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A new Early Liassic Caytoniales fructification from Hungary

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ABSTRACT. Several new seed bearing structures were collected in the Mecsek Mountains (Southern Hungary). Their structure undoubtedly shows affinity to the Caytoniales, however they differ from the hitherto known female reproductive organ, *Caytonia*. Good preservation of the cuticles, isolated both from the seed-bearing cupules and seeds *in situ*, allowed detailed examination of their position and structure. The results obtained have confirmed our knowledge of Caytoniales and have further provided new information on the structural variability of reproductive organs in Caytoniales. For the Hungarian material a new genus and species, *Reymanownaea kvacekii* is proposed.

KEY WORDS: Caytoniales, Early Liassic, Hungary, female reproductive organ, coalified seed, cuticle autofluorescence

INTRODUCTION

The Caytoniales are a small group of seed plants known from the Late Triassic to the Early Cretaceous (Jongmans & Dijkstra 1959, 1964, Harris 1951, 1964, Taylor & Taylor 1993). The group includes a single family containing five genera based on different organs (leaves, seed bearing structures, isolated seeds, pollen organs and dispersed pollen). They are generally considered to represent a single type of plant referred to the *Caytonia* plant. Several species (mainly leaves) have been described particularly from Asia, Greenland, Great Britain, Sweden, Poland and Antarctica (Jongmans & Dijkstra 1959, 1964, Taylor & Taylor 1993). The leaves are assigned to the genus *Sagenopteris* Presl (Thomas 1925, Harris 1932, 1964, Reymanówna 1973), the pollen organs – to the genus *Caytonanthus* Harris (Harris 1937, 1964, van Konijnenburg-van Cittert 1971), and the seed bearing organ to the genus *Caytonia* Thomas (Thomas 1925, Harris 1964). The isolated seeds are known under the name *Amphorispermum* Harris (1932), and dispersed pollen are referred to the genus *Vitreisporites* Leschik (Taylor & Taylor 1993). The stem was described by Harris (1971).

The seed-bearing organs of *Caytonia* and individual seeds were examined in detail based on material from Yorkshire, England (Thomas 1925, Harris 1940, 1964), Scoresby Sound, Greenland (Harris 1932) and from Poland (Reymanówna 1973, 1974). *Caytonia* was also reported from the Far East of Russia (Krassilov 1977), India (Bose & Banerji 1984), Antarctica (Banerji & Lemoigne 1987) and Iran (Schweitzer & Kirchner 1998).

Excellent preservation of many previously described specimens has allowed a complete reconstruction of the structure of *Caytonia* and draw in detail the mechanism of its pollination.

Species of *Caytonia* differ from each other mainly in size (Harris 1940, 1964, Reymanówna 1973, Schweitzer & Kirchner 1998), in the number of seeds (Harris 1940), and sometimes in epidermal characteristics (Harris 1940, 1964).

In the Mecsek Mountains (Hungary) the Caytoniales are represented by a new taxon of seed bearing structure described in this paper

as well as three species of *Sagenopteris: S. nilssoniana* Brongniart, *S. hallei* Harris and *S. pilosa* Barbacka (Barbacka 1992), some undetermined, poorly preserved leaves and numerous specimens of *Caytonanthus* sp. (Barbacka, unpublished data).

MATERIAL

Sixteen separate seed-bearing structures (cupules) were collected from a single piece of rock. It originated from unproductive layers of a coal mine and was collected on the dump of the Zobák shaft near Komló (The Mecsek Mountains, Southern Hungary). The coal production in this area is limited to the Lower Liassic.

The specimens are preserved as imprints or coalified and compressed seed-bearing cupules with outer cuticles fully or only partly intact. They include entire seed-bearing organs with their seeds, as well as isolated seeds occurring in groups or individually. While most of the cupules are probably mature, three of them are small and seem to be immature. The seeds enclosed in the cupules as well as the isolated ones seem to be fully mature. They are coalified and have their 3D-structure preserved.

The material is stored in the Hungarian Natural History Museum in Budapest, palaeobotanical collection (BP).

METHODS

The state of preservation of the material allowed multiple examinations. The cuticles of the cupules and the seeds were macerated in Schulze's solution and treated with 3% KOH. They were fixed in glycerine with phenol and protected by paraffin. The stone layer of the seeds was fixed directly in canada balsam under a cover glass, since it dissolves in glycerin. Whole cupules were examined with a SEM, without a gold coating; the seeds were coated with gold before investigation. The chemical composition of the fleshy-tissue of the cupule was examined under a reflected light fluorescence microscope at blue exciting light. In addition to the standard preparation of seed cuticles the seeds were also examined in polished sections. The seeds were embedded in the epoxy Durcupan and metacrylate (LR white) resins, then polished in three directions: in two longitudinal planes – one parallel to the flattened side, the other perpendicular to it, and one transversal section. The observations were made during different phases of the polishing but generally the surfaces were polished until they reached the middle of the seed.

The sectioning method was used by Thomas (1925), Harris (1940) and Reymanówna (1970), but they concentrated mainly on cupules. Thomas (1925) made sections of cupules containing seeds and in this way he also obtained seed sections of different directions (as they were compressed inside the cupule). The figure 31 in Thomas' (1925) paper shows the inner structure of a sectioned seed which is almost identical to a picture of one of the Hungarian seeds observed under a fluorescence microscope (Pl. 7 fig. 5). However, our method of polished section avoids the long chemical treatment (which was necessary for cupule preparation).

Under the fluorescence microscope the seed cuticles show a yellow colour and are easily recognized allowing observation of their arrangement and thickness. Utilizing the autofluorescence of the cuticle in blue exciting light made our method shorter in time and considerably simpler. The polished sections were made using sand paper (Auto-paper P 280A, P 400 A, P 600 A, Klingspor, Germany) and Al_2O_3 polishing powder (5 μm, 1 μm, 0.3 μm) in two ways: a) on the glass plate, b) on the polishing cloth (microcloth). The best results were obtained with method "b". The cloth removed the softer coal from inside the seeds, so the cuticle, which was harder, as a result protruded slightly from the surface. Under the fluorescence microscope it gave a more intensive fluorescence (increased by immersion oil), and under the reflected light microscope the cuticle was more shaded.

SYSTEMATIC DESCRIPTION

CAYTONIALES

Reymanownaea Barbacka & Bóka **gen. nov.**

Type: ***Reymanownaea kvacekii*** Barbacka & Bóka **sp. nov.**

Diagnosis. Fleshy, multi-ovulate cupules on short stalk. Cupule reniform in outline, fully surrounding seeds; lip placed at the base of the cupule near stalk, possibly surrounding it, showing numerous canals. Cupule and stalk filled with amorphous substance with sclereids. Cupule containing numerous orthotropous seeds, arranged in more than one row; micropyles facing the mouth of the cupule.

Derivatio nominis: Named in honour of the late Dr. Maria Reymanówna from the W. Szafer Institute of Botany, Polish Academy of Sciences in Cracow, Poland, a prominent palaeobotanist, in respect her scientific works.

Reymanownaea kvacekii Barbacka & Bóka **sp. nov**.

Pls 1–9

(?) 1998 *Caytonia* sp., Schweitzer & Kirchner, p. 37; Pl. 8, figs 1–5; text fig. 10.

Holotype. BP 96.305.1., Pl. 3 fig. 1.

Repository. Botanical Department of the

Hungarian Natural History Museum, Budapest.

Type locality. Zobák shaft near Komló (dump), the Mecsek Mountains, Hungary.

Stratygraphic horizon. Lower Liassic (Hettangian), Karolinavölgy Formation.

Derivatio nominis: Named in honour of Prof. Zlatko Kvaček, (Faculty of Sciences, Charles University, Praque, Czech Republic) in respect his scientific results.

Material. BP 96.283.1.E, K-O, 96.294.1, 96.301.1, 96.303.1, 96.305.1, 98.350.1.F, 96.402.1.B, 96.403.1.A, 96.513.1.C, 98.14.1.A, 98.121, slide (polished) Nos 1040, 1048, 1050, 1037, 1062, 1064, 1066, 1068

Diagnosis. Cupule reniform in outline, ca. 3–5 mm high and ca. 7–8 mm wide, covering 20–30 seeds. Cuticle of cupule thick, outer epidermis cells with straight cell walls. Stomata absent. Hair bases in two rows at the base of the cupule. Lip not recurved, mouth seemingly running all around the cupule (no connection between the cupule and the stalk being found; no internal structure of the cupule found so far), with numerous canals 75 μm wide. Stalk 2.5–4 mm wide at distal end, narrowing towards proximal end (0.5–0.8 mm wide). Epidermis of stalk with polygonal cells, numerous hair bases. Cupule and stalk filled with amorphous substance (fleshy substance) containing sclereids (80–120 μm in diameter). Orthotropous seeds arranged in two to three transversely oriented, parallel rows; seeds ca. 1.5 mm long, ca. 0.7 mm wide; micropyle directed towards mouth of cupule. Base of funiculus asymmetrical. Testa very thick.

