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Trapaceae pollen in the Cenozoic

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ABSTRACT. Plants belonging to the Trapaceae produce unique pollen grains. This enables the fossil record to be traced. A reexamination of pollen from various localities proves that there are at least four fossil species involved. Two of these (*Sporotrapoidites carlesii* Zetter & Ferguson sp. nov., *S. cesarei* Zetter & Ferguson sp. nov.) are described here for the first time. The changes in the pollen grains through time are discussed and the palaeoecology of the assemblages in which these are found reviewed.

KEY WORDS: pollen, *Sporotrapoidites, Trapa, Hemitrapa,* Trapaceae, palaeoecology, Miocene, Pliocene, Pleistocene

INTRODUCTION

Trapa is a genus of aquatic plants, which because of its edible fruits (water chestnut), has been the focus of human interest for thousands of years. This being so, it is surprising that there is still no concensus regarding its botanical affinities. While some botanists consider it to belong to the Lythraceae (e.g. Graham et al. 1998), others referred it to the Onagraceae. On the other hand, it is often considered to represent a separate family, the Trapaceae (syn. Hydrocaryaceae; Hutchinson 1969, Cronquist 1981, Cook 1996, Takhtajan 1997). This concept is supported, among others, by the unique nature of its pollen grains (Patel et al. 1984). This uniqueness moreover opens up the possibility of tracing its fossil record and thus contributing to a better understanding of the evolution of this fascinating aquatic plant.

Pollen grains which can be referred to the Trapaceae are regularly encountered in the course of palynological analysis of Cenozoic sediments. So far two species (*Sporotrapoidites illingensis*, *S. erdtmanii*) have been described based on light microscopic (LM) examination. In the present contribution these have been reexamined using both LM and scanning electron microscopy (SEM). This has yielded additional characters of taxonomic value and we believe it is now possible to recognize at least four fossil species based on pollen.

MATERIAL AND METHODS

Recent material

Recent pollen of different species of *Trapa* have been examined. In order to keep the amount of damage to the flowers to a minimum, just one of the four anthers was removed. This was placed in a drop of glycerine to prevent it being lost during dissection to release the pollen grains. The individual pollen grains were then transferred to a glass slide using a specially adapted dissecting needle with a human hair glued near its tip (Zetter 1989). The pollen were immersed in a drop of acetolysis mixture and heated over a spirit lamp to remove the protoplast and dye the exine a brown colour. Use of a spirit lamp enabled the process of acetolysis to be kept well under control.

In order to remove the acetolysis mixture and clean the pollen grains, these were transferred with the specially adapted needle to another slide in a drop of glycerine and photographed under a LM (Nikon Optiphot-2). Because no cover slip is used, it is possible to photograph the same grain in various orientations. Using a dissecting needle to apply pressure to the grains and split them, some of the pollen was prepared for a detailed examination of the stratification of the exine. These and the intact grains were then transferred to an aluminium SEM stub to which a drop of absolute ethanol had been applied with a pipette. As the alcohol evaporates very rapidly, it is necessary it keep on adding more ethanol until all the pollen grains have been transferred to the stub. The ethanol removes any traces of the glycerine from the surface of the pollen grains, so that these can be examined in great detail under the SEM. However, it also has the effect of dehydrating the pollen, so the dimensions may vary somewhat from those recorded under LM. Prior to examination with a Jeol 6400 at 10 kV these were spattered with gold in a BIORAD Sputter Coater for 4 minutes. The advantage of the method outlined above is that the very same grain can be examined under both LM and SEM.

Fossil material

Sediment yielding Trapaceae pollen has also been analysed. The surface sediment was removed to prevent any possible contamination by recent pollen grains. The sediment was then ground down in a mortar and gently boiled in HF in a copper pan to remove the silicates. After this the sample was transferred to a large polyethylene beaker, to which 3–4 l water was added and left to stand until the solids had settled out. After decanting the liquid, the residue was boiled in conc. HCl in a glass beaker for 5 minutes to prevent the formation of calcium fluoride. Once this process was complete and the sample had settled to the bottom of the beaker, any remaining HCl was decanted. The sample was then washed in distilled water and centrifuged 3–4 times before undergoing acetolysis (chlorination plus acetylation).

First the material was placed in a test tube, then ca. 1.5 cm glacial acetic acid added, followed by ca. 3 cm freshly prepared solution of saturated sodium chlorate, making sure that these liquids did not mix. Then 3–4 drops of conc. HCl were added and the mixture stirred with a glass rod. The test tube was placed in a bath of boiling water for 3 minutes. The sample was then centrifuged at 2000 rpm for 20 seconds and the liquid fraction decanted. To eliminate any remaining chemicals, the sample was washed and centrifuged at least three times. In order to remove the water, the sample was then washed in conc. acetic acid or acetic anhydride. A mixture of 9 parts acetic anhydride and one part conc. H_2SO_4 were now added to the test tube (Erdtman 1943). The test tube was placed in a warm water bath for 3–4 minutes, after which the mixture was centrifuged and the liquid fraction decanted. Finally the residue was washed once in acetic acid and at least three times in water. In a few cases it was necessary to separate the organic fraction from the inorganic material by heavy liquid separation using a solution of zinc bromide.

Some glycerine was mixed with the organic residue to form a suspension. With a pipette a drop of this liquid was transferred to a glass slide. Using the specially adapted needle (see above) those grains which were of particular interest were then brushed to the edge of the glycerine, where they could be located and transferred to another glass slide with a fresh drop glycerine for photography under a light microscope. The rest of the process is identical to that involving recent pollen grains (see above).

Pollen from a number of European and extra-European fossil localities have been investigated. While the smaller pollen grains are usually preserved in three dimensions, the larger ones tend to be somewhat compressed. This compression causes the pollen grains to appear asymmetrical.

