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Late Cretaceous *Palaeoaldrovanda*, not seeds of a carnivorous plant, but eggs of an insect

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Abstract. *Palaeoaldrovanda splendens* from the Late Cretaceous of the Czech Republic was originally described as a fossil seed closely related to the extant *Aldrovanda vesiculosa* (Droseraceae). *Palaeoaldrovanda* fossils are especially similar to seeds of *Aldrovanda* in their small size, ovoid shape with a neck-like structure at one end and a black, shiny surface. A reinvestigation of the fossil shows, however, that *Palaeoaldrovanda* is distinct from seeds of *Aldrovanda* in all critical characters such as organisation of the seed and in wall structure. After re-evaluation of all diagnostic characters, it is now clear that a close relationship between *Palaeoaldrovanda* and *Aldrovanda* and other Droseraceae can be excluded. Our study suggests that *Palaeoaldrovanda* may not be a seed of an angiosperm, but instead, several characters indicate that the fossil is most likely an insect egg. The diversity of insect eggs superficially resembling seeds is high, although as yet we have not been able to identify any egg groups with features exactly matching the fossil material.
Keywords. *Palaeoaldrovanda splendens*, Late Cretaceous, insect remains, carnivorous plant, Klikov Formation, Czech Republic.

INTRODUCTION

Many angiosperm lineages present in the extant flora were established during the Late Cretaceous e.g. Fagales, Laurales, Magnoliales, Nymphales, Piperales, Chlorantales (Crane et al. 1995, Friis et al. 1997, 2006). The majority of these are documented by numerous fossils of excellent preservation (e.g. Friis et al. 1997). However, there are still groups of Cretaceous angiosperms documented only by incomplete or equivocal material. For example, it has been suggested that angiosperms with special adaptations such as carnivory were already established early in the Cretaceous, based on reports of *Archaeamphora longicervia* Li (2005) from the Early Cretaceous of China and *Palaeoaldrovanda splendens* Knobloch et Mai (1984) from the Late Cretaceous of the Czech Republic. However, the interpretation of *Archaeamphora* is problematic and the fossil is in need of revision. The currently accepted classification of *Palaeoaldrovanda* is questioned in this paper.

As indicated by the name, *Palaeoaldrovanda splendens* was thought to be closely related to *Aldrovanda vesiculosa* L., an endangered aquatic carnivorous plant known from temperate to tropical regions of Eurasia and Australia (Knobloch & Mai 1986, Adamec 1995, Degreef 1997).

Fossil representatives of the genus *Aldrovanda* are known from the fossil record beginning in the Eocene (Reid & Chandler 1926) and the genus occurs continually through the whole Tertiary and Quaternary. *Aldrovanda* is well documented e.g. from the Miocene of Germany (Kirchheimer 1941), Denmark (Friis 1985), Russia (Dorofeev 1963a,b) and the Pliocene of Bulgaria (Palamarev 1970), indicating frequent occurrence of the genus in the fossil record of the Northern Hemisphere.

In this paper we show that *Palaeoaldrovanda splendens* is clearly distinct from seeds of both recent and fossil *Aldrovanda*, and that it may not represent seeds. Instead we propose that the fossils could be interpreted as insect eggs. We compared the morphology of *P. splendens* with numerous different kinds of insect eggs, primarily based on illustrations in Hinton (1981) with focus on the groups Phasmatodea and Lepidoptera, where we selected the most similar-appearing taxa for more detailed study. Both those groups are known from the Cretaceous period (Whalley 1977, Grimaldi & Engel 2005).

MATERIAL AND METHODS

The South Bohemian Basins consist of two elongated depressions, the Třeboň Basin and the Budějovice Basin. The two subbasins together occupy an area of about 2300 km^2. Sedimentation in both basins began in the Late Cretaceous and continued intermittently through the end of the Pliocene.

The fossil material studied here comes from clastic sediments of the Klikov Formation (Late Cretaceous). This Formation constitutes the most widely distributed stratigraphical unit in the South Bohemian Basins (Slánská 1974). The sediments consist of (A) light-gray or yellow conglomeratic, coarse- to medium-grain sandstone beds, (B) mainly fine grained red beds and (C) gray mudstone beds. All three types of beds occur repeatedly and irregularly in the Formation (Slánská 1976). Most of the fossils were found in gray beds as charcoalified specimens. Late Turonian–Santonian age of Klikov Formation using palynological data was suggested by Pacltová (1981) and adopted by Knobloch (1985).

We studied material from two sources. Historic material from the National Museum's archives comes from the boreholes Opatovice Hl-1, 41.9 m, 178.9 m; HP – VI, 51.3 m, 61.9 m; Třebeč Tj – 4a, 71.6 – 72.0 m; 72.0 – 72.2 m; Údolí P6, 107.0 – 107.5 m; Vráto Vo 38, 3.0 – 5.0 m; Vo 55, 11.0 – 12.0 m; Vo 61, 3.0 – 5.0 m; Vo 64, 3.5 – 4.0 m; Vo 66, 8.3 – 9.0 m (Knobloch & Mai 1986). New samples were collected in the Zliv Řídká Blana Quarry locality, in the South Bohemian Basins (49°04‘43“ N, 14°23‘04“ E). In our study, we did not distinguish between the two sources.