DESCRIPTION

The cupule containing seeds is placed on a short stalk (Fig. 1).

Stalk

The stalk (Pl. 1 figs 1, 2, Fig. 1) is short, 2.5–3 mm long, usually slightly curved. Its distal end is slightly protruding into the cupule, 2.5–4 mm wide, forming a convex bottom of the cupule similar to a receptacle. The proximal end of the stalk is slender, always broken and 0.5–0.8 mm wide (Pl. 1 figs 1, 2). The stalk shows dorsiventral cuticles, a thicker (Pl. 1 fig. 3) and a thinner one (Pl. 1 figs 4–5). The

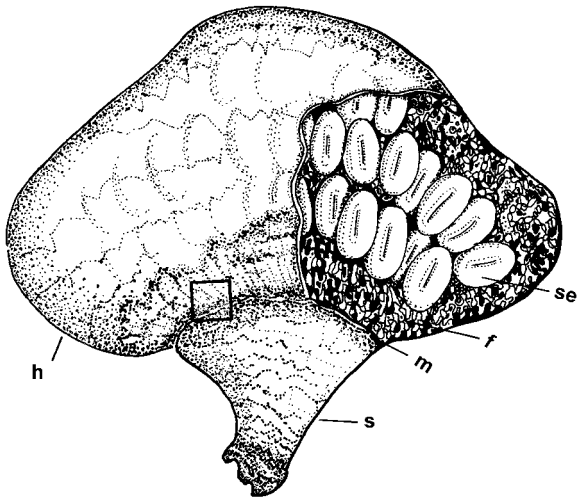

Fig. 1. The reconstructed cupule of the *R. kvacekii*: **h** – head, **se** – seed, **f** – fleshy substance, **m** – mouth, **s** – stalk. The square indicates the position of the fragment from Fig. 2

epidermis cells are about 25 × 24 μm, have rounded corners and straight cell walls. On both thicker and thinner cuticles are found hair bases but these are more frequent on the thinner cuticle. Each hair base consists of 4 thicker rounded cells with a central cavity in the middle of the structure (Pl. 1 fig. 7). On both cuticles structures consisting of two rounded cells were also observed, similar to undeveloped stomata in juvenile leaves of *Sagenopteris* (Barbacka & Bóka 2000), but they may also be hair bases (Pl. 1 fig. 6). Stomata were not observed.

Cupule

The cupule is transversely reniform in outline. Usually the mature cupules are about 4.5 mm × 7–8 mm. The largest cupule measures 5.5 × 8.5 mm, the smallest, probably immature, 2.5 × 6 mm. Compressed cupules without a cuticle shows two distinct and curved lines that separate three parallel zones in the internal structure. The first zone borders with the extended distal end of the stalk, the second, very narrow one, includes the mouth of the fructification, and the third, the widest, at the upper part of the cupule, contains the seeds (Pl. 1 fig. 2, indicated by arrows).

The cupule is covered by a thick outer cuticle (Pl. 2 fig. 1). The cells have thick and straight anticlinal walls. At the basal part of the cupule, near the stalk, the cells are small and slightly elongated, about 26 × 18 μm. Near

the base of the cupule there is a simple, horizontal row of hair bases consisting of about 5–6 cells surrounding a star-shaped central cavity with thickened margins (Pl. 2 fig. 2). Towards the middle part of the cupule the cells become more narrow and elongated, on average about 36 × 9 μm. They form slightly arcuate, vertical rows (Pl. 2 fig. 3). Towards the top of the cupule, the cells become rectangular and large, about 39 × 27 μm (Pl. 2 fig. 4). At the base of the cupule, the cuticle forms a 0.3 mm wide margin that covers the stalk, running seemingly all around it (Fig. 1). No stomata were observed.

Seeds fill almost the entire cavity of the cupule, leaving about 0.5 mm space between them and the outer cuticle of the cupule (Pl. 3 fig. 1).

Fleshy substance

The cupule is filled by a fleshy substance containing small egg-shaped bodies (sclereids?) (Pl. 2 fig. 5, Pl. 3 figs 1, 2). They are about 80–120 μm long and can easily be separated with a needle (Pl. 4 fig. 1). The fleshy substance fills the space between individual seeds and between the seeds and the outer cuticle of the cupule. It is also present at the basal part of the cupule and in the stalk, but here the bodies are only about half the size of those in the cupule. Their size and density decrease towards the proximal end of the stalk (Pl. 3 fig. 1). In many cases the seeds of *Reymanownaea kvacekii* are found in small groups, stuck to the flesh, and even the individual seeds are often surrounded by this substance (Pl. 4 fig. 2).

Chemical analysis of the fleshy substance proved that it contains lipids, remains of lignine and cellulose. Under a fluorescence microscope it shows a yellow colour at a blue exciting light. The enclosed bodies (sclereids ?) do not show any cuticular remains (no fluorescency) (Pl. 3 fig. 3).

Mouth

The mouth is placed at the base of the cupule. On all examined specimens the mouth extends the whole width of the cupule base. The opening of the mouth lies between the lip and the stalk.

The structure of the mouth shows thick cuticular bars, about 125 μm wide in the middle part, alternating with less cutinised strips, about 75 μm wide in the middle part (Pl. 4 figs 3–5). They form canals through which the pollen grains might penetrate towards the ovules. Their density is 6 bars and 5 canals per mm. At the proximal end the bars are slightly narrower and their tips are elongated. This end projects into the cuticle of the cupule. At the distal end of the mouth the bars extend and their rounded tips approach each other. This part of the mouth projects into the lip.

Lip

The lip is not recurved and covers the stalk for about 0.3 mm, being the basic margin of the cupule cuticle (Fig. 2). The lip consists of two adjacent cuticles: the outer cuticle, which is the continuation of the outer cuticular layer of the cupule, and the inner cuticle, which in its state of preservation does not show continuation. It may be the remains of the inner cuticle of the cupule which is now not detectable.

The outer cuticle of the lip shows irregular, polygonal cells with thick cell walls. Sometimes hair bases were observed (Pl. 4 fig. 6, Pl. 5 fig. 1). The inner cuticle shows rows of elongated cells (12–15 μm long and 7 μm wide) with very long papillae directed downwards. Each papilla covers part of the next cell in the

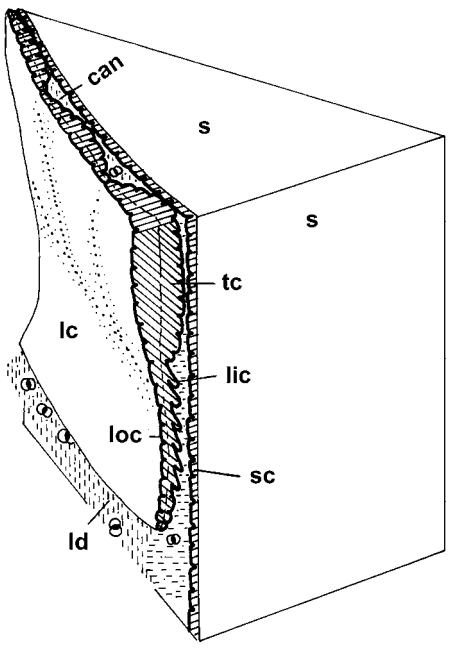

Fig. 2. Schematic drawing of the mouth of the cupule in transversal and radial longitudinal sections: **s** – stalk, **can** – canal, **tc** – thickening of the cuticle (bar), **lc** – lip cuticle, **loc** – lip outer cuticle, **lic** – lip inner cuticle, **sc** – cuticle of the stalk, **ld** – liquid drop

row, so they are arranged like rooftiles (Pl. 5 figs 4, 5).

Both cuticles have numerous *Vitreisporites* pollen grains on their surfaces (Pl. 5 figs 1–3).

Seeds

Inside the cupule, there are about 20–30 densely crowded seeds arranged in two or three transverse rows that partly cover each other. The seeds are oriented towards the "bottom" of the cupule, but do not touch it. Usually, in the first and second rows from the base of the cupule there are about 8–13 seeds and possibly 1–4 in a third row. The seeds are small and elongated, about 1–1.5 mm long and 0.7 mm wide, flattened – partly by compression – and are only about 0.1–0.3 mm thick (Pl. 5 fig. 6). The funiculus lies opposite the micropyle which is directed towards the mouth. Preserved whole funiculus was not observed, only their asymmetrical base on the seed (Pl. 6 fig. 1, between arrows).

Seed cuticles (nomenclature according to Harris 1940)

The outer cuticle, the cuticle of the testa (1.74 μm thick), shows cells with straight anticlinal walls. Their shape and size vary along the seed (Pl. 6 figs 2–5). At the funiculus the cells are elongated, from 100 × 10 to 137 × 20 μm, becoming wider (about 38 × 13 to 50 × 13 μm) towards the middle part of the seed. Towards the micropyle the cells become more rectangular, from 137 × 33 μm to 88 × 45 μm, until they are almost square, 30 × 28 μm near the micropylar canal. The cuticle of the testa at the micropyle shows conspicuous bulges. This was observed in only one seed, which was polished together with the surrounding rock (Pl. 6 fig. 6), because it usually breaks when a seed is removed.