The localities investigated are as follows:

AUSTRIA: Burgenland, Badersdorf (Upper Miocene: Pannonian), Upper Austria, Hausruck-Hinterschlagen (Upper Miocene: Sarmatian/Lower Pannonian)

GERMANY: North Rhine-Westphalia, Kreuzau (Middle Miocene), Bavaria, Pfaffenzell (Middle-Upper Miocene), Bavaria, Entrischenbrunn (Middle-Upper Miocene)

ITALY: Piedmont, Gifflenga (Pliocene)

SPAIN: Pyrenees, Cerdanya Basin, Sanavastre opencast mine (lowermost Upper Miocene: Upper Vallesian)

NEPAL: Kathmandu Basin, Thimi (Upper Pleistocene: Thimi Formation)

SYSTEMATIC RESULTS

***Trapa*-type pollen**

General description. Pollen generally prolate-spheroidal, E = 40–85 µm, P = 50–95 µm, equatorial view rhombic, polar view triangular obtuse, convex or concave, angulaperturate (see Pl. 3, Pl. 4 figs 1–6, 12, 13). Apertures 3, colpate or porate, protruding, with a collar of sexine. Sexine in the interapertural areas intectate, ca. 0.8–1.0 µm, much thinner than nexine (ca. 2–3 µm), composed of densely packed microclavae, these tending to be larger and less crowded in a broad (Miocene species) or narrow (Pliocene to recent) zone next the crests (Pl. 5 figs 1, 4, 5, 7, 11). Crests 3, meridional, 2–7 µm high, combining at the poles to form a 10–35 µm conical structure, cavernous, composed of sexine supported by columellae (Pl. 4 figs 9, 10, 14, 15, Pl. 5 figs 6, 9, 16). Sexine of crests tectate, tectum perforate, smooth but twisted or verrucate to rugulate at the poles, generally rugulate to verrucate over apertures, with germinal suture (Pl. 4 figs 9, 14, 15, Pl. 5 figs 6, 8, 9, 16).

Discussion. This description is based on our fossil material from Austria, Italy, Spain and Nepal (see above). Although Kohlman-Adamska (in Stuchlik 1994) criticized the use of the generic name *Sporotrapoidites* for a pollen grain, it is clear from Klaus' original paper (Klaus 1954) that he was referring to a microspore. We see no reason to reject the name of this morphotaxon. Most Miocene forms can be referred to as *Sporotrapoidites illingensis*

Klaus 1954 (syn. *Trapapollis illingensis* (Klaus) Kohlman-Adamska in Stuchlik 1994). They are characterized by a small corpus and broad transitional zone between corpus and crest in the interapertural areas (Fig. 1, Tab. 1). In Table 1 the height of the crest includes this transitional zone. Since the crest in the Spanish material was found to differ from the rest of the Miocene material, we feel obliged to refer this taxon to a new species. Moreover, in the Pliocene material the corpus is much larger and the transitional zone reduced or missing. Since we cannot apply the name *Sporotrapoidites illingensis* to this material, we erect a new binomial for this taxon.

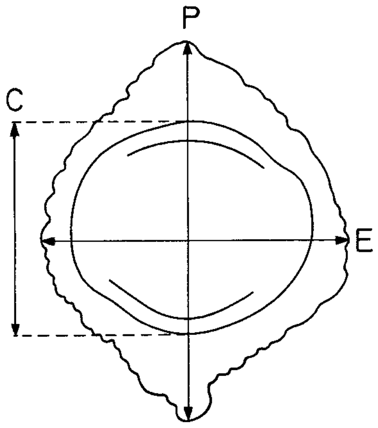

Fig. 1. Schematic shape of Trapaceae pollen: C – corpus, P – polar axis, E – equatorial diameter

NEW SPECIES

Sporotrapoidites carlesii

Zetter & Ferguson **sp. nov.**

Pl. 4 figs 1–11

Holotype. Institute of Palaeontology, University of Vienna (San-2, Pl. 4 fig 5)

Locus typicus. Spain: Pyrenees, Cerdanya Basin, Sanavastre opencast mine

Stratum typicum. *Trapa* horizon near the base of the outcrop.

Type horizon. Lowermost Upper Miocene: Upper Vallesian

Derivatio nominis. The new specific epithet pays tribute to Dr. Carles Martin-Closas (Barcelona), who has been working on the plant-remains of the Cerdanya Basin for several years.

Diagnosis. This pollen type differs from *Sporotrapoidites illingensis* Klaus (Klaus 1954) in the first place by its crest with a regularly verrucate surface at the poles (Pl. 4 fig 9). Moreover, near the apertures the heads of the microclavae tend to be conical (Pl. 4 fig 8), rather than rounded.

Comment. While Barrón (1997) referred the pollen grains from Sanavastre to *Trapa* sp., he pointed out that the fossil fruits from the Cerdanya Basin had been referred to a separate species, *Trapa ceretana*, by Rérolle (1884–1885).

Table 1. Major differences in Trapaceae pollen. The size (in µm) are based on 50 measurements

Taxa	P	E	C:P	Crest at pole height/width	Crest at equator height/width	Nature of crest at pole	Nature of crest at equator
Sporotrapoidites erdtmanii	34–51	37–65	1:1.6–1.8	5–8/4–7	3–4/4–7	smooth, wrinkled, perforate	smooth, wrinkled, perforate
S. illingensis, Badersdorf	78–95	75–85	1:2.2–2.4	30–35/3–6	5–7/4–7	irregularly rugulate	rugulate to verrucate
S. illingensis, Hausruck	80–95	70–80	1:2.3–2.6	30–35/4–9	4–6/4–7	irregularly rugulate	rugulate to verrucate
S. carlesii, Sanavastre	78–87	60–72	1:2.5–2.7	30–32/6–10	5–6/7–10	regularly verrucate	verrucate
S. cesarei, Gifflenga	60–80	45–60	1:1.6–1.8	15–17/2–4	3–5/4–6	twisted, smooth, perforate	regulate, perforate
Trapa cf. *quadrispinosa*	50–60	40–45	1:1.5–1.7	10–15/2–4	2–4/3–5	twisted, smooth to rugulate, perforate	smooth to rugulate, perforate

Sporotrapoidites cesarei Zetter & Ferguson **sp. nov.**

Pl. 3 figs 11–14, Pl. 4 figs 12–16

Holotype. Institute of Palaeontology, University of Vienna (Gif-1, Pl. 4 fig. 12)

Locus typicus. Italy: Piedmont, Gifflenga.

Stratum typicum. Bioturbated clay gyttja full of *Trapa* fruits.

Type horizon. Pliocene.

Derivatio nominis. The new specific epithet honours Dr. Cesare Ravazzi (Bergamo), who is currently studying the palynology of the Cervo River succession.

Diagnosis. This pollen type differs from *Sporotrapoidites illingensis* Klaus (Klaus 1954) in having a large corpus and only a narrow transitional zone.

Comment. The large corpus is also characteristic of recent pollen grains of *Trapa*.

