



## A new genus of Insecta based on egg structure from the Late Cretaceous Klikov Formation of the Czech Republic

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**Abstract:** A new genus, *Regentus* gen nov., is established here based on species originally described as *Spirellea trebecensis*, hence the new combination *Regentus trebecensis* (Knobloch et Mai, 1986) comb. nov. The material was collected and prepared by E. Knobloch from the Klikov Formation, from fluvial lacustrine sediments of upper Turonian – Santonian age, located in the South Bohemian Basins, Czech Republic. *Regentus trebecensis* fossils are broadly elliptical in outline, hollow inside, with a ribbed surface. Their apical end shows ridges irregularly arranged, pointing towards the tip; the ridges on the basal end form an irregular star-shaped structure. The wall of the fossil shows regular perforations arranged in two parallel rows leading from the inside to the surface. *Regentus trebecensis* was originally described as a seed, related to recent Stemonaceae Caruel. *R. trebecensis* resembles Stemonaceae seeds in shape and longitudinally ribbed surface. However, *R. trebecensis* lack an aril and uniseriate or vesicular hairs originating from hilum, raphe or micropyle, the characteristic for Stemonaceae seeds. The presence of perforations in the fossil wall precludes its interpretation as a fruit or seed. The shape and structure of the perforations resemble aeropyles of insect eggs, particularly the air-containing meshwork of insect eggs (e.g. Phasmatodea, Lepidoptera); this led us to interpret the studied fossils as insect eggs. The diversity of insect eggs resembling seeds is high, although no insect group with features exactly matching the fossil material has yet been identified.

**Keywords:** Fossil insect egg; Late Cretaceous; Czech Republic

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### Introduction

Dr. Ervín Knobloch was a prominent Czech paleobotanist. He collected a large amount of Late Cretaceous plant mesofossil reproductive structures, which he later described in a monograph together with Prof. Mai. As part of the geological mapping of the Czech Republic, he also had access to material from a number of boreholes. His collection of mesofossils is one of the largest

in Central Europe (Knobloch et Mai 1986). The collection contains cca 80 genera and several hundred species from the Kvikov Formation of the South Bohemian Basin (Knobloch et Mai 1983, 1984), the Moravian flysch (Knobloch 1977), Czech Bohemian Basin (Knobloch et Mai 1986), and numerous sites in Central Europe: the Austrian Gosau Formation (Knobloch 1975), the Polish Czerna Formation, Quedlinburg, Walbeck, Eisleben and Achen in Germany and Ajka in Hungary (Knobloch et Mai 1986). Shortly before his death, Knobloch donated his entire collection to the National Museum.

The aim of this paper is to revise one of Knobloch's taxons: *Spirellea trebecensis* Knobloch et Mai. *Spirellea trebecensis* was described as a seed of his fossil genus *Spirellea*, Erw.Knobloch, very remotely resembling seeds of recent Stemonaceae Caruel. (Knobloch et Mai 1984). *Spirellea trebecensis* differs considerably from the type species *Spirellea bohemia* Knobloch et Mai in ornamentation and micro composition of the fossil wall. Therefore, genus *Regentus* gen. nov. is designated here and *Spirellea trebecensis* is transferred here as *Regentus trebecensis* (Knobloch et Mai, 1986) comb. nov. Precise systematic identification of *Regentus* is not possible, but all studied characters: elliptical shape, ribbed surface and most importantly fossil wall with perforations leading from the inside to the surface indicate it is an insect egg.

Many different structures associated with insect eggs have been described to date. The earliest record of exophytic oviposition documents fossil structures consisting of small, circular impressions on plant fossils from the late Pennsylvanian (Gzhelian, Stephanian C) of the Saale Basin in Germany. The eggs were laid directly on the outer surface of plants (Laaß et Hauschke 2019), but more commonly, this insect-plant interaction has been recorded since the Triassic. Other findings document egg chorions from the Upper Triassic of Austria, found on the cuticles of *Nilssoniopteris haidingeri* (Stur ex Krasser) Pott, Krings et Kerp leaves by Pott et al. (2008). The small oval eggs were arranged in a circle (Pott et al. 2008). Two forms of imprints of fossil insect eggs, described as oviposition slits of endophytic eggs, are known from Lower Jurassic plants in Bavaria, Germany. They occur on *Schmeissneria microstachys* (C.Presl) Kirchner et Van Konijnenburg-Van Cittert leaves (Ginkgoales) (Van Konijnenburg-Van Cittert et Schmeissner 1999). Early Jurassic rare insect ovipositories occurring on *Pterophyllum* sp., bennettitalean (cycadeoidalean) leaves, were described from Pregheda, a former open-cast mine for bituminous coal in the South Carpathians of Romania (Popa et Zaharia 2011). *Paleoovoidus flabellatus* Vasilenko was described as a taxon of insect ovipositions on aquatic plant leaves *Quereuxia*, from the Campanian locality of Udurchukan (Amur Region) (Vasilenko 2008). Additionally, macerated carbonized leaf material of a scale-leaved conifer from the Lower Cretaceous of Germany yielded a portion of a fossil insect egg chorion (eggshell). It was assigned to a new genus and species, *Merangia horricomis* Fisher et Watson (Fisher et Watson 2015).