Below this cuticle a thick layer of stone cells (Pl. 7 fig. 5) follows. This is the thickest layer, which occupies about 5/6 of the whole thickness of the seed, being about 60.6 μm thick. The stone cells are of different sizes, the largest are 88 × 38 μm, the smallest 30 × 25 μm. The shape is characteristically elongated, hexagonal, and with a small central pit in each cell. Sometimes striations are visible on the cells, extending more or less radially from the pit (Pl. 7 fig.1). Because of the non-cuticular nature of the stone cells, they do not show fluorescency under a fluorescence microscope, while the central pits do show a strong fluorescency (Pl. 7 fig. 2). Under the reflected light microscope the central pits were observed as shallow cavities (Pl. 7 figs 3–4).

Under the layer of stone cells there is a "spotted" layer. It is very thin (0.8 μm), membrane-like, without any indications of cell walls (Pl. 7 fig. 6).

The inner cuticle of the integument has a long micropylar canal which is about 88 μm wide and more than 100 μm long, and composed of well-cutinized small (15 × 13 μm), nearly rounded cells (Pl. 8 fig. 1). In this micropylar canal *Vitreisporites* pollen grains are found (Pl. 8 fig. 2). The length of the pollen grains from saccus to saccus is about 28 μm.

The cuticle of the nucellus (the perisperm cuticle) is relatively thick (2.16 μm) (Pl. 8 figs 3–6, Pl. 9 figs 1–4). It shows rectangular or elongated, large cells. Their size varies from 63 × 33 μm to 145 × 63 μm. The cell walls are sinusoid, most conspicuously so towards the micropyle.

Internal to the nucellus cuticle is a non-cellular layer i.e. an aleurone layer (Pl. 9 figs 3–5). It is thick (about 25 μm) and shows a strongly fluorescent, granular structure. On the polished section a 110 μm long incision of the aleurone layer was observed at the end of the seed. Over the complete length it is surrounded by a thin cuticle (Pl. 9 fig. 6).

DISCUSSION

In its general structure the Hungarian fossil corresponds closely with features of the *Caytonia* (Thomas 1925, Harris 1940, 1960, 1964, Reymanówna 1973). The presence of a mouth, the structure of its lip, the *Vitreisporites* – type pollen grains in its micropyle, and its seed structure show strong similarity to the proper characteristics of *Caytonia*. Details which distinguish *Reymanownaea kvacekii* from previously described species of *Caytonia* are discussed below and the most important differences shown in Table 1.

Morphology

The most significant difference between the genera *Reymanownaea* and *Caytonia* is in the

Table 1. Comparison between the *Caytonia* and the *Reymanownaea*

characteristics	*Caytonia*	*Reymanownaea*
mouth	on one side, usualy 1 mm wide (Thomas 1925, Harris 1940, Reymanówna 1973)	all around the base of the cupule
seeds arrangement	along the midvein of macrosporophyl (Thomas 1925, Taylor & Taylor 1993)	on the side of the cupule
connection head/stalk	on one side the cuticle of the stalk continues into the head cuticle	no observed continuation of the stalk into the head
lip	recurved	not recurved
"bottom" of the cupule	not observed	present
fleshy substance in the stalk	not observed	present
funiculus	symmetrical (according to reconstruction drawing, Thomas 1925, text fig. 7, and Harris 1960, Pl. 1 fig. 2, Pl. 2 figs 9, 10)	asymmetrical
shape of the stalk	almost constant width along the stalk	distal end of the stalk much wider than its proximal end
papillae on the lip	present on lip and stalk (both sides of the mouth opening)	only on lip (one side of the mouth opening)
nucellar cuticle	similar cells on both chalazal and micropylar ends	cells on chalazal and micropylar ends different in shape and size

width and position of the mouth which gives rise to other differences in the structure of the new seed-bearing organ. In *Reymanownaea* the mouth seems to run all around the cupule: none of the examined cupules showed a connection between the cupule and the stalk. It may suggest that the connection is very narrow (one point) or that it runs inside the cupule – but any proof in internal structure of the cupule has not been found. The cuticle parts for the preparation of the mouth were taken from different places along the lower margin of the cupule and each preparation showed the usual lip structure. In *Caytonia* the mouth is usually about 1 mm wide while the rest of the cupule is connected to the stalk forming characteristic "encurved megasporophyl" (Reymanówna 1974).

The protruding distal end of the stalk forming the "bottom" of the cupule is the second important feature that distinguishes the two genera. These two differences may suggest a different way of cupule development. In *Caytonia* the morphology and the structure of the cupule show clearly that its reproductive organ was formed from one developmental unit, namely from the curved megasporophyl containing ovules. In all specimens of *Reymanownaea* however, the cupule and stalk seem to form separate units. Nevertheless, it could not be corroborated because of internal structural elements not having been preserved. The presence of a fleshy substance and of sclereids in both the cupule and stalk suggests their close developmental relation, while the mouth being all around the stalk and the lack of a joining point between stalk and cupule emphasize their separation. Therefore the connecting elements might run inside the fructification and are not observable from the outside. On some specimens the fleshy substance in the stalk has a fan-like arrangement which suggests a symmetrical construction. In these cases the anatomy of *Reymanownaea* differs considerably from *Caytonia*. Unfortunately we have no proof or hypothesis for the interpretation of the developing process.

The seeds of *Reymanownaea* might join with the lateral side of the cupule. This is suggested by the asymmetrical base of the funiculus, the position of the seeds observed *in situ* in parallel, horizontal rows, and the space between the seeds and the top of the cupule (Fig. 1). In *Caytonia* the seeds were born along the midvein of the cupule (Thomas 1925, Taylor & Taylor 1993). Furthermore, there are some further secondary differences which clearly distinguish the genus *Reymanownaea* from *Caytonia* (Table 1).

The cupule of the *Reymanownaea* is about twice as wide as it is high, making its shape transversely oval, while the *Caytonia*'s is round or longitudinally elongated (Thomas 1925). They also differ in size: while the largest samples of *Caytonia* are 4.5 mm wide and the average is about 3.5 mm (Harris 1940),

Reymanownaea with its 8–8.5 mm width is about twice as large as *Caytonia*. The lip of the *Reymanownaea* is not recurved which the *Caytonia*'s generally is; it forms an straight, uncurved margin only. The stalk of *Reymanownaea* is usually curved and considerably wider at the distal end. Its proximal end is narrow. The stalk of *Caytonia* is straight and its width is almost constant (Thomas 1925). The fleshy substance inside the cupule is similar in type to that of *Caytonia* (Thomas 1925, Harris 1940, Reymanówna 1973), but the sclereids are of a different type than those described by Reymanówna (1973). They rather agree with the oval bodies discussed by Thomas (1925). The fleshy substance is present in the stalk as well, which was not mentioned for any species of *Caytonia*.

Cuticle

In general the cuticular structure of the various parts of *Reymanownaea* corresponds with the cuticles described of *Caytonia*.

The cuticle of the cupule is very simple and thick, without many characteristics. However, the distribution and structure of the hair bases in *R. kvacekii* is different from those described by Reymanówna (1973) in *Caytonia harrisii* Reymanówna (the only species with hair bases on the cupule). The inner cuticle of the cupule as described by Reymanówna (1973), Krassilov (1977) and Harris (1940), was not found near the seeds in *R. kvacekii*. Its presumed remains were observed only in the lip.

The cuticle of the stalk is different from that of the *Caytonia*. *R. kvacekii* does not show either rows of cells on the upper surface or differentiation in cell shapes between the upper and lower cuticle as in the *Caytonia* (Thomas 1925, Harris 1940, Reymanówna 1973). There are no papillae on the stalk cuticle of *R. kvacekii* and the hair bases are of a different type from the described ones in *Caytonia* (Reymanówna 1973).

The cuticles of the mouth and lip of *Reymanownaea* and *Caytonia* are similar in structure. The significant difference is in the width of the bars and canals. In *C. sewardii* Thomas, the bars are 70 μm wide and the canals are about 28–30 μm (Harris 1940). The width of the bars in *R. kvacekii* is 125 μm and the canals are about 75 μm wide. This comparison regards *C. sewardii* only, because of the lack of data for the other species. However, considering the usual density of bars per mm of lip in the different species of *Caytonia* (Harris 1940) being higher than in *R. kvacekii*, they could not be as wide as those in *Reymanownaea*, they would even be narrower.

The structure of the lip essentially agrees with that of *Caytonia*. In *R. kvacekii* the papillae are of a different type; they are all extended in the same direction and cover the lip's inner surface, while in *Caytonia* they are also present on the stalk opposite the lip.