OTHER REPRESENTATIVES OF THE TRAPACEAE

Mohr (1983) and Mohr and Gee (1990) described pollen with crests from Miocene sediments of Gallenbach (South Germany) and compared it to that of recent and fossil *Trapa*. The major distinction proved to be one of size: the Gallenbach pollen was only 34–49 μm long from pole to pole. It is noteworthy that while these beds did not contain any megafossils of *Trapa*, those of *Hemitrapa* (Oligocene-Miocene) were recorded. While resembling *Trapa* fruits in shape and number of spines, *Hemitrapa* had the spines arranged in a whorl, lacked an apical corona and had a persistent peduncle. For this reason Miki (1952a, 1952b) initially emphasized its similarity to *Trapella* (Trapellaceae). However, no pollen resembling that of *Trapella* has ever been found in sediments containing *Hemitrapa*, only *Trapa*-like pollen described as *Sporotrapoidites erdtmanii* (Nagy) Nagy (Nagy 1979, 1985, Mohr 1983, Mohr & Gee 1990, T. Saito pers. comm.). It would thus seem that the two dispersed plant parts can be equated and *Hemitrapa* referred to the Trapaceae. Miki (1959, 1961) later came to the same conclusion.

Sporotrapoidites erdtmanii (Nagy) Nagy 1985

Basionym. *Goerboepollenites erdtmanii* Nagy (Nagy 1979)

Synonym. *Sporotrapoidites cucculatus* Seitner (Seitner 1987)

Description. Pollen generally oblate-spheroidal, E = 37–65 μm, P = 34–51 μm, equatorial view rhombic obtuse, polar view triangular obtuse, convex or concave, angulaperturate (Pl. 1). Apertures 3, colpate to porate, protruding, with a collar of sexine (Pl. 1). Sexine in the interapertural areas intectate, ca. 0.5–0.7 μm, much thinner than nexine (ca. 1.5–1.7 μm), composed of densely packed microclavae, these tending to be larger and less crowded in the apertural areas (Pl. 2 figs 1, 3, 12, 13). Crests 3, meridional, 3–4 μm high and 4–7 μm wide over the aperture, only slightly higher (5–8 μm) at the poles, cavernous, composed of sexine supported by columellae (Pl. 2 figs 5–11). Sexine of the crests tectate, tectum perforate, smooth but wrinkled, with germinal suture over apertures (Pl. 2 figs 2, 4, 6, 9–11).

Discussion. The pollen from the three German localities (Entrischenbrunn, Kreuzau, Pfaffenzell) which we have examined proved to be very uniform. Similar pollen has also been found in Gallenbach (Mohr 1983, Seitner 1987, Mohr & Gee 1990) and Japan (Yamanoi 1992a, 1992b, Yamanoi et al. 1993, T. Saito pers. comm.), which would suggest that this aquatic plant was widely distributed in the Miocene. Although Seitner (1987) described a second species, based on differences in the size of the corpus and vestibulum, we believe that these differences fall within the normal range of variation. The most variable character in this morphotaxon is the shape of the aperture, ranging from porate to colpate (Pl. 1 figs 1–8).

CHANGES IN THE POLLEN OF THE TRAPACEAE THROUGH TIME

Sporotrapoidites erdtmanii with its small pollen grains seems to represent the plesiomorphic form within the Trapaceae. The *Hemitrapa* plants producing this pollen type would appear to have given rise to *Trapa* in middle to late Miocene times. These plants produced larger pollen grains, with a broad transitional zone with spongy nexine between the corpus and the expanded crest. The next step, which took place in the course of the Pliocene, involved the expansion of the corpus at the expense of the transitional zone. All recent species of *Trapa* have such a large corpus. As the descriptions and illustrations of pollen from Chinese *Trapa* spp. (Ding et al. 1991) show, a minor increase in the size of the pollen has occurred in the recent past. The dimensions of the pollen grains (P × E) are now 61–108 × 47–88 µm. Considering the contentious status of the infrageneric taxa, it is hardly surprising that the pollen of recent microspecies are difficult to differentiate.

HYDROPHILY IN THE TRAPACEAE?

If the crests were to be removed from the pollen of the Trapaceae, the resulting pollen grains would have a strong resemblance to those of some of the Onagraceae (Patel et al. 1984). It seems likely that the Trapaceae evolved from the Onagraceae during the Palaeogene. If this supposition is correct, the crests represent a apomorphic character. This raises the question: why did they develop and what is their function? As the crests are hollow, they would appear to act as bladders enabling the pollen to float. This in turn would suggest that they play a role in pollination by water (hydrophily). However, based on the floral morphology of recent *Trapa*, entomophily is to be expected.

The white or pale pink petals can be assumed to attract insects and certainly the flowers are visited by a variety of Coleoptera, Diptera and Hemiptera (Kadono & Schneider 1986). In addition, a coronary disc is present, which might suggest the production of nectar. However, the presence of nectar has not yet been confirmed (Kadono & Schneider 1986). Moreover, little pollen was to be found on the insects, which would imply that cross-pollination by insects is limited (Kadono & Schneider 1986). It would appear that the major role of the insects is to inadvertently push the anthers up against the stigma, thereby aiding self-pollination. That self-pollination is probably the norm (Kühn 1982, Cook 1996) is suggested by exclusion experiments (Kadono & Schneider 1986), as well as the fact that the anthers are forced up against the stigma just as the flower is opening (Arima et al. 1999). Each flower only remains open for a few hours. As it closes the peduncle bends over and the flower comes into contact with the water surface (Arima et al. 1999). At this stage it is possible that some of the pollen are rinsed out of the flower and effect cross-pollination (hydrophily) in those flowers not already pollinated by autogamous or entomophilous means. In this way the Trapaceae increase the chances of fertilization.

The pollination syndrome has important repercussions for the systematics of the Trapaceae. The demonstration of autogamy in *Trapa* would indicate that any mutations which arose would tend to be retained, leading to a plethora of microspecies. This could lend credence to the narrow species concept currently employed by Russian and Chinese systematists. However, the matter is not that simple. Although Kadono and Schneider (1986) doubted the presence of hybrids in the genus, evidence for a wider range of pollination syndromes, including cross-pollination, shows that hybridization can, on occasion, occur. This would explain the presence of amphiploids in the genus (Oginuma et al. 1996).

