu geologického, 37: 161–170. (in Czech)

Němejc, F. (1956): Paleobotanická studie k otázce stratigrafie uloženin jihočeské pánve [Palaeobotanical study on the stratigraphy of sediments from the South Bohemian Basin]. – Sborník Ústředního ústavu geologického, oddíl paleontologický, 32: 335–377. (in Czech)

Němejc, F. (1957): Fossil plants from the iron stones of Hrutov (near Lišov in S. Bohemia). – Sborník Národního musea v Praze, B, 13: 97–122.

Němejc, F. (1961): Fossil plants from Klikov in S. Bohemia (Senonian). – Rozpravy Československé akademie věd, řada matematických a přírodních věd, 69: 1–48.

Němejc, F., Kvaček, Z. (1975): Senonian plant macrofossils from the region of Zliv and Hluboká (near České Budějovice). – Univerzita Karlova, Praha, 83 pp.

Pacltová, B. (1955): Mikropaleontologický výzkum v oblasti jihočeského terciéru [Micropalaeobotanical investigations from the South Bohemain Tertiary]. – Zprávy o geologických výzkumech v roce 1954: 132–134. (in Czech)

Pacltová, B. (1958a): Palynologický výzkum křídových, terciérních a kvartérních hornin v jihočeských pánvích v roce 1956 [Palynological investigations of Cretaceous, Tertiary and Quaternary sediments in South Bohemian basins in the year 1956]. – Věstník Ústředního ústavu geologického, 33: 330–338. (in Czech)

Pacltová, B. (1958b): Zajímavé výsledky palynologického výzkumu strukturního vrtu z Budějovické pánve [Interesting results of palynological investigation of structural borehole from the Budějovice Basin]. – Časopis pro mineralogii a geologii, 3: 419–421. (in Czech)

Pacltová, B. (1961): Některé rostlinné mikrofosilie ze sladkovodních uloženin svrchní křídy (senon) v jihočeských pánvích I. [Some plant micro-fossils from fresh-water sediments of the Late Cretaceous (Senonian) of the South Bohemian basins I.]. – Sborník Ústředního ústavu geologického, 26: 47–102. (in Czech)

Pacltová, B. (1981): The evolution and distribution of Normapolles pollen during the Cenophytic. – Review of Palaeobotany and Palynology, 35: 175–208.
https://doi.org/10.1016/0034-6667(81)90108-1

Polette, F., Batten, D. J. (2017): Fundamental reassessment of the taxonomy of five Normapolles pollen genera. – Review of Palaeobotany and Palynology, 243: 47–91.
https://doi.org/10.1016/j.revpalbo.2017.04.001

Schönenberger, J., Pedersen, K. R., Friis, E. M. (2001): Normapolles flowers of fagalean affinity from the Late Cretaceous of Portugal. – Plant Systematics and Evolution, 226: 205–230.
https://doi.org/10.1007/s006060170066

Sims, H. J., Herendeen, P. S., Lupia, R., Christopher, R. A., Crane, P. R. (1999): Fossil flowers with Normapolles pollen from the Upper Cretaceous of south-eastern North America. – Review of Palaeobotany and Palynology, 106: 131–151.
https://doi.org/10.1016/S0034-6667(99)00008-1

Slánská, J. (1974): Continental Cretaceous and Tertiary sedimentation in the South Bohemian Basin. – Neues Jahrbuch für Geologie und Paläontologie, 146(3): 385–406.

Slánská, J. (1976): A red-bed formation in the South Bohemian Basins, Czechoslovakia. – Sedimentary Geology, 15: 135–164.
https://doi.org/10.1016/0037-0738(76)90041-5

Tiffney, B. H. (1984): Seed size, dispersal syndromes, and the rise of the angiosperms: evidence and hypothesis. – Annals of the Missouri Botanical Garden, 71: 551–576.
https://doi.org/10.2307/2399037

Váchová, Z., Kvaček, J. (2009): Palaeoclimate analysis of the flora of the Klikov Formation, Upper Cretaceous, Czech Republic. – Bulletin of Geosciences, 84(2): 257–268.
https://doi.org/10.3140/bull.geosci.1100

Vangerow, E. F. (1954): Megasporen und andere pflanzliche Mikrofossilien aus der Aachener Kreide. – Palaeontographica, Abt. B, 96(1-2): 24–38.