Late Cretaceous *Palaeoaldrovanda splendens* Knobloch et Mai from fluvial lacustrine sediments of the Czech Republic, preserved as charcoal, was originally described as a fossil seed related to the extant carnivorous genus *Aldrovanda* L. (Droseraceae). However, reinvestigation of the fossils showed that *Palaeoaldrovanda* differs from recent seeds of *Aldrovanda* in having only unelaborated matter in the areas of the micropyle and hilum, and in having uniform wall structure showing files of rectangular cells in the inner surface. After re-evaluation of all diagnostic features, it became clear that a close relationship between *Palaeoaldrovanda* and *Aldrovanda*, as well as other Droseraceae, can be excluded. Several characters, such as wall structure and shape of projections indicate that *Palaeoaldrovanda* is most likely an insect egg (Heřmanová et Kvaček 2010).

The Cretaceous genus *Knoblochia* Heřmanová et al. from the Moravian flysch of the Czech Republic was established for small, longitudinally ridged, ovoid to round fossils with projections on both ends, similar in surface morphology to our material. Comparison of *Knoblochia* with insect eggs of Phasmatodea and Lepidoptera species showed clear affinity of *Knoblochia* to insects (Heřmanová et al. 2013). Part of the fossil material belonging to *Costathea diskoensis* Miner was also discussed as possible insect eggs (Batten et Zavattieri 1996).

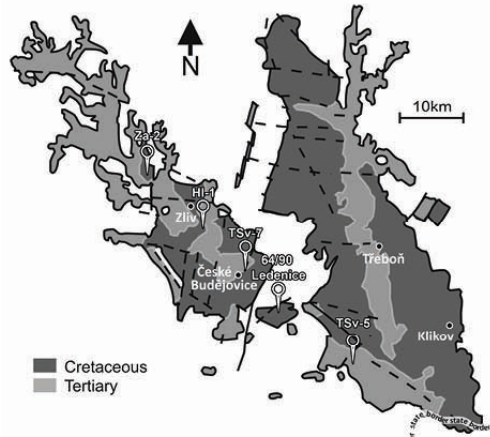
## Material and method

All specimens are three-dimensionally preserved, small, charcoalfied mesofossils. The material was originally prepared by E. Knobloch and his collaborators. The mesofossils were extracted from grey claystone by bulk maceration, followed by washing on a sieve. After sieving, some of the organic residue was treated with  $H_2O_2$ , rinsed in water, and dried in air. The original method of gluing the holotype to the SEM stub, used by E. Knobloch or his technician, used an unsuitable glue. The glue has covered the entire holotype over time and no details were visible. The specimen was removed from the adhesive using acetone, and cleaned with hydrofluoric acid for one hour. Unfortunately, after cleaning, the holotype broke into three pieces (Fig. 2B). However, the original publication (Knobloch et Mai 1986, pl. XLV, fig. 1) where the holotype was illustrated provides a good overview of how the fossil looked (Fig. 2A). The studied material of *Regentus trebecensis* is housed in the National Museum Prague and accessible for study.

Sorting and preliminary studies were carried out using an Olympus SZX 12 binocular microscope. All specimens for SEM observation were mounted on aluminum stubs using nail polish. They were studied using a Hitachi S3700 field emission scanning electron microscope. Specimens were coated by gold and studied under high vacuum at 2 kV. Specimen NMP F 3308 was studied using X-ray micro-tomography in a SkyScan 1172 at 250  $\mu$ A and 40 kV, without a filter. N-Recon Software was used for reconstruction.

Because of the specific topic, we use the rules/constraints for both botany and zoology in one article, including the different ways of writing of Latin name authorities (Turland 2025, ICZN 1999). The studied extant material of Lepidoptera was obtained from the Prague Botanical Garden; Phasmatodea eggs were received from a private collector Mr. Zajíček; fossils of *Regentus trebecensis* were compared with extant insect eggs figured in Hinton (1981).