THE ECOLOGY AND PALAEOECOLOGY OF THE TRAPACEAE

Although it can produce land forms, *Trapa* is typically an aquatic plant of neutral to somewhat alkaline (pH 6.7–8.2), eutrophic lakes (http://www.magi.com/~ehaber/factnut.html). While it produces some submerged leaves (commonly referred to as photosynthetic roots because of their role in nutrient assimilation), almost all the photosynthetic activity in the mature plant is concentrated in the apical leaves (Arima et al. 1988). These are kept afloat by means of aerenchyma present in the petioles. The leaves spread out over the water surface to produce a rosette, only becoming emergent if competition for space occurs (Arima et al. 1990, Arima 1994). This habit means 1) that *Trapa* is restricted to open water, as it is unable to compete with taller helophytic plant communities close to the shoreline, and 2) that the floating canopy tends to shade out submerged aquatics (Groth et al. 1996). As a result the plant communities in which *Trapa* occurs (*Nupharetum*, *Trapetum*, etc.) are inclined to be oligotypic. An individual

Table 2. A selection of Neogene localities to illustrate the range of aquatic plants present in the assemblages. D – diaspores, L – leaves, P – palynomorphs

Taxa	Kreuzau (D)	Gallenbach (D)	Pfaffenzell (D)	Entrischenbrunn (D)	Hausruck (A)	Badersdorf (A)	Bełchatów (PL)	Gifflenga (I)
	Ferguson et al. 1998	Schmid & Gregor 1983 Mohr & Gee 1990	Günther & Gregor 1989 Meller pers. comm. 2001	Meller pers. comm. 2001	Present study	Present study	Wójcicki & Zastawniak 1998	Martinetto 1998
Aldrovanda								D
Azolla						P		P
Botryococcus					P	P		
Brasenia					D			
Ceratophyllum		D	D	D	D			D
Characeae		D	D					
Euryale/Eoeuryale/Pseudo-euryale		D	D	D	D	P	D	D
Hemitrapa	D+P	D+P	D+P	D+P				
Lemnaceae					D	P		D
Myriophyllum					P	P		P
Nelumbo					P	P		
Nuphar								D+P
Nymphaea					D	P		
Pediastrum					P	P		
Potamogeton		D+P	D	D	D			P
Proserpinaca					P		D	
Ranunculus subg. *Batrachium*					D+P	P	D	P
Salvinia	L+P		L	P				P
Stratiotes	D			D	D			
Trapa					D+P	P	D	D
Utricularia					P			
Zygnemataceae					P	P		
Number of aquatic taxa	3	5	6	6	16	11	4	11

Trapa plant can reach a length of 1–6.5 m (Arima et al. 1990). As the plants are initially attached to the substrate by adventitious roots, this means that they are largely confined to shallow water. Due to self-shading the submerged parts eventually die back and the plant becomes free-floating. At this stage the plants and their fruits may be swept downstream (Ridley 1930). Consequently, megafossils may be either allochthonous or autochonous. The fact that the trapaceous pollen, which is produced earlier in the year, is confined to those horizons in which fruits have been found endorses autochthony. Thus the presence of these pollen grains can be used in establishing the local environmental conditions. Since the water chestnut is normally an annual (hydrotherophyte), the winter temperature is not critical. However, in order to flower and fruit *Trapa* requires a water temperature in excess of 20°C for some months (Mai 1985, Arima et al. 1992, Tornadore et al. 2000). Knowledge of these parameters should be helpful in interpreting the palaeoecology of the fossil representatives.

One way of testing whether the Trapaceae has always occupied its present ecological niche is to compare the aquatic plants present in the fossil assemblages with those in recent plant communities. The various localities containing *Sporotrapoidites illingensis* and *S. cesarei* indicate that *Trapa* species were confined to sluggish water along with the free-floating hydrophytes *Azolla*, *Salvinia*, *Stratiotes* and Lemnaceae (Tab. 2). These backwaters must have acted as sinks for clastic sediment brought down during floods. This muddy substrate enabled a variety of fixed aquatics such as lotus (*Nelumbo*), waterlilies (*Brasenia*, *Nuphar*, *Nymphaea*, *Euryale* etc.), pondweed (*Potamogeton*), water-crowfoot (*Ranunculus* subg. *Batrachium*), water-milfoil (*Myriophyllum*) and mermaid-weed (*Proserpinaca*) to become established in the shallows. The diversity of the aquatic angiosperms and the presence of the green algae *Botryococcus*, *Pediastrum* and Zygnemataceae are indicative of eutrophic or even hyper-eutrophic conditions (Rauh 1951, Reynolds 1984). This would appear to suggest that the ecology of *Trapa* has changed little in the course of time.

On the other hand, it is noticeable that the assemblages in which *Hemitrapa heissigii* and *Sporotrapoidites erdtmanii* are found are much poorer in aquatic plants. This could indicate that the water contained fewer nutrients than that of the *Trapa* communities. Although eutrophic floating aquatics such as *Salvinia* and *Stratiotes* were present, *Azolla* and Lemnaceae were apparently absent. While the seeds of the Lemnaceae can survive periodic desiccation, seed production in the various species is a very rare phenomenon (Landolt 1997). The plants can only survive seasonal desiccation if they are covered by a layer of mud or silt. Does this perhaps mean that *Hemitrapa* grew in shallow water prone to drying out? An oscillating water-level would inevitably result in a reduction in the number of fixed aquatics. On the other hand, the absence of *Nuphar* and *Nymphaea*, which prefer a muddy substrate in which to establish their rhizomes (Hynes 1970), might indicate that *Hemitrapa* favoured an environment with a lower rate of clastic input. The presence of Characeae gyrogonites in Gallenbach and Pfaffenzell would certainly suggest that *Hemitrapa* was growing in fairly clear water.

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PLATES

Plate 1

Sporotrapoidites erdtmanii (Nagy) Nagy

1–8.	Equatorial view, LM, Kreuzau to display variation in shape and aperture
9–10.	Polar view, LM, Pfaffenzell
11–12.	Polar view, LM, Kreuzau
13–14.	Equatorial view, LM, Entrischenbrunn
15–16.	Equatorial view, LM, Pfaffenzell
17–19.	Equatorial view, SEM, Kreuzau
20–22.	Equatorial view, SEM, Pfaffenzell