In total, 33 samples of *Palaeoaldrovanda splendens* were studied, ranging from mere fragments to complete specimens. The material is housed in the National Museum, Prague, Czech Republic (NMP), under numbers F 03219–03222, F 03237, F 03305, F 03387 and F 03391–03412. The specimens from boreholes are from the collection of

Ervín Knobloch; specimens from Zliv Řídká Blana were collected by the present authors in 2007.

The Zliv Řídká Blana fossils were separated from the sediment by washing on a 0.090 mm sieve and dried in air. Subsequently, they were treated by hydrofluoric and hydrochloric acids. The material from the collection of Ervín Knobloch was also treated by hydrofluoric and hydrochloric acids.

The material was studied using a binocular microscope (Olympus SZX 12) as well as scanning electron microscopes (Hitachi S3700 and JEOL JSM 6380). For the SEM, fossils were mounted on aluminium stubs using nail polish and sputter coated with gold.

For comparison with the fossils specimens, we studied eggs of phasmatodea species Psg 009 *Extatosoma tiaratum* MacLeay 1826, Psg 010 *Phyllium bioculatum* Gray 1832, Psg 014 *Eurycnema goliath* Gray, Psg 019 *Lonchodes brevipes* Gray, Psg 029 *Lonchodes hosei* Kirby, Psg 100 *Lonchodes amaurops* Westwood, Psg 195 *Sungaya inexpectata* Zompro 1996, Psg 214 *Diapherodes jamaicensis,* Psg 283 *Diapherodes venustula, Lonchodes* sp., *Pharnacia* sp., *Phyllium* sp.; eggs of lepidopteran species: *Attacus atlas* L., *Caligo memnon* C. & R. Felder, *Cossus cossus* L., *Eryphanis polyxena* Meerburgh cca, *Papilio memnon* L. The eggs were prepared by boiling in water for few seconds and then drying in air.

RESULTS

***Palaeoaldrovanda splendens* Knobloch et Mai**

1984 *Palaeoladrovanda splendens* Knobloch et Mai, p. 24, pl. 9 fig. 11, pl. 14, figs. 7–11.
1986 *Palaeoladrovanda splendens* Knobloch et Mai; Knobloch et Mai, p. 98, pl. 25, figs. 20, 2.
1991 *Palaeoladrovanda splendens* Knobloch et Mai; Knobloch et Mai, p. 261, pl. 2, fig 5.

Holotype: Specimen NMP F 03387 (Fig. 1A); originally described by Knobloch & Mai (1984: pl. 9, fig. 11).

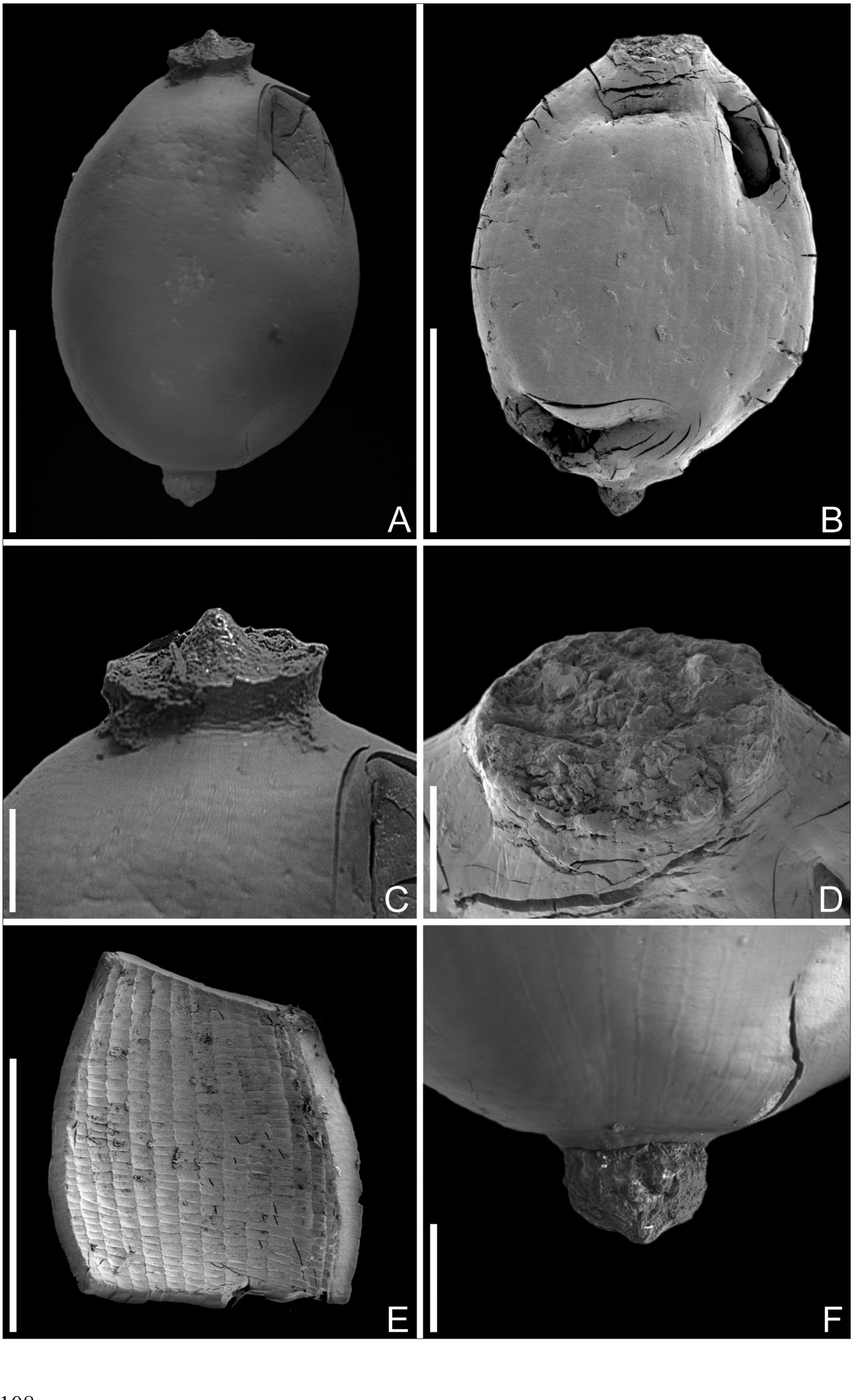
Type horizon: Klikov Formation, Late Cretaceous.