The seed cuticles of *Reymanownaea* generally agree with descriptions made on *Caytonia* seeds (Thomas 1925, Harris 1932, 1940, 1960, 1964, Reymanówna 1973) as regarding their types and arrangement. The differences are visible in their structure. In *R. kvacekii* the outer cuticle of the testa is thicker and the cell walls are strongly marked. Its cells are different in size and shape, depending on their position along the seed. The cells of the nucellus also show various shape at the ends of the seed, being narrow and elongated at the funiculus and smaller and rectangular towards the micropyle. In *Caytonia* both the chalazal and the micropylar ends of the nucellar cuticle show the same small cells, and only in the middle part of the nucellar sack the cells are elongated and narrow (Harris 1960). The "micropylar collar", as described by Harris (1960) was not observed in *R. kvacekii*.

The bisaccate pollen grains in the micropylar canal are, with regard to their size (25–30 μm, usually 28 μm), similar to the pollen grains of the *Caytonanthus oncodes* Harris or of the *C. arberi* (Thomas) Harris (Harris 1964, van Konijnenburg-van Cittert 1971).

With respect to its morphology, *R. kvacekii* seems to be much closer to the fructification described by Schweitzer and Kirchner from Alborz, Iran (1998) under the name *Caytonia* sp. They agree in shape of cupule and stalk, and size of the cupule is also similar, *Caytonia* sp. is 6–7 mm wide and 4–5 mm high. Although Schweitzer and Kirchner could not give any exact data about the length of the mouth, the wide zone above the extended distal end of the stalk is similar to the wide mouth in *Reymanownaea*. In the material from Iran we can also observe the same zonation of the cupule as in *R. kvacekii* (Schweitzer & Kirchner 1998, text fig. 10, Pl.8 figs 1–5). Moreover, the seed

arrangement of *R. kvacekii* is like that in *Caytonia* sp. from Iran (Schweitzer & Kirchner 1998, text fig. 10, Pl. 8, figs 1–5).

Unfortunately, we know nothing about the axis or the position of the cupules on it in Hungarian specimens. Considering the Schweitzer and Kirchner paper (1998) we may presume, that the arrangement of the *Reymanownaea* cupules was similar, i.e. spirally, to that in the *Caytonia* sp. from Iran.

POSSIBLE ATTRIBUTION OF *REYMANOWNAEA KVACEKII*

In the Mecsek Mountains the Liassic *Reymanownaea kvacekii* occurs with *Sagenopteris nilssoniana, S. harrisii* and *S. pilosa* (Barbacka 1992), but none of these were collected at the same time as the cupules. The fructifications were accompanied by a new type of *Sagenopteris* leaf, which differs in morphology from the other species. It has a characteristically wide and extended midrib at the base of its two middle pinnules (Fig. 3). Unfortunately its cuticular examination was impossible because the state of its preservation (Barbacka, unpublished data).

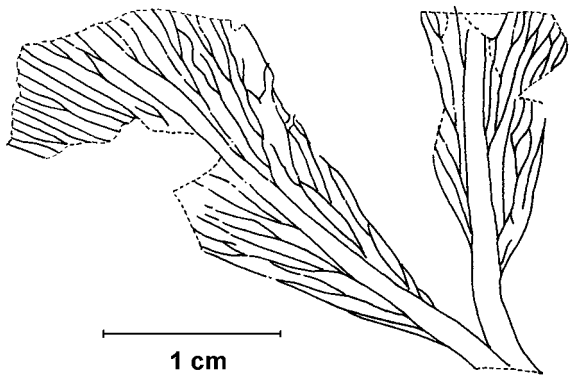

Fig. 3. Leaf of *Sagenopteris* sp., the new type, with extended midrib at the base of its two middle pinnules

Comparison of the known cuticles of the leaves with cuticles belonging to the cupule and stalk of *R. kvacekii* has not helped to establish the exact attribution of *R. kvacekii*. Some *Sagenopteris* species have poorly preserved cuticles. Irrespective of that, cuticles of leaves and fructifications might be slightly different. The *Caytonia sp.* (Schweitzer & Kirchner 1998) was found together with *Sagenopteris* cf. *phillipsii* (Brongniart) Presl in Iran, in the Middle Jurassic (Dogger) layers and also *S.* cf. *colpodes* Harris was mentioned from the same deposits. Therefore the ages of the *R. kvacekii* and *Caytonia* sp. from Iran are different, and also the species of *Sagenopteris* leaves that accompanied the cupules might be different. However, the Hungarian deposits are still being explored and material collected in the future may give new data for the resolution of this question.

Recently, five pieces of fructification very similar to *R. kvacekii* were found among material collected in Bayreuth (Liassic, Germany; J.H.A. van Konijnenburg-van Cittert, pers.com.). The material is stored at the Natural History Museum in Leiden, The Netherlands. If the specimens really belong to *Reymanownaea*, this genus may be related to *S. nilssoniana*, since this is the only species of *Sagenopteris* from the German Liassic.

CONCLUSION

A new genus of fructification belonging to the Caytoniales was established on the grounds of the difference in position of the mouth all around the base of the cupule. This difference also suggests a different way of cupule development from that of the *Caytonia*. On the basis of the available data a full interpretation was not possible. This question needs further study.

The appearance of the *Reymanownaea* (Liassic) is parallel in time with that of *Caytonia* known from the Liassic as well as from the Middle Jurassic and the Lower Cretaceous and shows that this group was more varied than was thought before.

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PLATES

Plate 1

Reymanownaea kvacekii gen. et sp. nov.

1. Fructification, SEM picture, bar = 1 mm, specimen No BP 96.283.1.E
2. The same fructification, bar = 2 mm (arrows indicate the lines that separate three parallel zones in the internal structure of the cupule)
3. The thicker cuticle of the stalk with hair bases, bar = 100 μm, slide No 1070

4, 5. The thinner cuticle of the stalk showing two types of hair bases, bar = 100 μm, slide No 1040

6. Hair bases (?) on the thinner cuticle of the stalk, bar = 25 μm, slide No 1070
7. Hair base on the thinner cuticle of the stalk, bar = 25 μm, slide No 1040

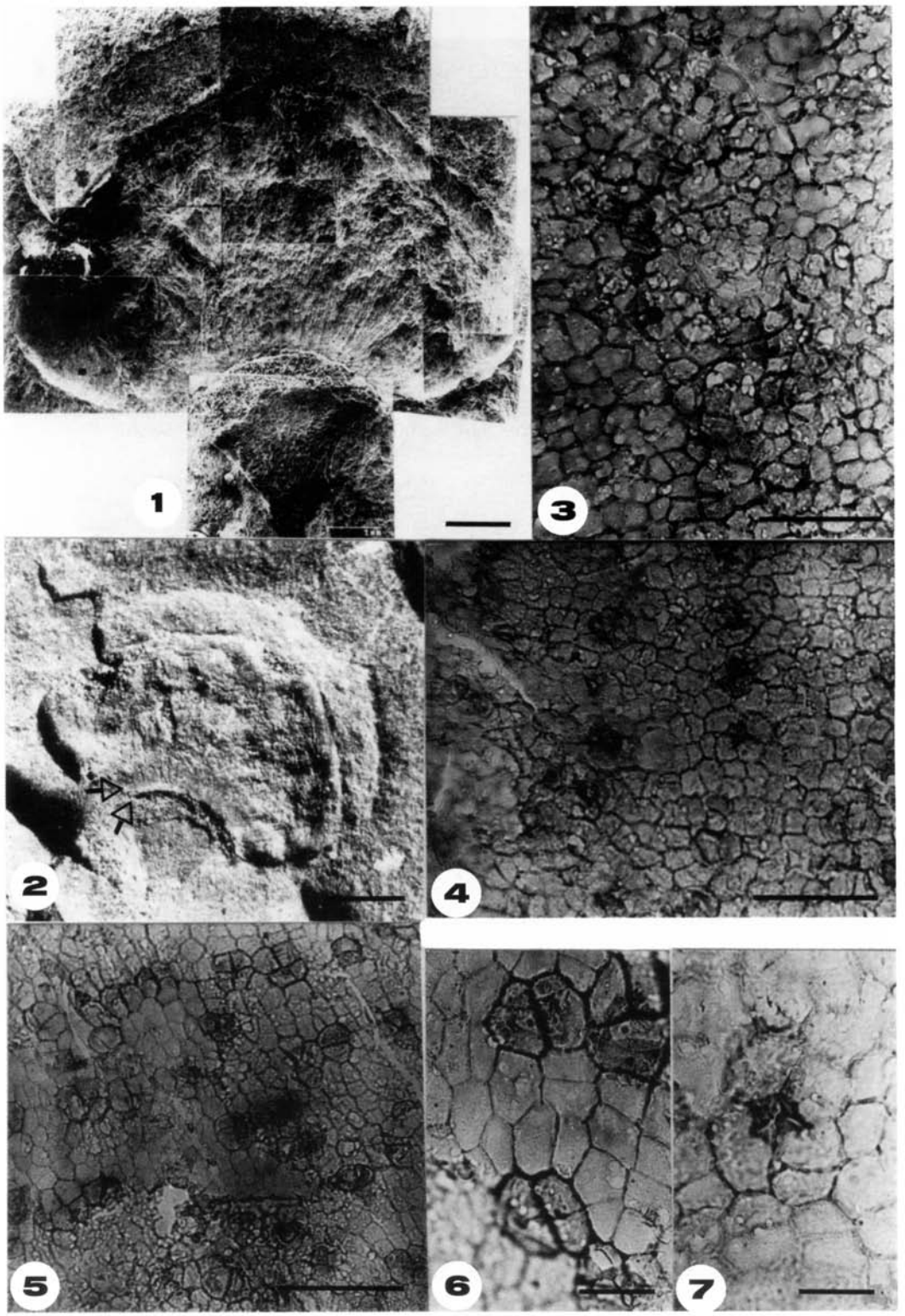
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Plate 2

Reymanownaea kvacekii gen. et sp. nov.