Scale bar – 10 μm


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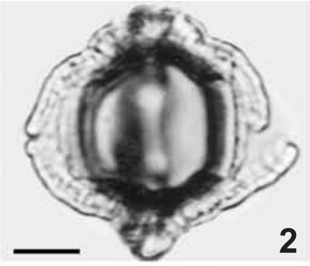
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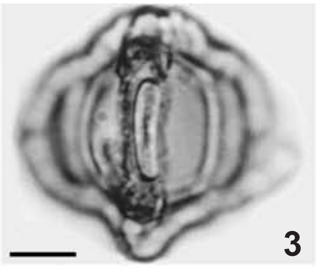
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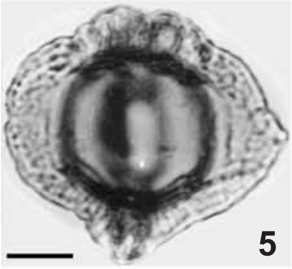
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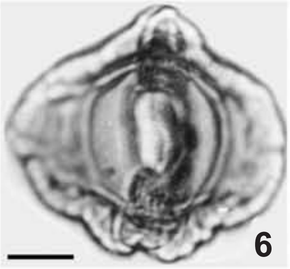
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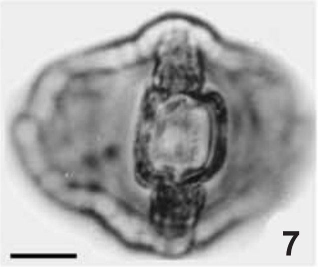
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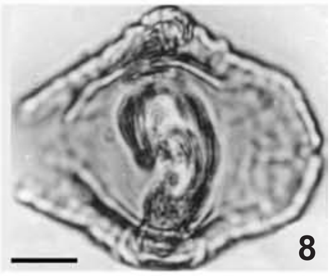
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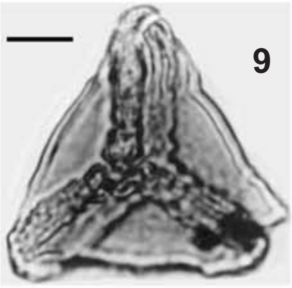
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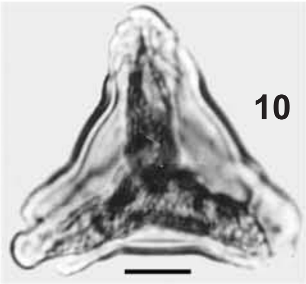
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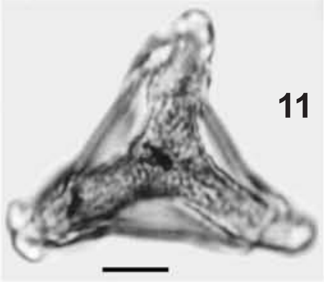
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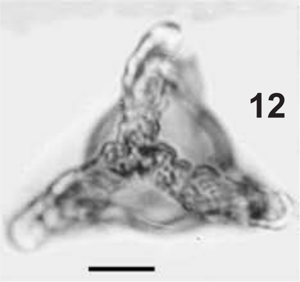
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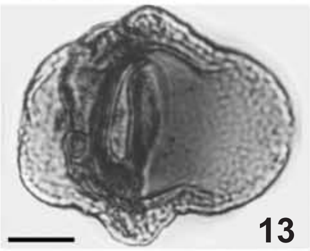
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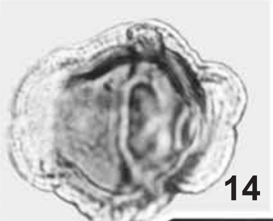
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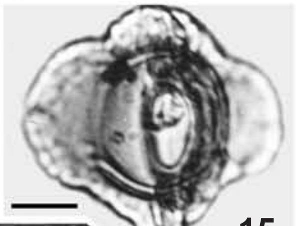
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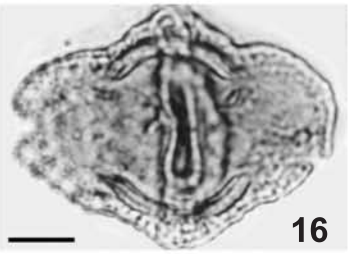
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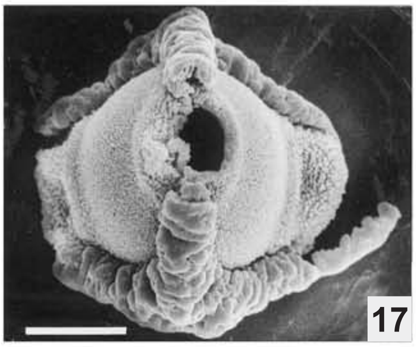
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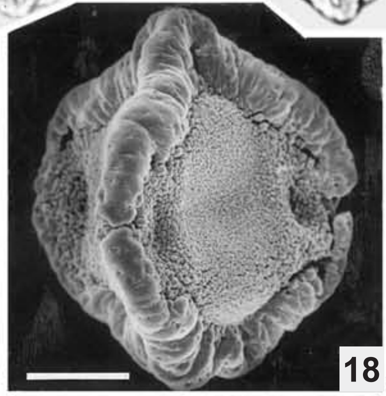
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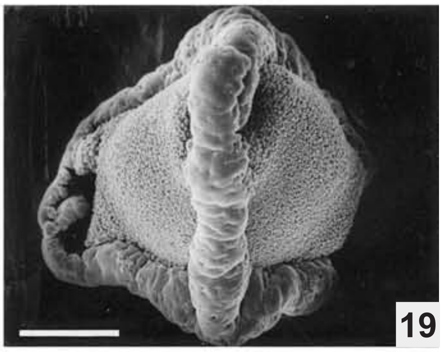
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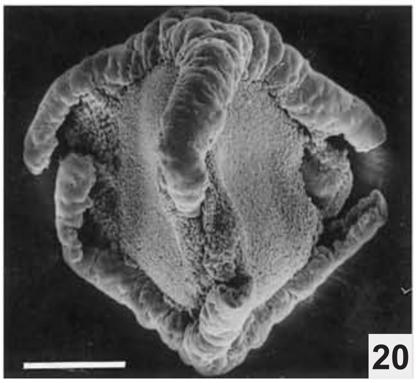
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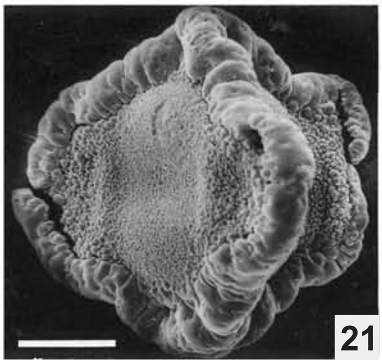
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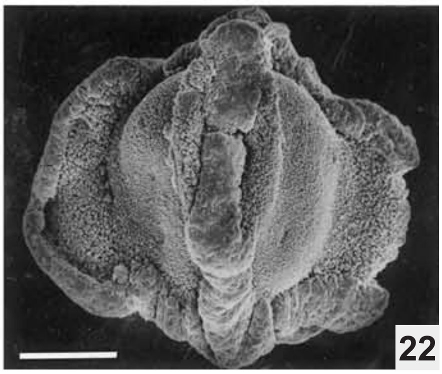
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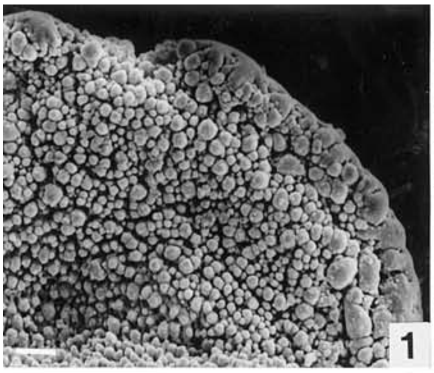
Plate 2