Type locality: Údolí near Nové Hrady, borehole P6 107.0 – 107.5 m.

Specimens studied: NMP F 03219–03222, F 03237, F 03305, F 03387, F 03391–03412.

Occurrence: Boreholes Opatovice Hl-1, 41.9 m, 178.9 m; HP – VI, 51.3 m, 61.9 m; Třebeč Tj – 4a, 71.6–72.0 m; 72.0–72.2 m; Údolí P6, 107.0–107.5 m; Vráto Vo 38, 3.0–5.0 m; Vo 55, 11.0–12.0 m; Vo 61, 3.0–5.0 m; Vo 64, 3.5–4.0 m; Vo 66, 8.3–9.0 m, and locality Zliv Řídká–Blana.

Description: The fossils are charcoalified, small ovoid, with shiny surface 0.4 - 1.6 mm long and 0.7 - 1.4 mm broad. The holotype (Figs. 1A, 5A) shows a small conical projection surrounded by an coronal rim in the apical part, 200 µm in diameter with pitted surface (Fig. 1C). In the basal part it shows a cap-like projection, 100 µm in diameter, with irregularly pitted surface (Fig.1F). Other specimens in the type collection show in the basal part a cap-like projection similar to the holotype (Fig. 1B). The apical part is frequently broken, leaving an irregular scar (Fig. 1D). The inner structure of the wall is well preserved and observed in numerous fragments. The wall is formed by only one very


A
B
C
D
E
F

compact layer 25 µm thick (Fig. 1E). The surface of this layer is black and shiny. The inner surface of this layer is covered by rectangular cell-like structures arranged in rows (Fig. 1E). Each cell is 45 µm x 10 µm. In rare cases the pattern of the rectangular cell-like structure is also seen on the outer surface, but not so distinctly pronounced as on the inner part (Fig. 1F).

Seeds of *Aldrovanda vesiculosa* (Droseraceae, Angiospermae)

Fruits of *Aldrovanda vesiculosa* are unilocular and do not open (Boesewinkel 1989). The ovule is anatropous and bitegmic (Terehin 1986). Seeds of *Aldrovanda vesiculosa* display ovoid shape (Figs. 2A, 5D) with a short neck at the micropylar end (Fig. 2D) and a slightly pointed chalaza (Fig. 2C) on the opposite end. The raphe is indistinct, in some cases indicated by a slightly raised ridge. The micropylar aperture is circular, exhibiting a micropylar plug and hilum (fig. 2D). The seeds average 1 mm broad and 1. 2 – 1.5 mm long. The seed wall is approximately 200 µm thick. The outer epidermis of the seed wall is shiny (Fig. 2E), consisting of polygonal cells (15-25 µm) with pores distributed irregularly between them (Fig. 2F). The epidermis displays various surface patterns. In some cases it is very smooth (Fig. 2E); in other cases it shows cell structure very well (Fig. 2F). The seed wall is formed by two layers of columnar sclereids with polygonal facets. The outer layer is formed by thick-walled cells, with their outer periclinal and anticlinal walls strongly thickened. Their inner periclinal walls are thin. For more details of inner structure of the seed and the seed wall see Terehin (1986).

Insect eggs

PHASMATODEA: Memebers of this group produce eggs that may resemble seeds in their gross morphology. The eggs in Phasmatodea are distinct in having an operculum in the anterior part of the egg where the nymph is hatched. Some, but not all species also have a raised structure on the operculum, known as the capitulum. On the dorsal side there is a micropylar plate and medial line, which is one of diagnostic characters (Seelick 1994). The median line of the egg resembles in some extent a raphe of an angiosperm seed (Fig

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Fig. 1. *Palaeoaldrovanda splendens*. A – Holotype with shiny surface showing ovoid shape, small conical projection surrounded with coronal rim in apical part; cap-like projection in basal part, no. F 03387, Opatovice borehole HL-1 178.9 m, scale bar = 0.5 mm. B – Ovoid shiny fossil showing irregular scar in apical part, cap-like projection in basal part, no. F 03220, Údolí near Nové Hrady borehole P6, 107.0 – 107.5 m, scale bar = 0.5 mm. C – Holotype showing small conical projection surrounded with coronal rim having pitted surface, no. F 03387, Opatovice borehole HL-1 178.9 m, scale bar = 0.1 mm. D – Irregular scar in apical part of object, no. F03220, Údolí near Nové Hrady-borehole P6, 107.0 – 107.5 m, scale bar = 0.1 mm. E – Wall of object formed by rectangular cells arranged in rows, no. F 03222, Vráto borehole Vo 66, 8.3 – 9.0m, scale bar = 0.5 mm. F – Holotype showing cap-like projection with irregularly pitted surface in apical part, no. F 03387, Opatovice borehole HL-1 178.9 m, scale bar = 0.1 mm.