1. Cuticle of cupule, bar = 200 μm, slide No 1066
2. Cuticle at the base of cupule, the hair bases indicated by arrows, bar = 50 μm, slide No 1066
3. Cuticle towards the middle of cupule, bar = 50 μm, slide 1066
4. Cuticle towards the top of the cupule, bar = 50 μm, slide 1066
5. Fleshy substance with sclereids, SEM picture, bar = 200 μm, specimen No BP 96.305.1.

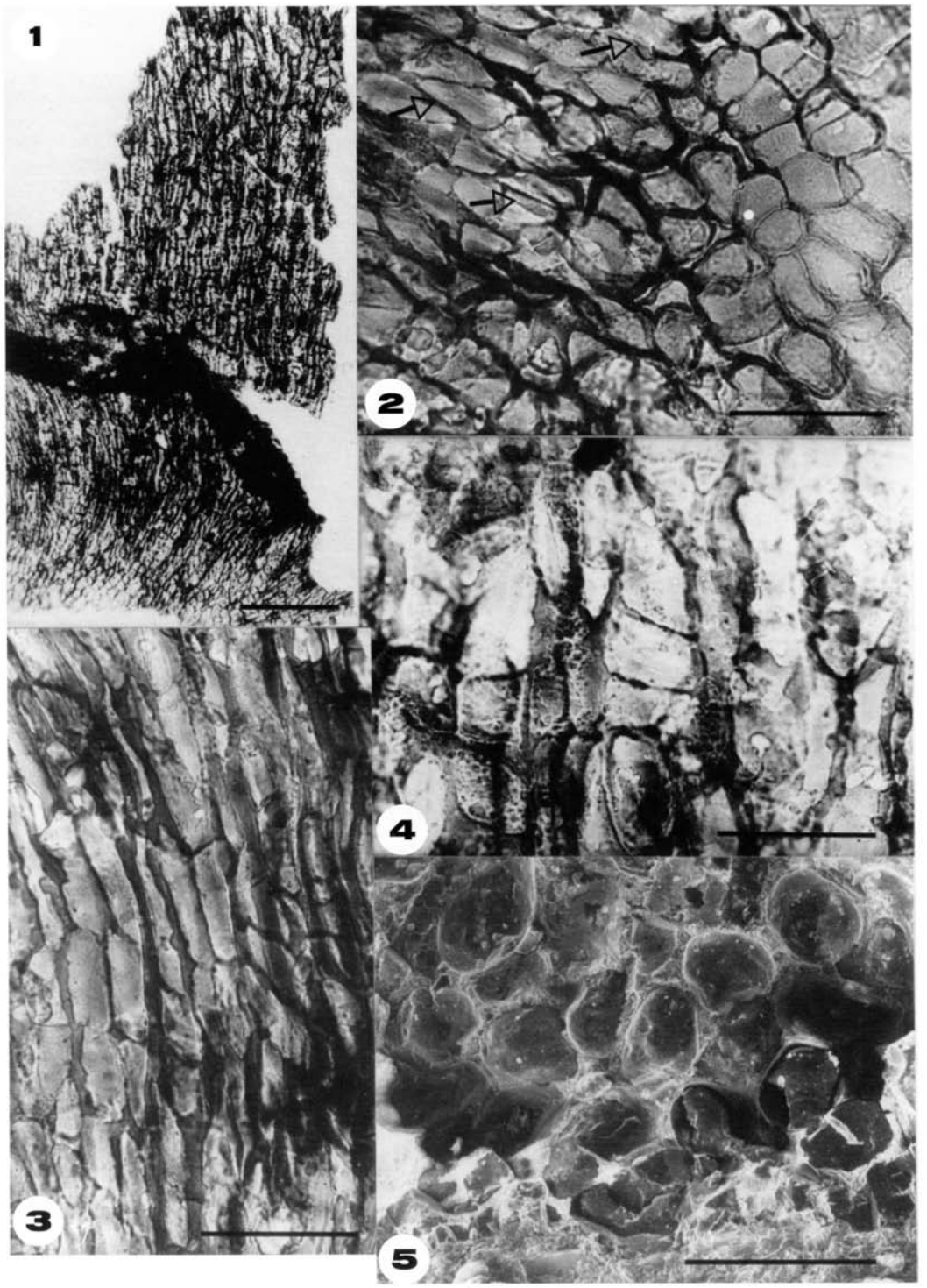
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Plate 3

Reymanownaea kvacekii gen. et sp. nov.

1. Holotype, SEM picture, bar = 1 mm, specimen No BP 96.305.1
2. The same specimen; SEM picture showing seeds surrounded by fleshy substance, bar = 500 μm
3. Fleshy substance under the fluorescence microscope, black sclereids in light flesh, bar = 50 μm

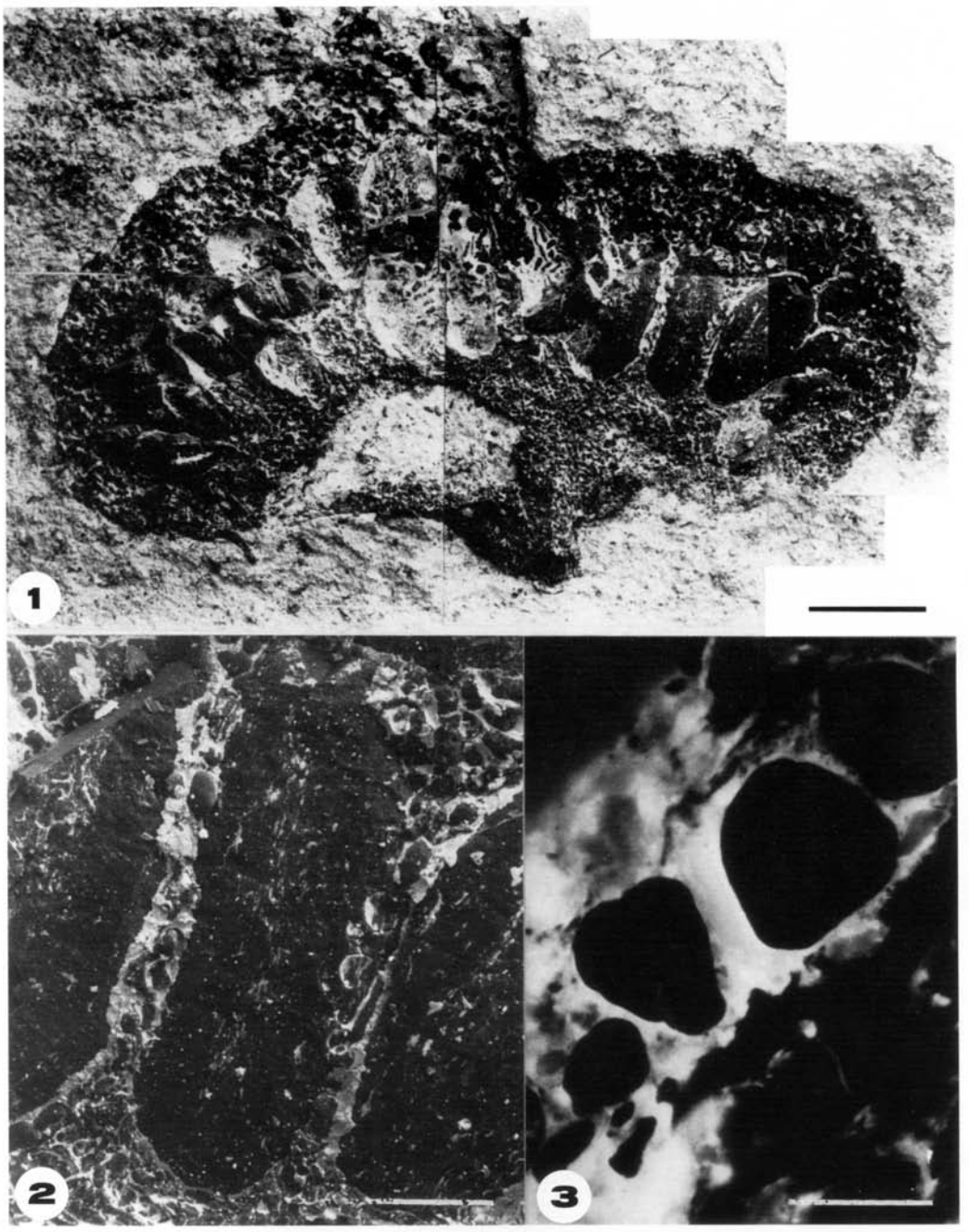
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Plate 4

Reymanownaea kvacekii gen. et sp. nov.