Details of *Sporotrapoidites erdtmanii* (Nagy) Nagy under SEM

1. Sculpture next the pore
2. Crest with germinal suture, lateral view
3. Change in sculpture at transition between corpus (above) and collar (below)
4. Separation of crest at aperture
5. Rounded aperture with remains of hollow crest after partial separation. Note the columellae inside the crest.
6. Germinal suture viewed from above, displaying columellae over the aperture
7. Crest removed to show short columellae over the aperture
8. Crest removed to reveal elongated columellae away from the apertural zone
9. Narrow germinal suture
10. Crest displaying perforations in polar area
11. Wrinkled crest with perforations in equatorial area
12. Fractured exine demonstrating thick nexine and thin intectate sexine
13. Bald patch exposing the microclavae of which the sexine is composed

Scale bar – 1 μm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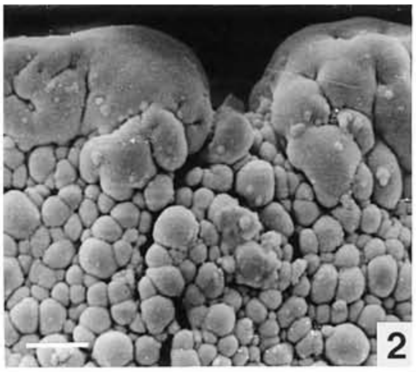
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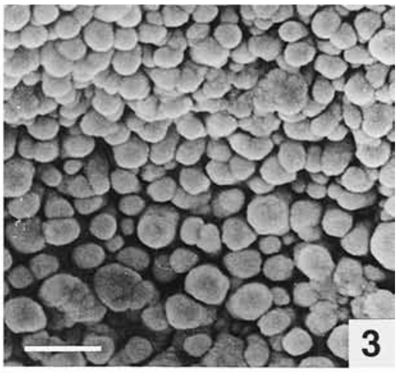
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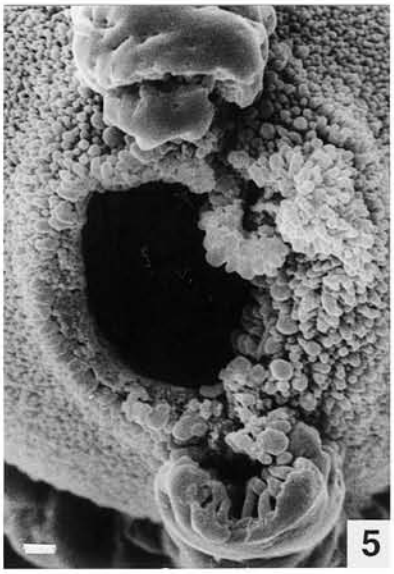
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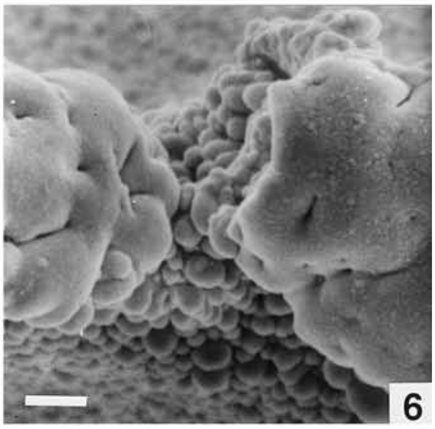
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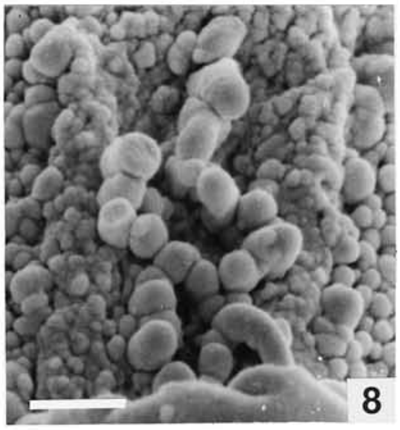
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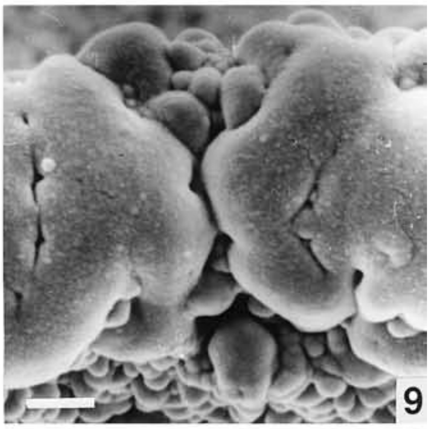
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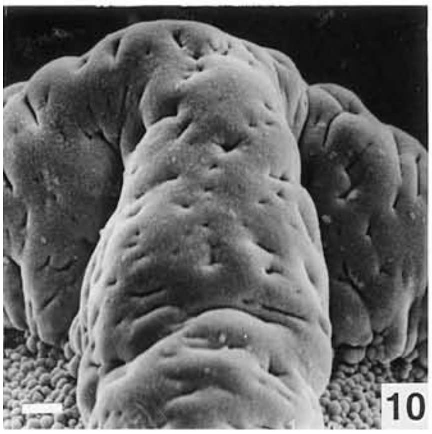
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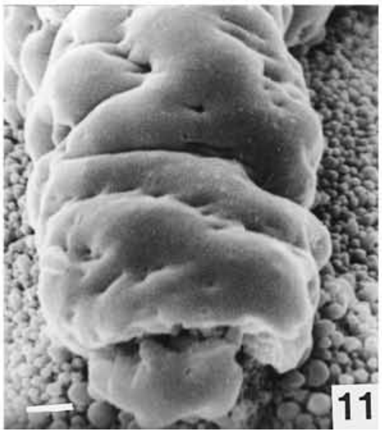
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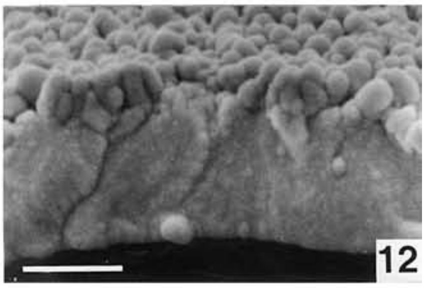
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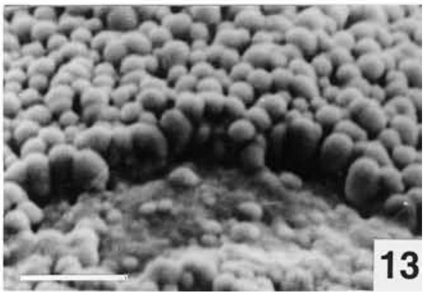
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Plate 3

Sporotrapoidites illingensis Klaus

1–5. Equatorial view, LM, Badersdorf
6. Aberrant form with single crest, LM, Badersdorf
7–10. Equatorial view, LM, Hausruck-Hinterschlagen

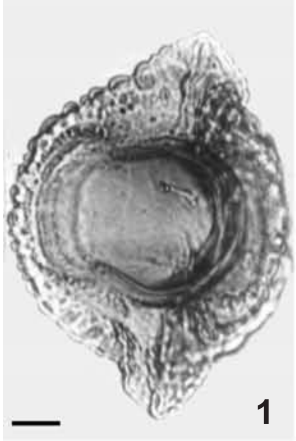
Sporotrapoidites cesarei Zetter & Ferguson sp. nov.