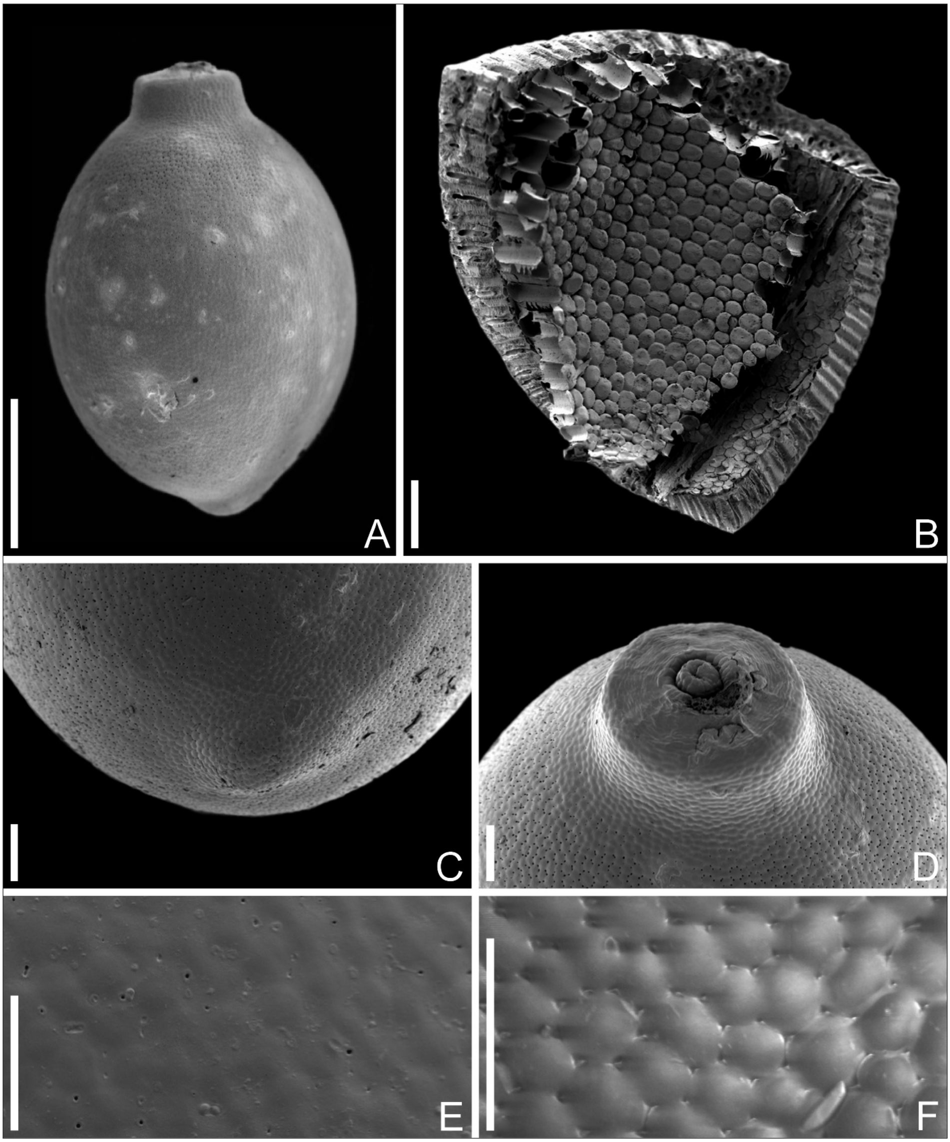

Fig. 2. Extant *Aldrovanda vesiculosa*. A – Ovoid seed showing micropylar plug, raphe and raised chalaza, scale bar = 0.5 mm. B – Seed coat consisting of inner and outer layers of cells; outer layer formed by thick walled cells, inner layer consists of thin wall cells, scale bar = 0.1 mm. C – Detail of chalaza, scale bar 0.1 = mm. D – Micropylar area exhibiting micropylar plug and hilum, scale bar = 0.1 mm. E-F – Outer epidermis of seed consisting of polygonal cells, scale bar = 50 µm.