Material of *Regentus trebecensis* comes from five different boreholes: HI-1 Opatovice 208.7 m; 64/90 Ledenice 29.20 m; TSv-5 Třebeč 293.6–293.8 m; borehole Za2 Zahájí 17.6–17.90 m, and TSv-7 České Budějovice – Vrátó 42.2–42.3 m. These five boreholes are among the many that were drilled in the South Bohemian Basins in the second half of the twentieth century. The material was collected and prepared by E. Knobloch from the Klikov Formation, the lowermost part of the South Bohemian Basins (Fig. 1.). The Klikov Formation consists 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 late Turonian-Santonian, based on palynology and geological correlation (Knobloch, 1985; Pačtová, 1981). The South Bohemian Basins occupy an area of about 2300 km<sup>2</sup> and consist of two subbasins: The



**Fig. 1. Geological map of South Bohemia Basins. Material of *Regentus trebecensis* comes from five different boreholes: HI-1 Opatovice 208.7 m; 64/90 Ledenice 29.20 m; TSv-5 Třebeč 293.6 - 293.8 m; borehole Za2 Zahájí 17.6 – 17.90 m, and TSv-7 České Budějovice – Vrátó 42.2–42.3 m.**

Budějovice Basin and the Třeboň Basin. The two basins are elongated depressions developed on the Moldanubian crystalline bedrock of the Bohemian Massif, separated by the Lišov Horst. Sedimentation in the basins began in the Late Cretaceous and continued sporadically until the Pliocene (Slánská 1974).

## Results

**Classis:** Insecta Linnaeus, 1758

**Ordo:** uncertain

### *Regentus* Heřmanová et J.Kvaček gen. nov.

**Type species.** *Spirellea trebecensis* Knobloch et Mai 1986, p. 150, pl. 45, figs. 1–3.

**Stratigraphic and geographic range of genus.** Klikov Formation, Upper Turonian – Santonian age, Late Cretaceous.

**Diagnosis.** Based on egg structure: Fossils broadly elliptical in outline, ribbed, hollow inside, apical end rounded, ridges coming together in basal region forming irregular star-shaped structure; wall showing tiny perforations leading from inside to surface, perforations arranged in two rows running in parallel forming a band, surface of fossil papillated.

**Differential diagnosis.** Genus *Regentus* differs from genus *Spirellea* represented by the type species *Spirellea bohemica* (Knobloch et Mai 1986) in several characters. While *S. bohemica* has a round shape, *Regentus* is broadly ellipsoid in shape. While *S. bohemica* shows the epidermal cells larger, irregularly shaped and the lumen (botany) is sunken with the cell margins rising upwards, the surface of *Regentus* is papillate, and its wall shows tiny perforations leading from the inside to the surface.

*Regentus* has several features in common with *Palaeoaldrovanda* (Heřmanová et Kvaček 2010, Heřmanová 2017): its size and elliptical shape. However, *Regentus* differs from *Palaeoaldrovanda* in having a ribbed surface, and in the presence and shape of projections on its surface on both sides. Additionally, the wall of the *Palaeoaldrovanda* is formed by rectangular cell-like structures arranged in rows, while *Regentus* has a smooth inner surface. *Regentus* resembles *Knoblochia* Heřmanová et al. in size, elliptical shape and ribbed surface (Heřmanová et al. 2013). However, *Knoblochia* differs from *Regentus* in the presence and shape of projections on both sides of the fossil, *Knoblochia* shows a small conical projection surrounded by a coronal rim in the apical end, and a round collar with central projection in the basal part.

**Etymology.** The Latin name is derived from Regent, a notable brewery in the Třeboň city.

### Zoobank.

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### *Regentus trebecensis* (Knobloch et Mai, 1986) Heřmanová et J.Kvaček comb. nov.

Figs. 2A–I; 3A–I

Syn. 1986 *Spirellea trebecensis* sp. n.; Knobloch et Mai, p. 150, pl. 45, figs. 1–3.

**Original combination.** *Spirellea trebecensis* Knobloch et Mai, 1986.

**Holotype.** No. NMP F3669; housed in the National Museum Prague; published by Knobloch et Mai 1986, pl. 45 fig. 1.

**Type locality.** České Budějovice – Vráto, TSv-7 borehole 42.2–42.3 m.

**Type horizon.** Klikov Formation, Upper Turonian – Santonian age, Late Cretaceous.

**Emended diagnosis.** Same as for the genus.

**Differential diagnosis.** Same as for the genus

**Specimens studied.** NMP F3308, F3309, F3311, F3313, F3314, F3669.

**Occurrence.** Boreholes Hl-1 Opatovice 208.7 m; 64/90 Ledenice 29.20 m; TSv-5 Třebeč 293.6–293.8 m; borehole Za2 Zahájí 17.6–17.90 m and TSv-7 České Budějovice – Vráto 42.2–42.3 m.

**Description.** The holotype is a small, ribbed fossil, elliptical in outline, hollow inside (Fig. 2A). For the purposes of this publication, we consider one end to be apical and the other to be basal, regardless of the original orientation. It contains approximately 16 anastomosing ribs running from the apex to the base of the fossil. The inner surface of the fossil wall is structureless (Fig. 2B). The surface of the holotype is papillated, and tiny holes perforate the wall of the fossil (Fig. 2C). Other material of *R. trebecensis* from different localities in Klikov Formation consists of fossils of broadly ellipsoid shape, with ribbed surface (Fig. 2D, 2G, 3D). The fossils are 0.65–0.9 mm long and 0.55–0.7 mm broad. Some of the fossils are flattened according to their perpendicular axis (Fig. 2G). The apical end is rounded; ridges vaguely aimed generally towards the tip (Fig. 2E). In the basal end, the ridges come together, forming an irregular star-shaped structure (Fig. 2H). The surface of the fossil is papillated (Fig. 2I). The fossil wall shows tiny perforations leading from the inside to the surface, arranged in two rows side by side (Fig. 2C, 2F, 3C, 3F).