1. Sclereids in fleshy substance, SEM picture, bar = 25 μm
2. Separated group of seeds surrounded by fleshy substance, bar = 5 mm
3, 4. Lip canals, bars = 100 μm and 200 μm, slide No 1040
5. Lip canals, the lower part projecting into the lip, bar = 100 μm, slide No 1068
6. Outer cuticle of the lip, bar = 50 μm, slide No 1068

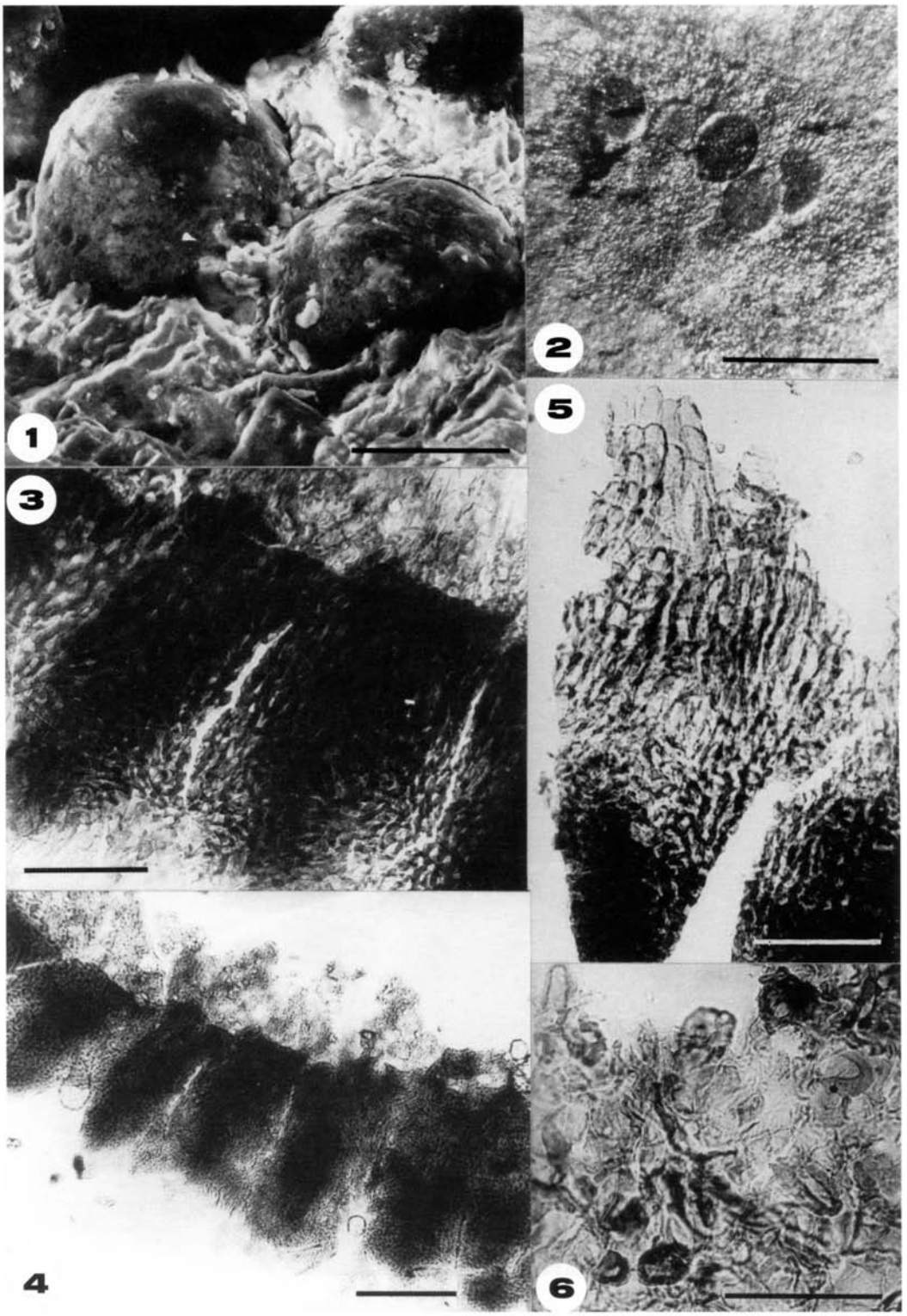
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Plate 5

Reymanownaea kvacekii gen. et sp. nov.

1. Outer cuticle of the lip with attached pollen grains, bar = 50 μm, slide No 1068
2, 3. Pollen grains of *Vitreisporites* type, bar = 25 μm, slide No 1068
4, 5. Inner cuticle of the lip, long papillate cells, bar = 50 μm, slide No 1068
6. Seed, arrows indicating the nucellus cuticle, SEM picture, bar = 500 μm

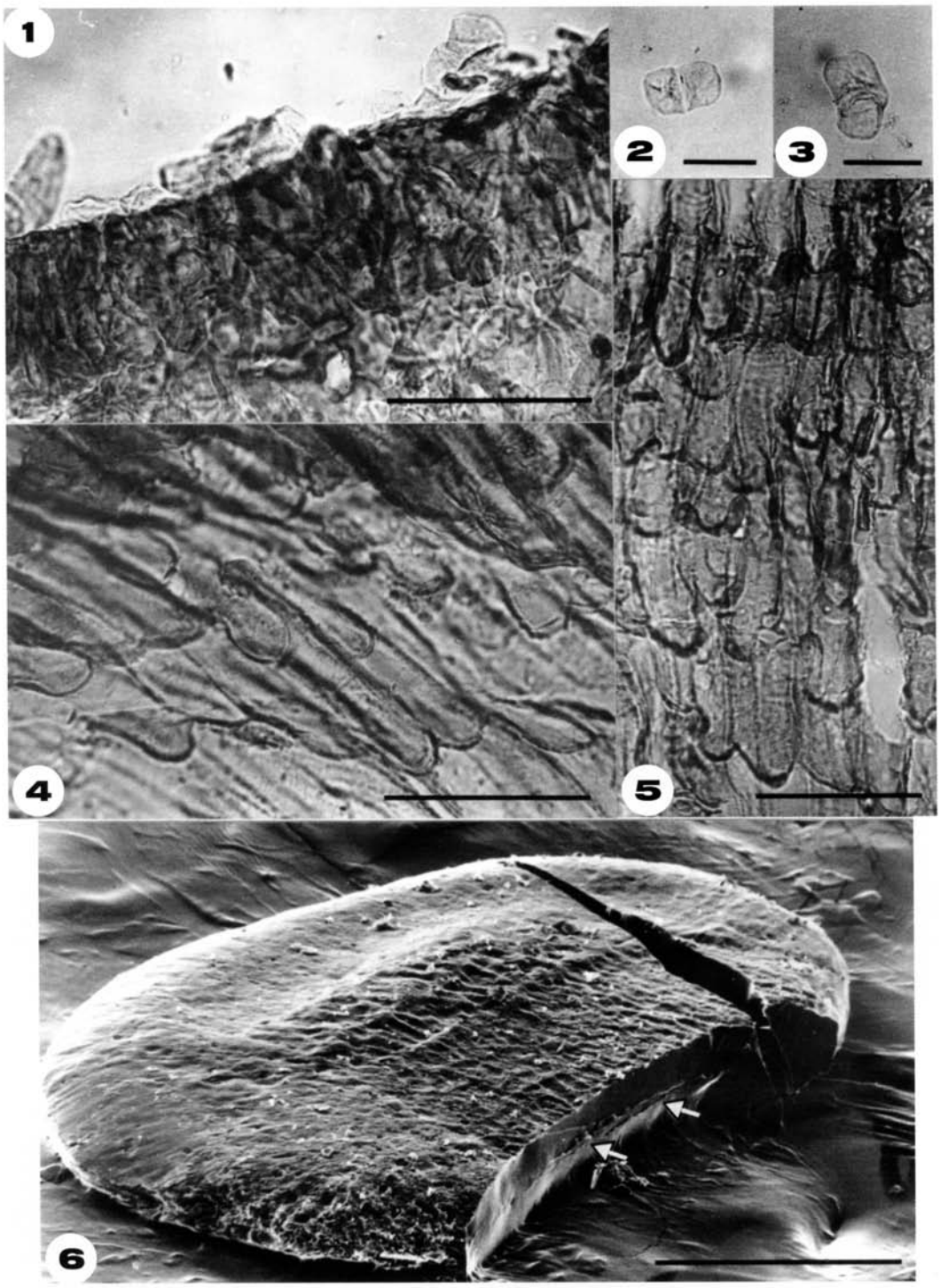
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Plate 6

Reymanownaea kvacekii gen. et sp. nov.