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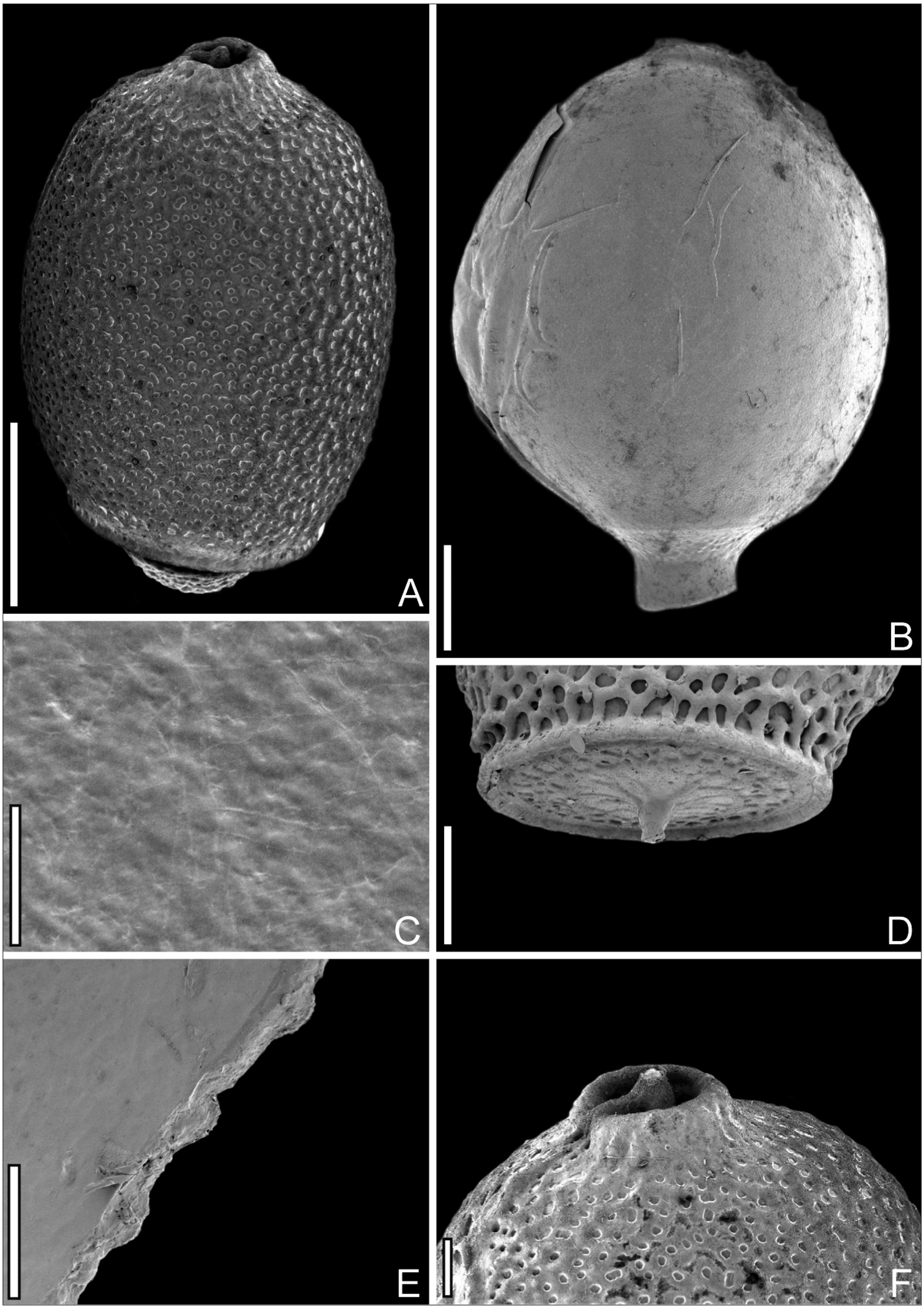
Fig. 3. Extant Phasmatodea eggs. A – *Lonchodes brevipes* ovoid egg, scale bar = 1 mm. B – *Extatosoma tiaratum* egg, scale bar = 1 mm. C – *Extatosoma tiaratum* detail of egg showing shiny surface, scale bar = 0.1 mm. D – *Lonchodes amaurops* egg showing round operculum in



anterior part with small projection (capitulum), scale bar = 0.5 mm. E – *Lonchodes amaurops* egg with smooth inner membrane, scale bar = 0.1 mm. F – *Lonchodes brevipes* detail of posterior part of egg, showing conical projection surrounded by coronal rim, scale bar = 0.2 mm.