11. Polar view, LM, Gifflenga
12–14. Equatorial view, LM, Gifflenga

Trapa cf. *quadrispinosa* Roxb.

15–17. Equatorial view, LM, Thimi

Scale bar – 10 µm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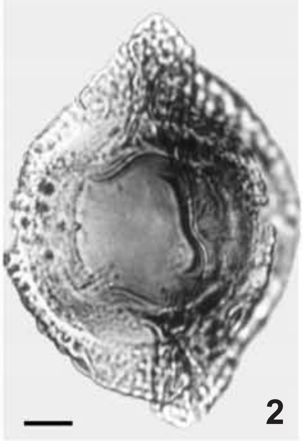
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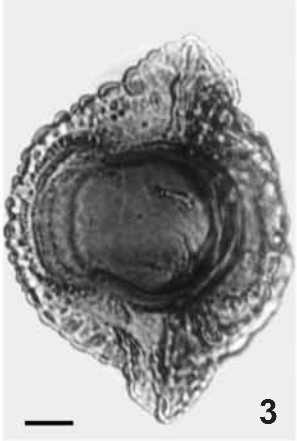
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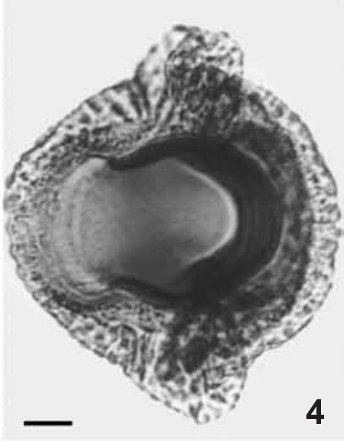
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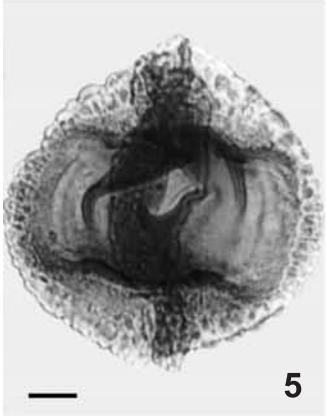
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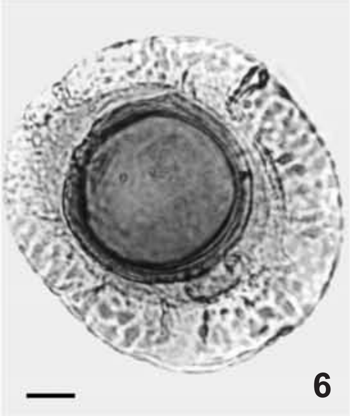
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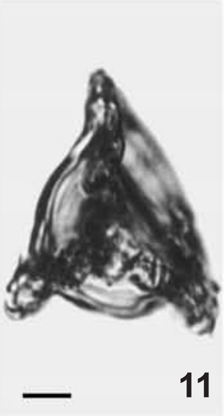
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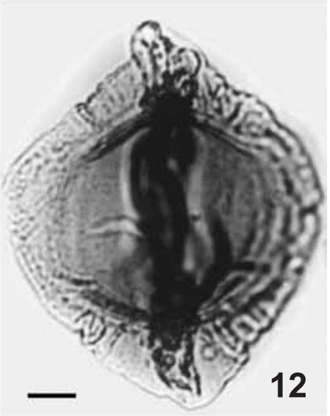
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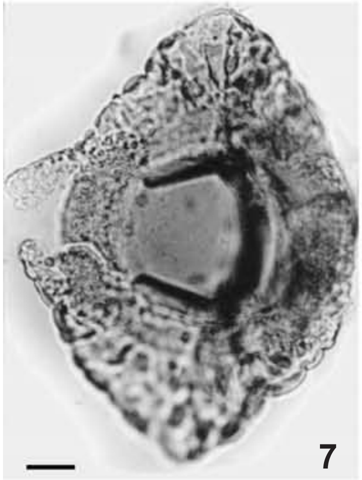
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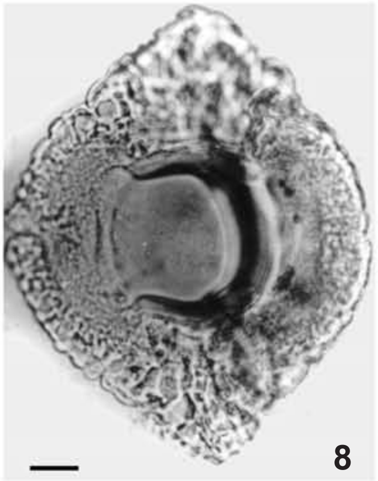
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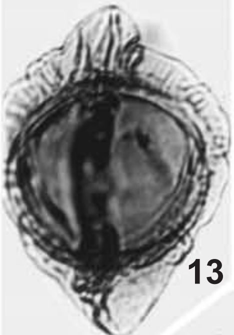
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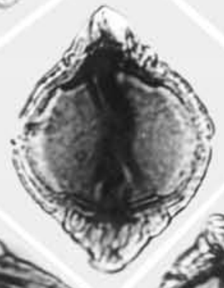
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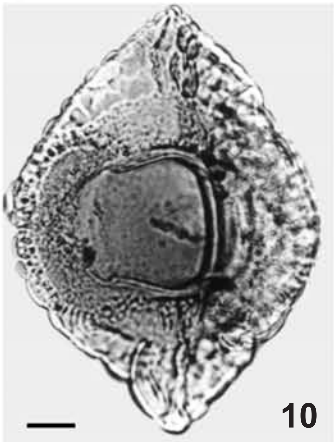
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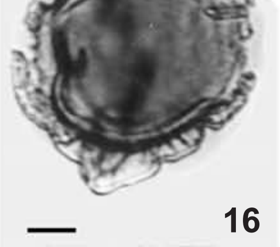
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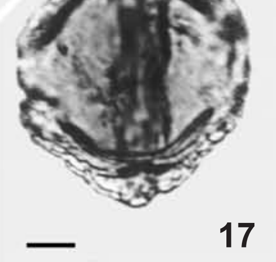
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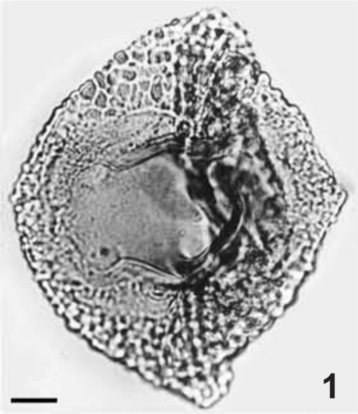
Plate 4