## Discussion

### Comparison with fossil insect eggs

The relation between *Regentus trebecensis*, *Palaeoaldrovanda splendens* and *Knoblochia cretacea* has been discussed in the differential diagnosis. Mesozoic insect eggs are usually described as imprints on fossil leaves: for example, two forms of oviposition slits from Lower Jurassic on *Schmeissneria microstachys* (Ginkgoales) (Van Konijnenburg-Van Cittert et al. 1999), and Early Jurassic imprints occurring on *Pterophyllum* sp., bennettitalean (cycadeoidalean) leaves, from the South Carpathians of Romania (Popa et al. 2011), and *Paleoovoidus flabellatus* Vasilenko 2008. *Paleoovoidus flabellatus* was described as a taxon of insect ovipositions on aquatic plant leaves *Quereuxia* from the Campanian (Vasilenko 2008). Zygopteran egg sets from the Albian of Makhtesh Ramon, central Negev, Israel, were deposited on narrow leaves of an angiospermous *Acaciaephyllum*-like morphotype (Krassilov et al. 2007). Their main feature is the arrangement in rows of individual eggs in relation to each other, but details of individual imprints were not preserved. In contrast, *Regentus trebecensis* are described as charcoalfied and interpreted as individual eggs, and nothing is known about their oviposition.

Small cuticles on *Nilssoniopteris haidingeri* leaves interpreted as oval eggs arranged in a circle (Pott et al. 2008) resemble *Regentus trebecensis* in small size and oval shape. The difference is in their preservation: while *Regentus trebecensis* is preserved as charcoal, the eggs on leaves of *Nilssoniopteris haidingeri* are preserved as cutinized fossils. The eggs on *Nilssoniopteris haidingeri* have ribbed walls and a strongly cutinized aperture at one end only, unlike *Regentus trebecensis*, which has no protrusions at the ends of the fossil.

Insect chorion *Merangia horricomis* Fisher et Watson occurring on conifer foliage from the Early Cretaceous of Germany (Fisher et al. 2015) resembles *Regentus trebecensis* in their small size. While *Merangia horricomis* is cylindrical to barrel-shaped, *Regentus trebecensis* is generally ovoid. While *Merangia* shows a slightly sunken operculum *Regentus*