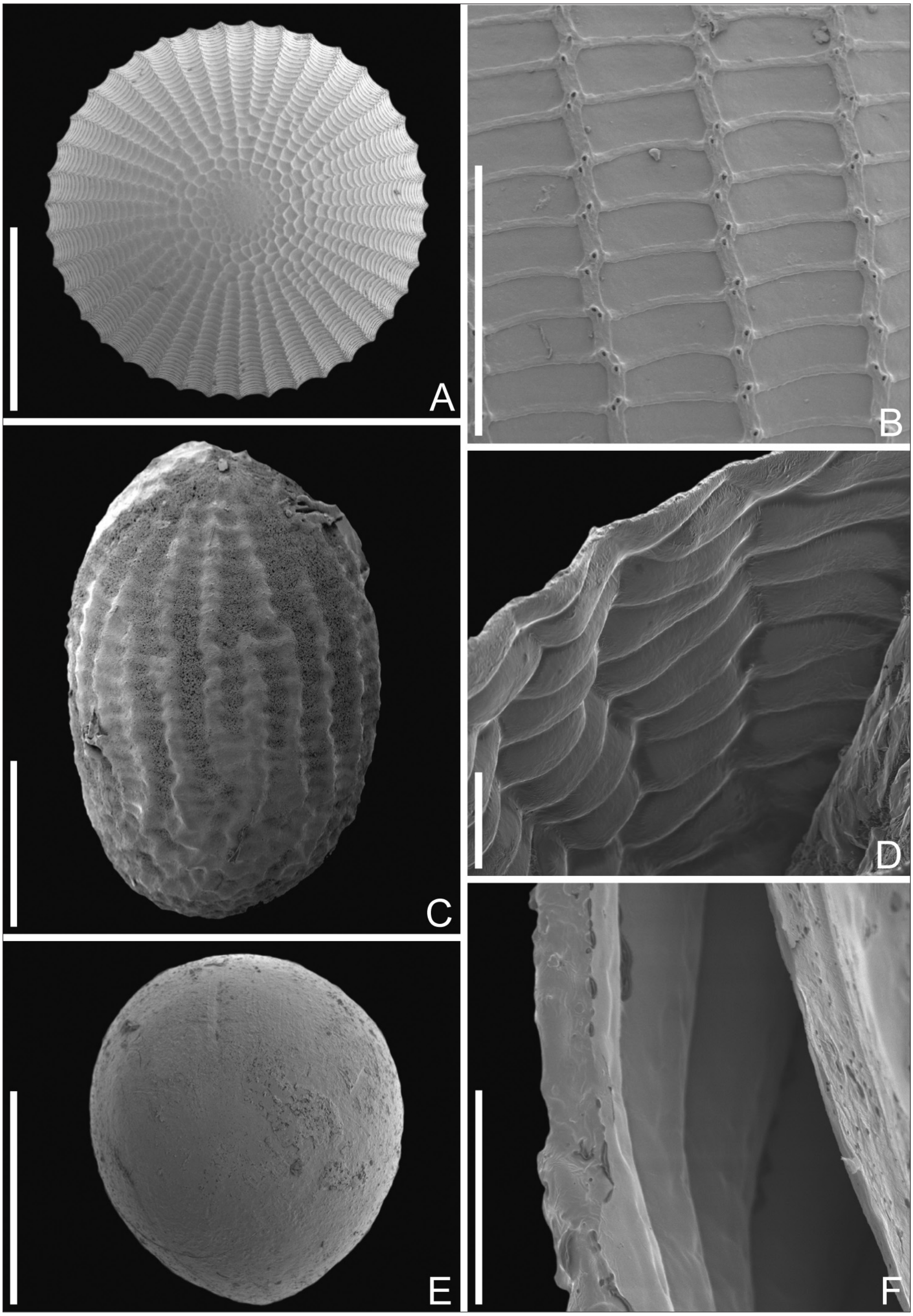


Fig. 4. Extant Lepidoptera eggs. A – *Eryphanis polyxena* round egg, scale bar = 1 mm. B – *Eryphanis polyxena* outer surface of chorion covered with transversal and longitudinal ribs, aeropiles arranged regulary in ribs, scale bar = 0.3 mm. C – *Cossus cossus* ovoid egg covered

3F). Other diagnostic characters such as adhesiveness cannot be observed in fossils and are not considered here.

The eggs of *Lonchodes brevipes* are ovoid in shape (Figs. 3A, 5B) with pitted surface of egg capsule. Eggs are approximately 3.1 mm long and 2 mm broad; in the anterior part of the egg there is a round operculum with a distinct conical stalked capitulum. A posterior polar mound shows a conical structure surrounded with a coronal rim bearing fine pitting. The micropylar plate is elliptical.

The eggs of *Lonchodes amaurops* are ovoid in shape with distinctly pitted surface of egg capsule. Eggs are approximately 2.6 mm long and 2 mm broad; in the anterior part of the egg there is a round operculum with a small raised capitulum (Fig. 3D). A posterior polar mound shows a conical structure surrounded by a coronal rim bearing fine pitting. The micropylar plate is elliptical.

The eggs of *Extatosoma tiaratum* are ovoid, with shiny surface of egg capsule (Figs. 3B, 5C). Eggs are approximately 4.6 mm long and 4 mm broad; micropylar plate abruptly expanded at micropylar area; capitulum hollow, often collapsed (Clark 1979).

Lepidoptera: The eggs of *Eryphanis polyxena* are round, about 2 mm in diameter (Fig. 4A), the outer surface of the chorion is covered by transversal and longitudinal ribs. Aeropiles occur in pairs at each intersection of transversal and longitudinal ribs (Fig. 4B). The ribs are arranged radially from the micropyle. In the micropylar area the rib pattern gradually changes to an anastomosing, net-like structure. The inner surface of the chorion is structureless. The outer surface of the vitelline envelope is also structureless. The inner part of the vitelline envelope is ribbed.

The eggs of *Cossus cossus* are ovoid, approximately 1.3 mm long and 0.8 mm broad, and are covered by around 15 anastomosing longitudinal ribs, grading into a reticular structure. (Fig. 4C). The inner surface of the chorion is covered by rectangular cells arranged in rows (Fig. 4D).

Caligo memnon eggs are round, approximately 1.5 mm in diameter. The outer layer of the chorion is covered by transverse and longitudinal ribs. The longitudinal ribs are much thicker than the transverse ones. Aeropiles occur in pairs at each intersection of transversal and longitudinal ribs. The inner part of the chorion is ribbed. The vitelline envelope is thin and structureless (Fig. 4F).

The egg of *Papilio memnon* are round, approximately 1.5 mm in diameter, and the outer layer of chorion is structureless (Fig. 4E).

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by 15 anastomosing longitudinal ribs topped with micropyle, scale bar = 0,5 mm. D – *Cossus cossus* inner surface of chorion covered with rectangular cells arranged in rows, scale bar = 0,3 mm. E – *Papilio memnon* round egg with smooth outer layer of chorion, scale bar = 1 mm. F – *Caligo memnon* detail of inner part of chorion showing ribbed, vitelline envelope, thin and structureless, scale bar = 0.1 mm.