1. Chalazal end of the polished seed showing the asymmetric attachment of the funiculus (between arrow heads) and possible vascular cells (arrow); reflected light microscope picture, bar = 100 μm
2. Outer cuticle of the seed, bar = 200 μm, slide No 1048
3. The same cuticle, cells of middle part of the seed, bar = 50 μm
4. The same, cells near the chalazal end of the seed, bar = 50 μm
5. The same, cells near the micropylar end of the seed, bar = 50 μm
6. Bulging cells at the micropylar end of the polished seed, bar = 100 μm

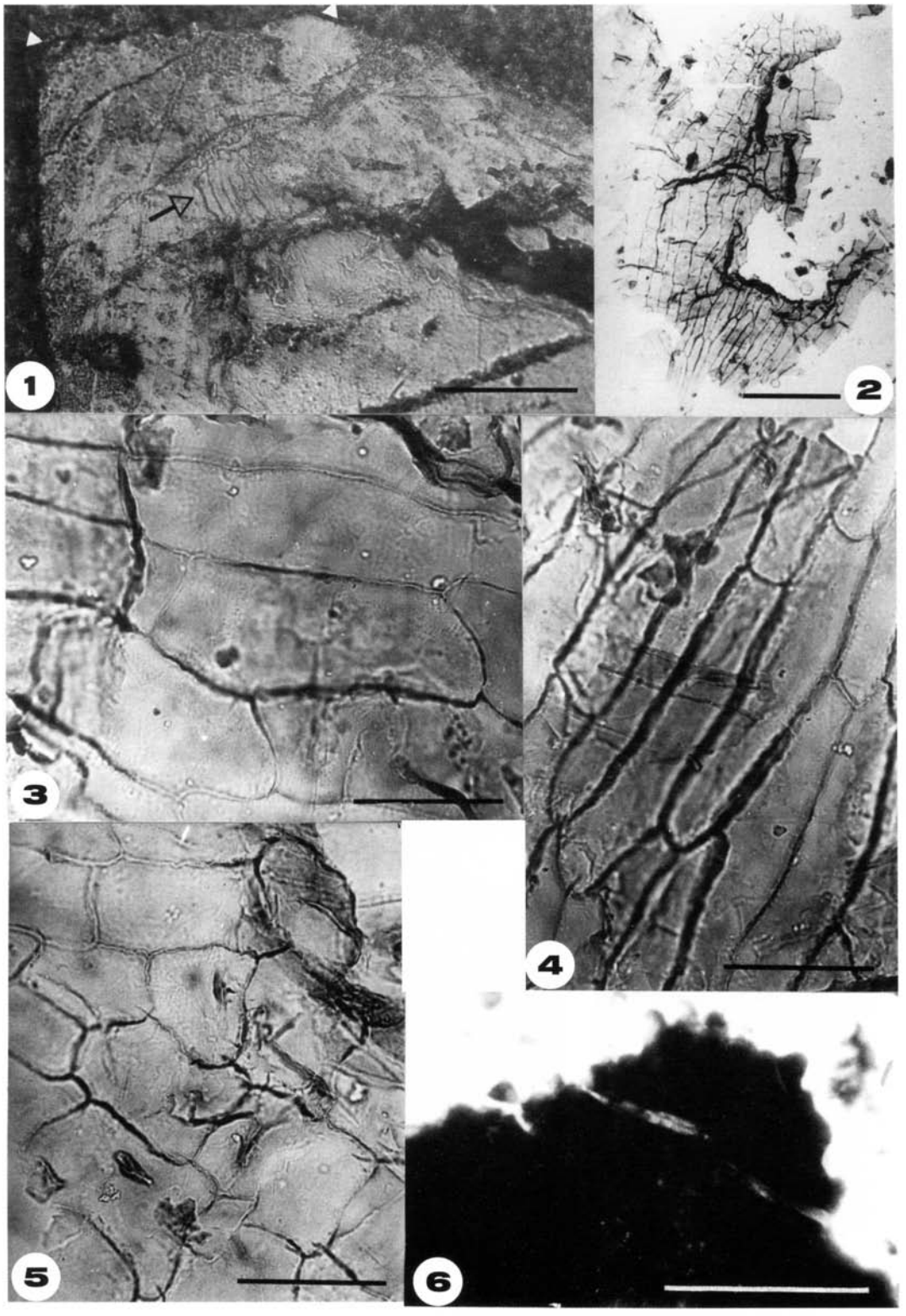
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Plate 7

Reymanownaea kvacekii gen. et sp. nov.

1. Stone cells of the seed, bar = 50 μm, slide No 1057
2. Stone cells with central pits that light up under the fluorescence microscope; bar = 50 μm
3, 4. Stone cells under the reflected light microscope, the central pits indicated by arrows, bars = 100 μm and 50 μm
5. Stone layer in the cross-sectioned seed, the black wide area between the edge of the seed and fluorescent inner cuticles under the fluorescence microscope, bar = 200 μm
6. Spotted layer of the seed, bar = 50 μm, slide No 1050

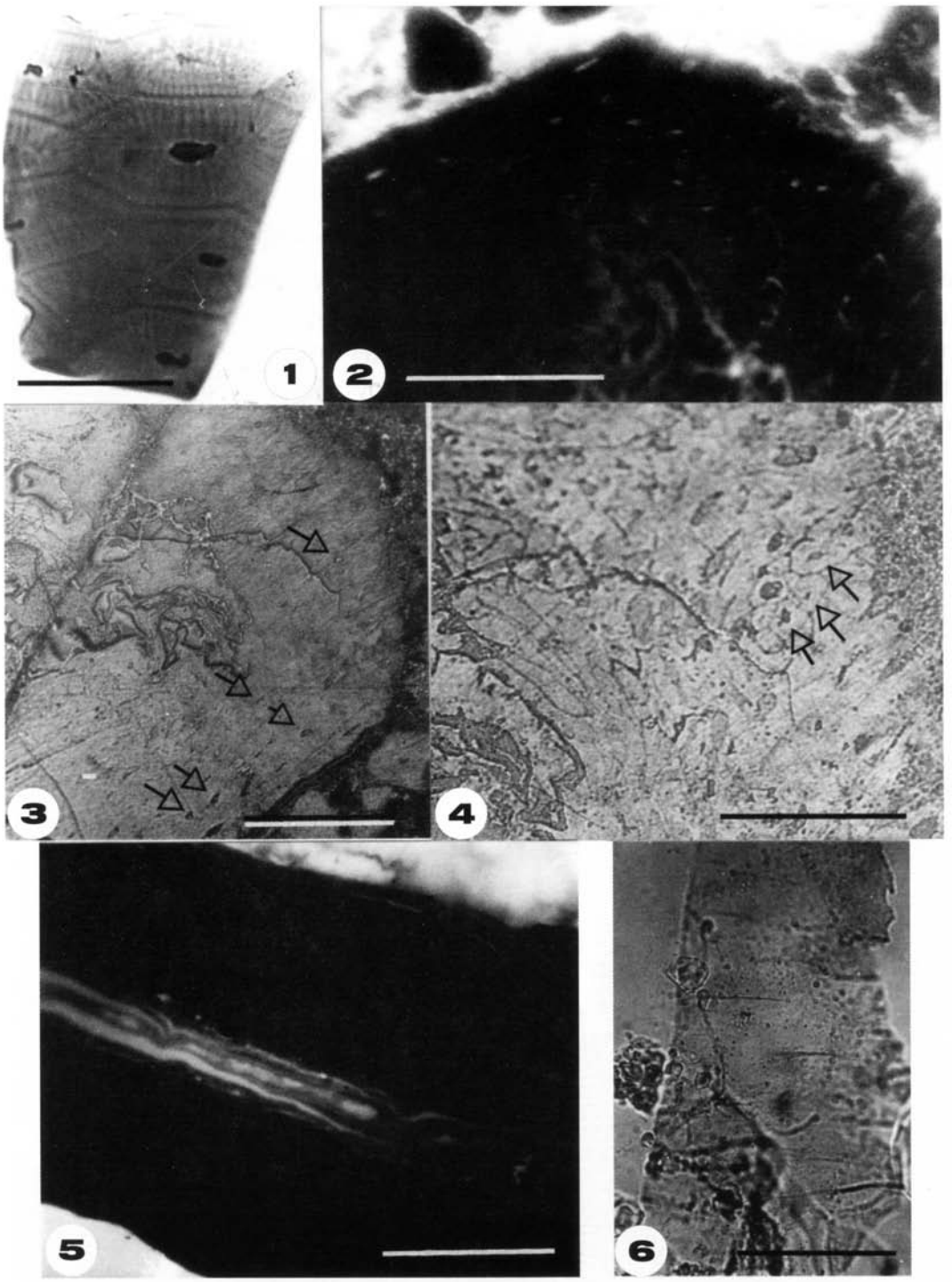
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Plate 8

Reymanownaea kvacekii gen. et sp. nov.