Appendix

List of taxa described from the locality Zliv-Řídká Blana, the Czech Republic (Klikov Formation, Late Cretaceous).
Abbreviations: PA – proposed affinities; NA – name of species; OT – organ types; SN – specimen number, all housed in National Museum, Prague; ST – specimens in total; OP – ovary position; W – width (mm); L – length (mm); A – Angiospermae; F – Fagales; E – Ericales; UA – uncertain affinity; e – ovary inferior and flower epigynous; h – ovary superior and flower hypogynous; 5*– pentacarpellate capsule; 3* – tricarpellate capsule; & – endocarp; b – broken.

PA	NA	OT	SN	ST	OP	W	L
Bryophyta	*Eopolytrichium* sp.		NM-F 3631	1	–	0.5	3.1
Fern	Taxon 1	leaf	NM-F 4130	1	–	1.6	1.4
Fern	Taxon 2	leaf	NM-F 3459, NM-Fs 52	10	–	0.9–3.27	0.85–2.78
Conifers	*Pagiophyllum* sp.	leaf	NM-F 4132	1	–	2.4	4.6
A: F	*Budvaricarpus serialis*	fruit	NM-F 3160 – NM-F 3171, NM-F 3205 – NM-F 3207, NM-F 3289 – NM-F 3298, NM-F 3388 – NM-F 3389, NM-F 3413 – NM-F 3458	400	e	0.7–2.7	0.8–2.5
A: F	*Budvaricarpus* sp.	fruit	NM-F 3619	1	e	1.7	1.8
A: F	*Calathiocarpus* sp.	fruit	NM-F 4631	1	e	0.6	0.7
A: F	*Caryanthus trebecensis*	fruit	NM-F 3286, NM-F 3634	2	e	0.8	1.4
A: F	*Caryanthus triasseris*	fruit	NM-F 3300, NM-F 4629	20	e	0.8	1.1
A: F	*Caryanthus* sp. 1	fruit	NM-F 3208	1	e	0.9	1.4
A: F	*Caryanthus* sp. 2	fruit	NM-F 3627	1	e	0.8	0.8
A: F	*Caryanthus* sp. 3	fruit	NM-F 4628	1	e	1.1	1.1
A: F	*Dahlergeniantus* sp.	fruit	NM-F 4495	3	h	0.6	1.0
A: F	Taxon 3	fruit	NM-F 3724	1	e	1.2	1.8
A: F	*Zlivifructus vachae*	fruit	NM-F 3172, NM-F 3173, NM-F 3174, NM-F 3229, NM-F 3230	120	e	0.5–1.1	0.5–1.1
A: F	*Zlivifructus microtriasseris*	fruit	NM-F 3626, NM-F 3630	2	e	0.6–0.7	0.6–0.7
A: ?E	Taxon 4	5*	NM-F 3188, NM-F 3235	70	h	1.1–1.68	1.2–2.2
A: ?E	Taxon 5	5*	NM-F 3193	1	h	1.3	2.6
A: ?E	Taxon 6	5*	NM-F 3194	2	h	1.1	2.1
A: ?E	Taxon 7	5*	NM-F 4091, NM-F 4498	20	h	1.6	1.5
A: ?E	Taxon 8	5*	NM-F 4492	1	h	1.4	1.2
A: ?E	Taxon 9	5*	NM-F 4621	1	h	0.75	1.0
A: ?E	Taxon 10	5*	NM-F 4500	1	h	1.1	1.9
A: ?E	Taxon 11	5*	NM-F 4622	1	h	1.7	3.1
A: ?E	Taxon 12	3*	NM-F 3302	1	h	0.8	1.0
A: ?E	Taxon 13	3*	NM-F 4501	1	h	1.3	1.5
A: ?E	Taxon 15	3*	NM-F 4619	1	h	0.8	1.15
A: ?E	Taxon 16	3*	NM-F 4497	4	e	1.25	–
A: UA	*Trebecenia sarcocalis*	3*	NM-F 3637, NM-F 3197, NM-F 4509	3	h	1.25	1.75
A: UA	Taxon 17	fruit	NM-F 3201	1	?	0.7	0.75
A: UA	Taxon 18	fruit	NM-F 4626	1	?	2.4	1.4
A: UA	Taxon 19	fruit	NM-F 3181, NM-F 3180 – NM-F 3187, NM-F 3779 – NM-F 3784	350	–	1.5–1.9	1.4–2.5
A: UA	Taxon 20	fruit	NM-F 3200	1	h	0.65	0.7
A: UA	Taxon 21	fruit	NM-F 4491	1	e	0.8	1.7
A: UA	Taxon 22	fruit	NM-F 3195	1	h	2.0	2.8
A: UA	Taxon 23	fruit	NM-F 4502	1	h	2.0	2.6
A: UA	Taxon 24	&	NM-F 3217	1	–	1.0	1.5
A: UA	Taxon 25	&	NM-F 3218, NM-F 4496	2	–	1.1	1.5
A: UA	Taxon 26	&	NM-F 4625	1	–	5.0	3.0
A: UA	cf. *Sabia menispermoides*	&	NM-F 4624	1	–	2.2	1.8
A: UA	Taxon 28	fruit	NM-F 4494	1	?	0.6	0.75
A: UA	Taxon 14	flower	NM-F 3196, NM-F 3635, NM-F 4505, NM-F 4508	1	h	1.25–1.6	1.5-2
A: UA	Taxon 27	flower	NM-F 4504	1	e	2.5	1.0