DISCUSSION

Palaeoaldrovanda splendens was originally described by Knobloch & Mai (1984) as a small shiny ovoid seed related to the carnivorous plant *Aldrovanda* of the family Droseraceae. In the original diagnosis for the genus, the seeds were characterized as follows "Samen von allgemeinen Eigenschaften der *Aldrovanda*-Samen, aber mit Keimdeckelchen mit sehr spitze Micropyle. Chalaza als truncates Stielchen. Oberfläche der Testa sehr fein stria" (Knobloch & Mai 1984). Translated as: "Seeds with general characters of *Aldrovada* seeds, but with operculum with acute micropyle. Chalaza as a small truncate stalk. Surface of testa very finely striated". The small conical projection surrounded by a coronal rim at one end of the fossil was interpreted by Knobloch & Mai (1984) as an acute micropyle (Fig. 1C). The cap-like projection at the opposite end of the fossil was interpreted as the chalaza (Fig. 1F). The compact wall consisting of rectangular cells arranged in rows was considered as a part of the testa (Fig. 1E).

We compared Cretaceous *P. splendens* with some *Aldrovanda* species: extant *A. vesiculosa* L. and fossil *A. praevesiculosa* Kirchheimer). Fossil *A. praevesiculosa* occurs in the Miocene of Germany (Kirchheimer 1941) and Denmark (Friis 1985). While extant *A. vesiculosa* L. and the Tertiary *A. praevesiculosa* are closely similar in all critical features, the Cretaceous *P. splendens* stands out as very different. Characters such as a raphe and a seed wall composed of several layers known for *A. vesiculosa* L. and *A. praevesiculosa* are missing in *P. splendens.* The very characteristic thickening of the outer periclinal and anticlinal walls known for *A. praevesiculosa* (Friis 1985) is also missing in *Palaeoaldrovanda*. Other fossil species of *Aldrovanda* described from the Cenozoic (Reid & Chandler 1926, Dorofeev 1963a,b, 1968,) show similar differences from *Palaeoaldrovanda.*

Comparison between *Palaeoaldrovanda* and seeds of *Aldrovanda* and other Droseraceae

Superficially, *Palaeoaldrovanda* resembles *Aldrovanda* in the ovoid shape and shiny outer surface. However, the seeds of *Aldrovanda* are bigger than those of *Palaeoaldrovanda*, and there are several clearly different characters in morphology of the various seed structures. Thus, the micropylar area of *Aldrovanda* is round, exhibiting a micropylar plug and hilum (Fig. 2D). The conical projection surrounded by the coronal rim (Fig. 1C) in one end of *Palaeoaldrovanda* described by Knobloch & Mai (1984) as a micropyle does not show any hilum, and its pointed shape does not correspond to the micropyle of *Aldrovanda*. The chalaza of *Aldrovanda* (Fig. 2C) is slightly pointed. In the basal part of *Palaeoaldrovanda* (Fig. 1F) there is a very distinct cap-like projection with an irregularly pitted surface, different from the chalaza of *A. vesiculosa*. The raphe of *Aldrovanda* is rather indistinct, but still recognizable. *Palaeoaldrovanda* does not show any raphe.

Aldrovanda vesiculosa has anatropous ovules. The micropyle and hilum are close together in the apical part of the seed and the raphe is distinct. The chalazal area, opposite the micropyle and hilum, may be elevated, the raphe is internal and so does not leave a scar, but its presence shows as a raised ridge on the surface of the seed. In *Palaeoaldrovanda splendens*, structures are clearly present in both ends of the fossils and there is no indicat-

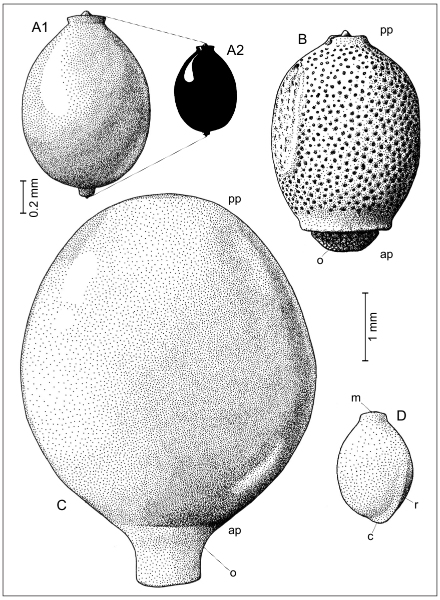

Fig. 5. A – Complete *Palaeoaldrovanda splendens* with shiny surface; small conical projection surrounded with coronal rim in apical part; cap-like projection in basal part. A1 – Object enlarged, bar = 0.2 mm. A2 – Object in natural (black) colour. B – *Lonchodes brevipes* (Phasmotodea, Insecta) egg showing conical projection structure in posterior part, surrounded by coronal rim bearing fine pitting; round operculum in anterior part of egg. C – *Extatosoma tiaratum* (Phasmotodea, Insecta) egg with fleshy surface. D – *Aldrovanda vesiculosa* (Droseraceae, Angiospermae) ovoid seed showing micropylar area and slightly pointed chalaza; raphe slightly raised. pp – posterior part; ap – apical part; o – operculum; m – micropyle; r – raphe; c – chalaza. All objects in the same magnification except A1.

ion of a raphe. If *Palaeoaldrovanda* is indeed a seed, this structure would indicate an orthotropous organisation, which does not correspond with the orientation of ovules in the genus *Aldrovanda* and the whole family Droseraceae.