1. Cuticle of the micropylar end of the seed, bar = 200 μm, slide No 1062
2. Micropyle with pollen grains inside, bar = 100 μm, slide No 1062
3, 4. Cuticle of the nucellus, bars = 200 μm and 100 μm, slide No 1050
5. Cells of the nucellus under the reflected light microscope, polished seed, bar = 20 μm
6. Nucellus under the reflected light microscope, cross section, bar = 50 μm

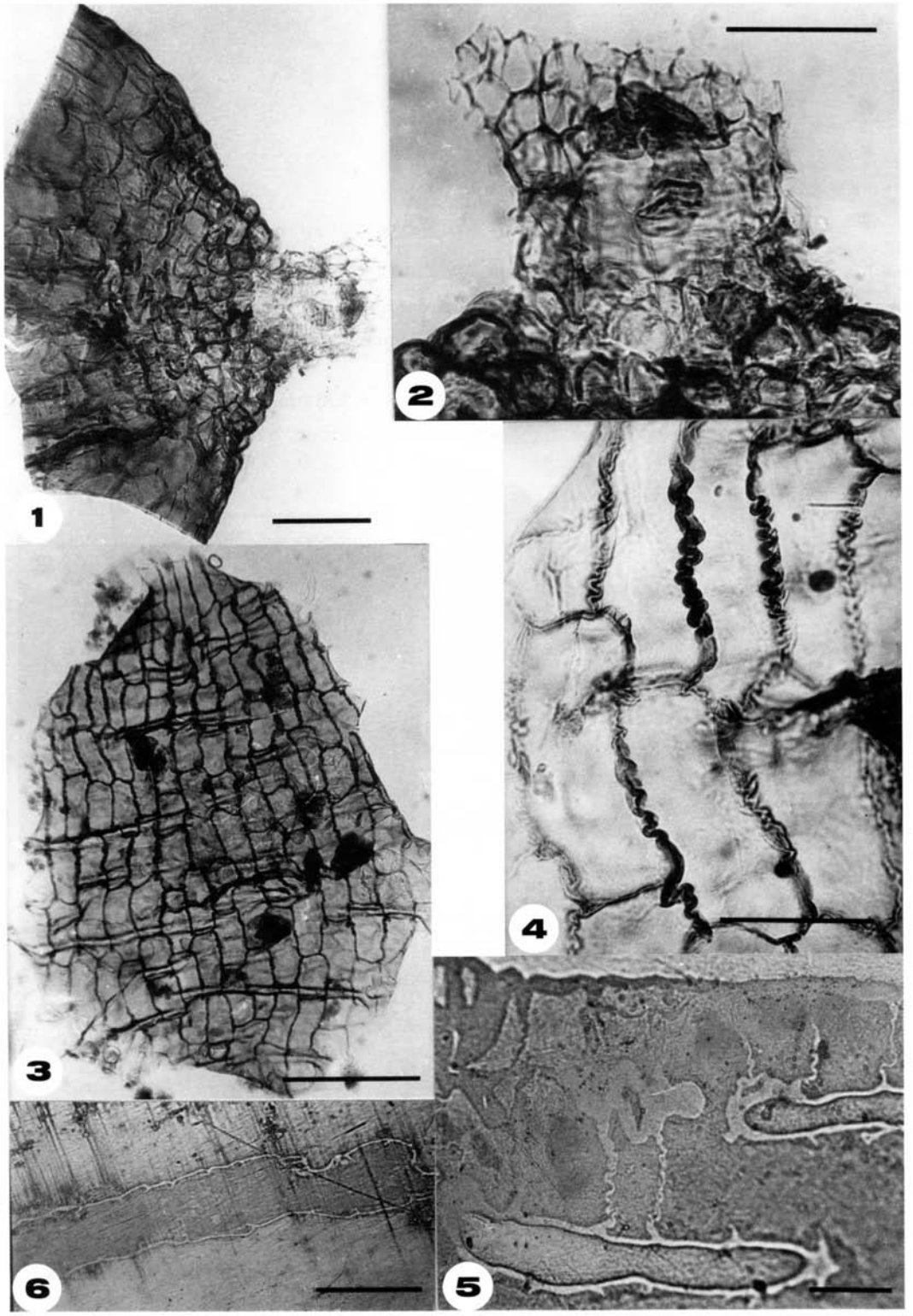
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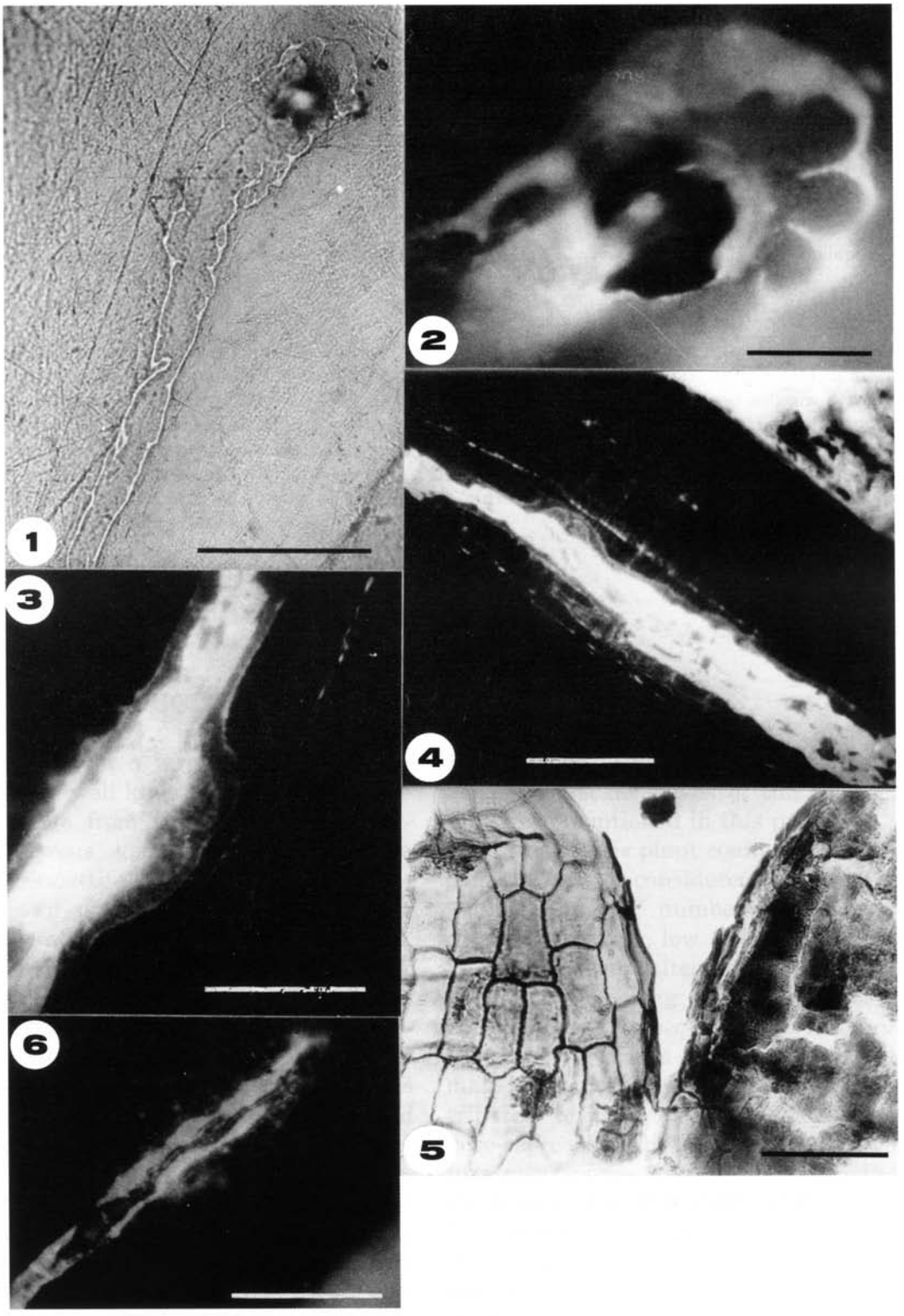
Plate 9

Reymanownaea kvacekii gen. et sp. nov.

1. Nucellus under the reflected light microscope near to the micropylar end, cross section, bar = 50 μm
2. The same as fig.1, but under the fluorescence microscope bar = 10 μm
3, 4. Cuticle of the nucellus under the fluorescence microscope, inside it the aleurone layer, bars = 25 μm and 50 μm
5. Nucellus cuticle (left) and its aleurone layer (right), bar = 200 μm, slide No 1064
6. Incision in the aleurone layer under the fluorescence microscope, bar = 50 μm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