PA	NA	OT	SN	ST	OP	W	L
A: UA	Taxon 29	flower	NM-F 3198	1	h	0.7	1.0
A: UA	Taxon 30	flower	NM-F 3199	1	e	1.0	1.1
A: UA	Taxon 31	flower	NM-F 4620	1	h	0.65	0.85
A: UA	Taxon 32	flower	NM-F 4503	1	h	1.3	1.1
A: UA	Taxon 33	flower	NM-F 3778a	1	e	1.5	2.3
A: UA	Taxon 34	flower	NM-F 3778b	1	e	1.7	1.0
A: E	*Eurya* sp. 1	seed	NM-F 3213	12	–	0.9	1.0
A: E	*Eurya crassitesta*	seed	NM-F 3211	1	–	1.3	1.3
A: E	*Eurya* sp. 3	seed	NM-F 3212, NM-F 3209	2	–	0.8	1.0
A: E	*Protovisnea* sp. 1	seed	NM-F 3177	1	–	1.9	1.5
A: E	*Protovisnea* sp. 2	seed	NM-F 3179	8	–	1.2–2.1	1.2–1.7
A: UA	*Klikovispermum* sp. 1	seed	NM-F 3203, NM-F 4633	2	–	2.0	2.5
A: UA	*Klikovispermum malechii*	seed	NM-F 3299	1	–	0.8	0.8
A: UA	*Klikovispermum* sp. 2	seed	NM-F 3638	1	–	0.7	1.1
A: UA	*Klikovispermum* sp. 3	seed	NM-F 4636	1	–	1.05	1.2
A: UA	*Klikovispermum* sp. 4	seed	NM-F 4635	1	–	0.7	1.3
A: UA	*Klikovispermum* sp. 5	seed	NM-F 4632	1	–	0.8	1.0
A: UA	*Klikovispermum* sp. 6	seed	NM-F 4638	1	–	b	–
A	? Nympheaceae sp. 1	seed	NM-F 3636	1	–	1.2	0.8
A	? Nympheaceae sp. 2	seed	NM-F 4634	1	–	0.75	1.25
A: UA	Taxon 35	seed	NM-F 3236	1	–	0.45	0.7
A: UA	Taxon 36	seed	NM-F 4637	1	–	1.8	2.1
A: UA	Taxon 37	seed	NM-F 4639	1	–	b	–
A: UA	Taxon 38	seed	NM-F 4641	1	–	1.4	1.4
A: UA	Taxon 39	seed	NM-F 4642	1	–	b	–
A: UA	Taxon 40	seed	NM-F 3640	1	–	1.2	0.8
Insecta	*Microcarpolithes hexagonalis*		NM-F 4520	1	–	0.5	0.7–1.0
Insecta	*Palaeoaldrovanda splendens*	egg	NM-F 3237	1	–	b	–