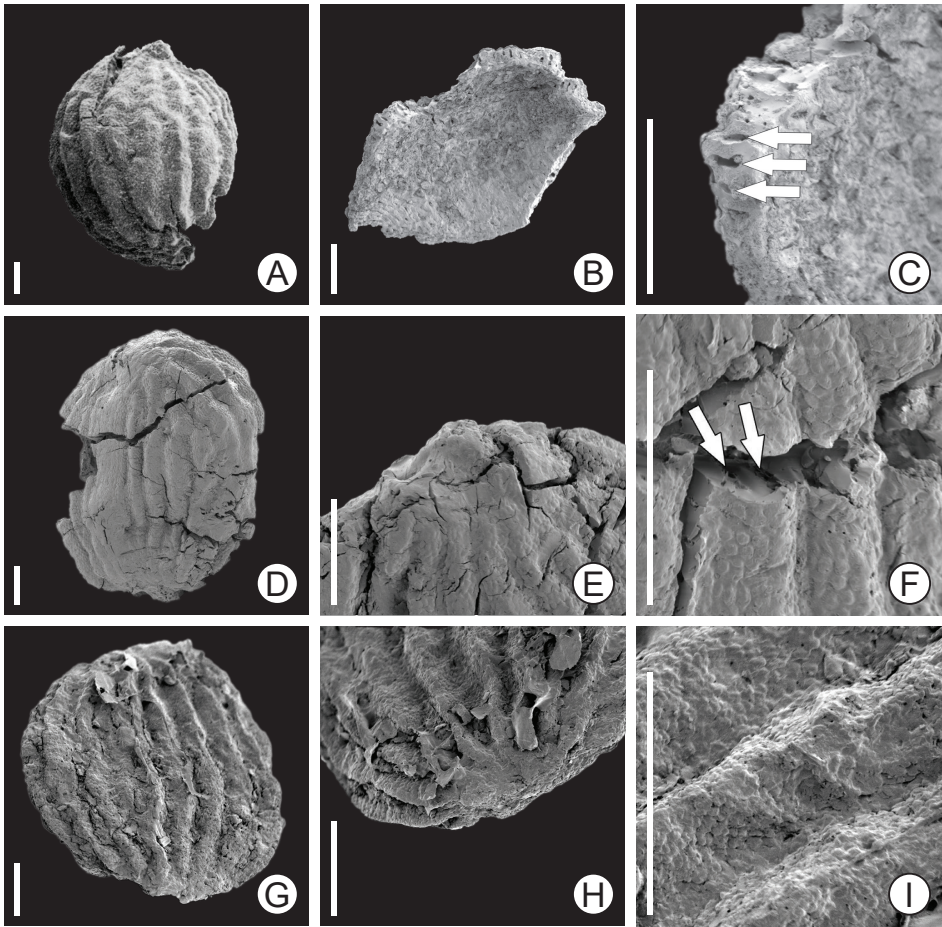


Fig. 2. *Regentus trebecensis* (Knobloch et Mai) comb. nov.: (A) reproduction of holotype published by Knobloch et Mai (1986, pl. XLV, fig. 1) showing ribbed fossil; no. NM F3669; (B) holotype, present state, one of three parts of specimen showing inner surface of fossil wall; no. F3669; (C) detail of holotype, present state, showing small holes penetrating fossil wall (arrows), no. F3669; (D) ribbed fossil, general view, showing ribs and elliptical outline; no. F3308; (E) same specimen as D, detail of apical end, ridges irregularly directed generally towards apical tip; (F) same specimen as D, detail of fossil wall showing tiny perforations (arrows) leading from inside to surface; (G) fossil, general view, showing ribs and elliptical outline, no. F3311; (H) same specimen as G, detail of polar region ridges coming together forming irregular star-shaped structure; (I) same specimen as G, detail of surface covered by papillae. All SEM micrographs. Scale bar 0.1 mm for all pictures.

*trebecensis* has no operculum at all. Long, narrow, sharp spines arising from circular pits present in *Merangia horricomis* do not occur in *Regentus trebecensis*.

*Costatheca dentata* Dijkstra fossils were also discussed as possible insect eggs (Batten et Zavattieri 1996, 1995). *Regentus trebecensis* differs from *Costatheca dentata* mostly in material composition. While *Regentus trebecensis* is found preserved as charcoal, specimens of *Costatheca dentata* are mostly found as cutinized fossils. The shape of *Costatheca dentata* is significantly more elongated than the *Regentus trebecensis*. No wall perforations were observed in *Costatheca dentata*. A ribbed surface is common for both *Regentus trebecensis* and *Costatheca dentata*.