The seed coat of *Aldrovanda vesiculosa* is formed by two layers of cells. The outer layer consists of columnar cells having thickly cutinised outer periclinal and anticlinal walls. Their inner periclinal walls are thin. The inner seed coat layer consists of irregularly arranged thin-walled cells (Fig. 2B). *Palaeoaldrovanda splendens* shows only one compact structure composed of rectangular cells arranged in rows (Fig. 1E). This structure does not correspond to any of the layers in *A. vesiculosa* and does not show the characteristic cell structure pattern of fossil representatives of the *Aldrovanda* genus (Friis 1985: pl. 15, fig.2).

There are also differences in seed micromorphology between *Palaeoaldrovanda* and *Aldrovanda*. The outer epidermis of the *Aldrovanda* seed consists of polygonal cells (15-25 µm; see Fig. 2F) while the outer epidermis of *Palaeoaldrovanda* (Fig. 1F) displays rectangular cells in rows.

Other members of the family Droseraceae – *Drosophyllum, Dionaea* and *Drosera* – have seeds with very different morphology. They have various shapes from ovoid to very elongated, but never show a shiny surface of the coat layer (for more details see Boesewinkel 1989).

Based on the above mentioned differences it is concluded that *Palaeoaldrovanda* is very probably not a relative of *Aldrovanda*.

Comparison between fossil *Palaeoaldrovanda* and eggs of insects

Palaeoaldrovanda and insect eggs exhibit a number of characters in common. They are of similar shape, showing in some cases similar wall construction, including cellular pattern.

Phasmatodea: If comparing representatives of Phasmatodea with *Palaeoaldrovanda* in terms of shape, their similarity is very conspicuous. *Palaeoaldrovanda* shows a small conical projection surrounded with coronal rim, resembling structures in the posterior part of eggs of the genus *Lonchodes*, and a well delimited cap-like structure resembling the operculum of Phasmatodea eggs. However, none of the studied eggs of Phasmatodea are completely identical with *Palaeoaldrovanda*. The principal difference is that the inner membrane of Phasmatodea is structureless, but *Palaeoaldrovanda* has an inner membrane consisting of rectangular cells in rows.

Lepidoptera: Lepidoptera eggs of *Cossus cossus* have the inner surface of the chorion built of rectangular cells in rows. This cell structure is similar to the inner structure of the *Palaeoaldrovanda* wall (cf. Figs. 1E and 4D), but the general shape and outer surface of the chorion is different from *Palaeoaldrovanda*. The same cellular pattern, rectangular cells in rows, as occurs on the inner surface of *Palaeoaldrovanda* (Fig. 1E), we have observed on the outer surface of the chorion in eggs of *Eryphanis polyxena* (Fig. 4B) and *Caligo memnon.* Rectangular cells in rows seem to be a common character among lepidoptera eggs (Hinton 1981). Additionally, eggs of *Papilio memnon* show similarities to *Palaeoaldrovanda* in having a smooth chorion (cf. Figs. 1A and 4E). However, we only studied eggs of five lepidopteran species and this number is not sufficient for general conclusions.

CONCLUSIONS

In this paper we provide only preliminary observations. However, even this brief revision clearly indicates that the interpretation by Knobloch & Mai (1984) of *Palaeoaldrovanda* as seeds related to *Aldrovanda* was not correct. There are no diagnostic characters which would support any relation to modern Droseraceae. Our studies clearly show that *Palaeoaldrovanda* is not a seed with a basic anatropical and bitegmic organisation; there is no evidence of a raphe, and the wall structure is simple. *Palaeoaldrovanda* does not show a clearly pronounced micropyle or chalaza. Except for the black, shiny surface and the shape and size of the fossils, there are no characters that link *Palaeoaldrovanda* with extant *Aldrovanda*. In conclusion, we suggest the fossils are not closely related to any fossil or extant members of Droseraceae and they cannot be included in this family. Whether the *Palaeoaldrovanda* fossils are seeds at all as first described is therefore very questionable.

Instead we have explored the possibility that the fossils could represent insect eggs. This is supported by the following characters: presence of a conical projection surrounded by a coronal rim, resembling a posterior polar mound in the genus *Lonchodes,* and inner surface covered by rectangular cells in rows, resembling the inner surface of the chorion in the genus *Cossus*. Diversity of insect eggs is very high and we have studied only a limited number of actual species samples; additional species were studied from literature. Eggs of insects have an ovoid shape and projections on both sides, characters that are also observed for *Palaeoaldrovanda*. The outer surface of the chorion is shiny in some species, and in others, the inner surface is covered by rectangular cells in rows, characters that are also observed for the wall of *Palaeoaldrovanda*. However, the wall structure of *Palaeoaldrovanda* is different from all insect eggs that we have studied, in having only one layer.

Our new interpretation of *Palaeoaldrovanda* significantly influences the current view of the family Droseraceae. It is at least possible that this family did not evolve until the Tertiary. It may also influence the hypotheses of the first unequivocal appearance of carnivorous plants in general.

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