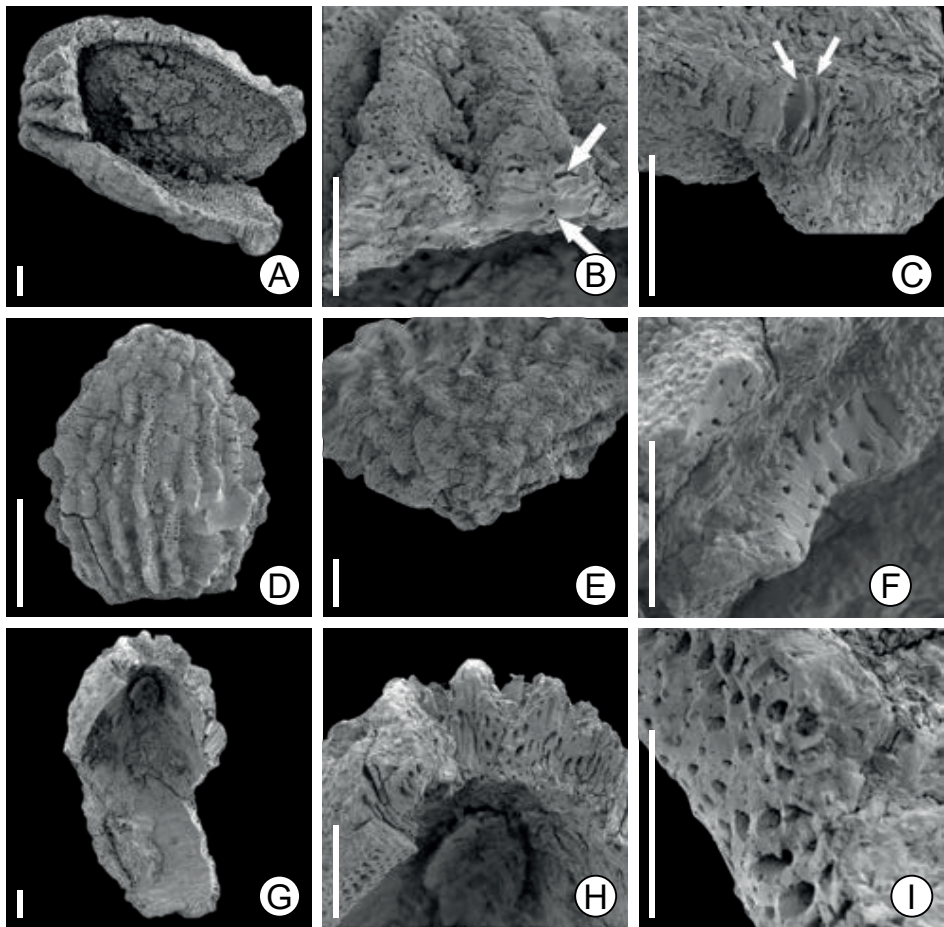


Fig. 3. *Regentus trebecensis* (Knobloch et Mai) comb. nov.: (A) fossil general view, broken specimen, no. F3313; (B) same specimen as A, detail of fossil wall showing tiny perforations (arrows) leading from inside to surface; (C) same specimen as A, detail of fossil wall showing tiny perforations leading from inside to surface; (D) fossil general view showing ribs and elliptical outline, no. F3309; (E) same specimen as D, detail of ridges forming irregular star-shaped structure; (F) same specimen as D, detail of perforations arranged in two parallel rows; (G) fossil general view, broken specimen, no. F3314; (H) same specimen as G, detail of fossil wall shows tiny perforations leading from inside to surface; (I) same specimen as G, detail of perforations. Scale bar 0.1 mm for (A–H), scale bar 50  $\mu$ m for (I).

### Comparison with recent material – plants

The relationship between genus *Spirellea* and recent Stemonaceae was discussed by Knobloch et Mai (1984): “Seeds of this type have been found in the Stemonaceae, a disjunct Southeast Asian-North American monocot family. *Stemona* Lour. in particular shows very similar characteristics in morphology and anatomy of the seeds.” Fruits of recent Stemonaceae are capsule similar to *P. trebecensis* in elliptical shape and longitudinally ridged surface. Seeds of recent Stemonaceae are similar to *P. trebecensis* in longitudinally ridged surface. However, the seeds of Stemonaceae differ substantially from *P. trebecensis* in being large (more than 5 mm long), having aril of uniseriate or vesicular hairs from originating from the hilum, raphe or micropyle (Kubitzki, 1998, Stevens 2001 onwards). On the other hand, none of the recent

Stemonaceae shows perforated fruit walls. The function of each seed or fruit is to protect the embryo as much as possible, therefore the wall of the fruit or seed is solid and contains no perforations, except for the micropyle. Close examination of the fossil wall of *Regentus trebecensis* shows perforations leading from the inside to the surface and penetrating the entire wall of the fossil. No regularly distributed perforations of a seed coat or testa are described anywhere in the plant kingdom (Corner 1976), so it is not possible to associate *Regentus trebecensis* with any plant propagule.

### Comparison with recent material – insects

Most heterotrophic organisms need oxygen, so like the insect eggs we discussed above, their eggs also contain variously formed respiratory structures. The respiratory system of insect eggs minimizes water loss but maintains an efficient oxygen supply (Hinton 1981). For this reason, the eggs are equipped with a special layer – an air-containing meshwork, a layer of gas inside the chorion shell. In addition to the eggshell layers, there are structures present on and inside the eggshell for respiration (aeropyles) and fertilization (micropyles), and inner eggshell structures for the distribution of oxygen in the egg (pillars, sometimes also referred to as struts or columns) (Hinton, 1981).

*Regentus trebecensis* shows a feature that is generally characteristic for eggs: tiny perforations permeating the entire fossil wall (compare figs. 3I – fossil and 4D – recent). Even the elliptical outline and ribbed structure of *Regentus trebecensis* are similar to insect eggs (compare figs. 3D – fossil and 4A – recent). As case studies, we mention the following species of Phasmatodea: *Lonchodes amaurops* (Westwood 1859), *Extatosoma tiaratum* (Macleay 1826) and *Phyllium* sp., and species of Lepidoptera: *Cossus cossus* (Linnaeus 1758) and *Attacus atlas* (Linnaeus 1758).

The eggs of *Lonchodes amaurops* are ovoid in shape with a distinctly pitted surface of the egg capsule. Eggs are approximately 2.6 mm long and 2 mm broad, similar to *Regentus trebecensis*; in the anterior part of the egg of *L. amaurops* there is a round operculum with a small raised capitulum, and a posterior polar mound shows a conical structure surrounded by a coronal rim bearing fine pitting. The micropylar plate is elliptical. The species *L. amaurops* shows a very similar wall structure in transverse section to the wall of *Regentus trebecensis* perforated by small holes. However, unlike *Regentus trebecensis*, *Lonchodes amaurops* has a distinct operculum containing a tip-like capitulum.

The egg of *Extatosoma tiaratum* has an oval shape, smooth surface and operculum with small capitulum and distinct micropillar plate. *Extatosoma tiaratum* is similar to *Regentus trebecensis* in its oval shape and small size. However, *Regentus trebecensis* has a ribbed surface and no operculum.

The eggs of *Phyllium* spp., like *Regentus trebecensis*, have a ribbed surface and a shell composed of several layers. However, *Phyllium* spp. differs from *Regentus trebecensis* in the number of ribs on the surface, and the number and shape of the layers of which the chorion is composed.

Lepidopteran eggs of *Cossus cossus* are small, have elliptical shape and a chorion surface built by primary and secondary ribs forming rectangular cells in rows. *Cossus cossus* eggs have similar characters to *Regentus trebecensis* – size, shape, ribbed surface and ridges in the polar region forming a irregular star-shaped structure, similar to *Regentus trebecensis* (compare Figs. 3E and 4B).

*Attacus atlas* shows small ovoid eggs; the outer chorion is smooth. Aeropyles regularly penetrate the egg chorion. The shape and structure of the *Attacus atlas* egg wall structure with aeropyles is similar to the fossil wall of *Regentus trebecensis* (compare figs 2C and 4E).

## Conclusion

The variability of shapes among both seeds and insect eggs is enormous. Based on the fact that the fossil *Regentus trebecensis* has a regularly perforated wall and holes arranged in two

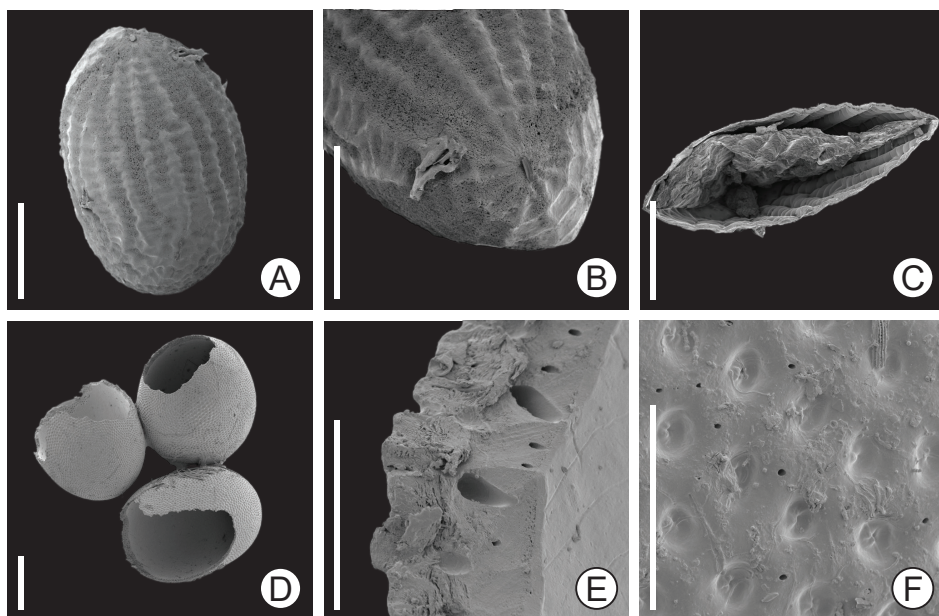


Fig. 4. Extant insect eggs (Lepidoptera). (A–C) *Cossus cossus* (Linnaeus, 1758) (Cossidae), scale bar 0.5 mm: (A) ribbed insect egg of elliptical shape, (B) irregular star-shaped structure in polar region, (C) cross section of the individual egg; (D–F) *Attacus atlas* (Linnaeus, 1758) (Saturniidae), scale bar 0.1 mm: (D) three eggs accidentally adhering together, broken, (E) egg wall with aeropyles, (F) detail of outer chorion.

rows side by side that strongly resemble surface structure of aeropyles, we are inclined to think that this is an egg and not the seed of a plant. Other features, such as the overall shape, ribbing and surface ornamentation of *Regentus trebecensis* are more consistent with insect eggs.

Precise systematic identification of *Regentus trebecensis* remains open, because of the large number and variability of eggs of extant insects. The diversity of insect eggs superficially resembling seeds is high, although as yet it has not been possible to identify any insect group with features exactly matching the fossil material.

## Acknowledgements

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## References

- Batten D.J., Zavattieri A.M., 1996: Re-examination of seed cuticles from Cretaceous deposits in West Greenland. – *Cretaceous Research* 17: 69–714.
- Batten D.J., Zavattieri A.M., 1995: Occurrence of dispersed seed cuticles and similar microfossils in mainly Cretaceous successions of the Northern Hemisphere. – *Cretaceous Research* 16: 73–94.

- Corner E.J.H., 1976: The Seeds of Dicotyledons, volume 1. Cambridge University Press, Cambridge.
- Fisher H., Watson J. 2015: A fossil insect egg on an Early Cretaceous conifer shoot from the Wealden of Germany. – *Cretaceous Research* 53: 38–47. <https://doi.org/10.1016/j.cretres.2014.10.013>
- Gaunt M.W., Miles M.A., 2002: An insect molecular clock dates the origin of insects and accords with palaeontological and biogeographic landmarks. – *Molecular Biology and Evolution*: 748e761.
- Grimaldi D., Engel M.S., 2005: *Evolution of the Insects*. Cambridge University Press.
- Heřmanová Z. 2017. Inner structure of Cretaceous insect egg *Palaealdrovanda splendens* Knobloch et Mai, studied using X-ray microtomography. – *Geoscience Research Reports* 50: 99–102. <https://doi.org/10.3140/zpravy.geol.2017.14>
- Heřmanová Z., Bodor E. R., Kvaček J. 2013: *Knoblochia cretacea*, Late Cretaceous insect eggs from Central Europe. – *Cretaceous Research* 45: 77–85. <https://doi.org/10.1016/j.cretres.2013.07.001>
- Heřmanová Z., Kvaček J. 2010: Late Cretaceous *Palaealdrovanda*, not seeds of a carnivorous plant, but eggs of an insect. – *Journal of the National Museum (Prague), Natural History Series* 179: 105–118.
- Hinton H.E., 1981: *Biology of Insect Eggs*, volume 1. Pergamon Press, Oxford.
- Knobloch E. 1975: Früchte und Samen aus der Gosaufarmation von Kössen in Österreich. – *Věstník Ústředního Ústavu geologického* 50: 83–91.
- Knobloch E., 1977: Paläokarpologische Charakteristik der Flyschzone der mährischen Karpaten. – *Sborník geologických věd, paleontologie* 19: 79–135.
- 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.: *Miscellanea micropalaeontologica: A memorial volume dedicated to the 18th European colloquy on micropalaeontology. Moravské naftové doly, Hodonín*: 305–332.
- Knobloch E., Mai D. H. 1984: Neue Gattungen nach Früchten und Samen aus dem Cenoman bis Maastricht (Kreide) von Mitteleuropa. – *Feddes Repertorium* 95: 3–41.
- Knobloch E., Mai D. H. 1986: Monographie der Früchte und Samen in der Kreide von Mitteleuropa. – *Ústřední ústav geologický v Academii, Praha*.
- Krassilov V., Silantjeva N., Hellmund M., Hellmund W. 2007: Insect egg sets on angiosperm leaves from the Lower Cretaceous of Negev, Israel. – *Cretaceous Research* 28: 803–811. <https://doi.org/10.1016/j.cretres.2006.11.004>
- Kubitzki K. (Ed.), 1998: *Stemonaceae*, in: *The Families and Genera of Vascular Plants*, Volume 3. Springer, Berlin.
- Laaß M., Hauschke N. 2019: Earliest record of exophytic insect oviposition on plant material from the latest Pennsylvanian (Gzhelian, Stephanian C) of the Saale Basin, Germany. – *Palaeogeography, Palaeoclimatology, Palaeoecology* 534: 109337. <https://doi.org/10.1016/j.palaeo.2019.109337>
- Pacltová B., 1981: The evolution and distribution of Normapolles pollen during the Cenophytic. – *Review of Palaeobotany and Palynology* 35: 175–208.
- Popa M., Zaharia A. 2011: Early Jurassic ovipositories on Bennettitalean leaves from Romania. – *Acta Palaeontologica Romaniae* 7: 285–290.
- Pott C., Labandeira C. C., Krings M., Kerp H. 2008: Fossil insect eggs and ovipositional damage on bennettitalean leaf cuticles from the Carnian (Upper Triassic) of Austria. – *Journal of Paleontology* 82: 778–789. <https://doi.org/10.1666/06-094.1>
- Slánská J., 1976: A red-bed formation in the South Bohemia Basins, Czechoslovakia. – *Sedimentary Geology* 15: 135–164.

- Slánská J., 1974: Continental Cretaceous and Tertiary Sedimentation in the South Bohemian Basin. – Neues Jahrbuch für Geologie und Paläontologie 146: 385–406.
- Stevens P. F. (2001 onwards): Angiosperm Phylogeny Website. Version 14, July 2017 [and more or less continuously updated since].” will do. <http://www.mobot.org/MOBOT/research/APweb/>.
- Turland, N.J., Wiersema, J.H., Barrie, F.R., Gandhi, K.N., Gravendyck, J., Greuter, W., Hawksworth, D.L., Herendeen, P.S., Klopper, R.R., Knapp, S., Kusber, W.-H., Li, D.-Z., May, T.W., Monro, A.M., Prado, J., Price, M.J., Smith, G.F. & Zamora Señoret, J.C. 2025. International Code of Nomenclature for algae, fungi, and plants (Madrid Code). Regnum Vegetabile 162. Chicago: University of Chicago Press. <https://doi.org/10.7208/chicago/9780226839479.001.0001>
- Van Konijnenburg-Van Cittert J. H. A., Schmeissner S. 1999: Fossil insect eggs on Lower Jurassic plant remains from Bavaria (Germany). – Palaeogeography, Palaeoclimatology, Palaeoecology 152: 215–223. – [https://doi.org/10.1016/s0031-0182\(99\)00059-0](https://doi.org/10.1016/s0031-0182(99)00059-0)
- Vassilenko D. 2008: Insect ovipositions on aquatic plant leaves *Quereuxia* from the Upper Cretaceous of the Amur Region. – Paleontological Journal 42: 514–521. <https://doi.org/10.1134/S003103010805006>