1–11. *Sporotrapoidites carlesii* Zetter & Ferguson sp. nov.
1–4. Equatorial view, LM, Sanavastre
5, 6. Equatorial view, SEM, Sanavastre
7. Sculpture of corpus, SEM, Sanavastre
8. Sculpture next the pore, SEM, Sanavastre
9. Crest in polar area, SEM, Sanavastre
10. Detail of crest in polar area, SEM, Sanavastre
11. Crest with germinal suture, SEM, Sanavastre

12–16. *Sporotrapoidites cesarei* Zetter & Ferguson sp. nov.
12, 13. Equatorial view, SEM, Gifflenga
14. Crest in polar area, SEM, Gifflenga
15. Germinal suture viewed from above, SEM, Gifflenga
16. Sculpture of transitional zone between corpus and apertural collar, SEM, Gifflenga

1–6, 12–13 Scale bar – 10 μm
7–11, 14–16 Scale bar – 1 μm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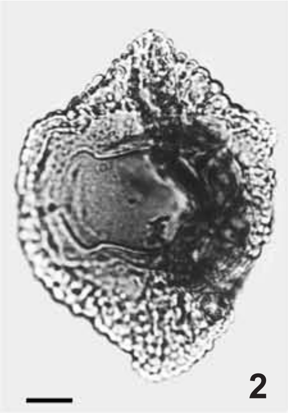
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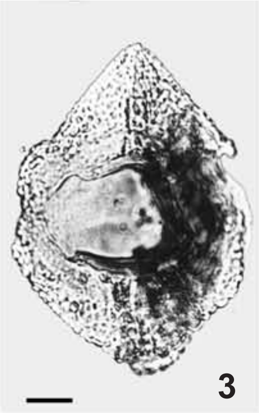
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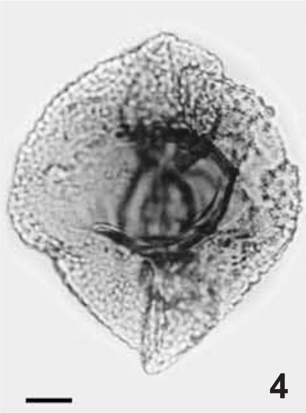
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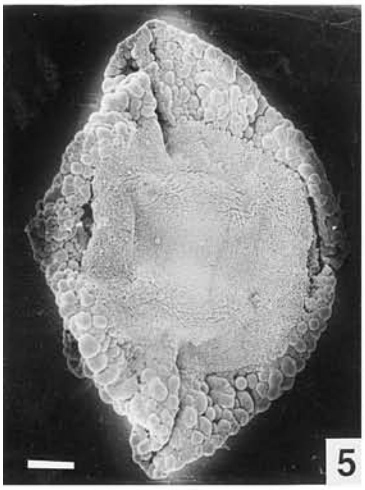
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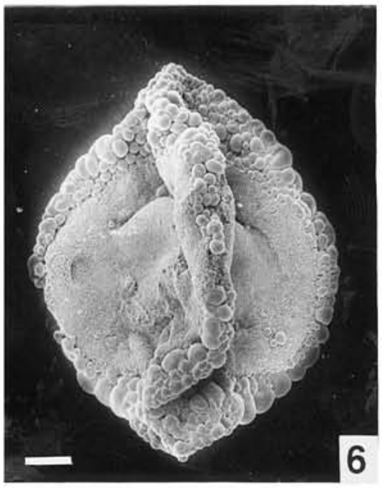
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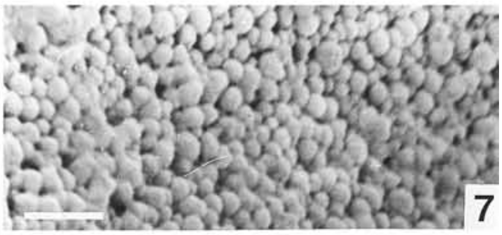
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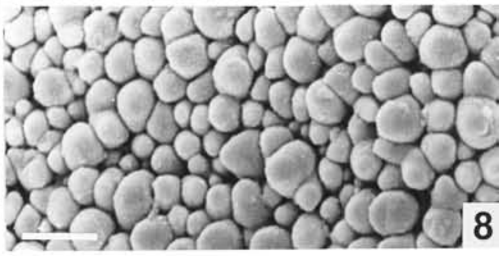
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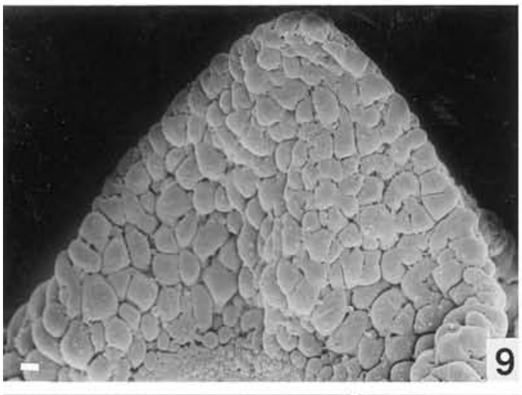
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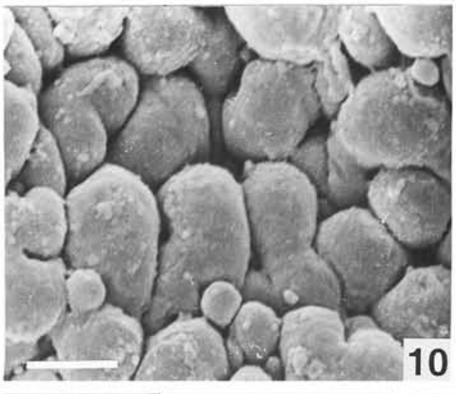
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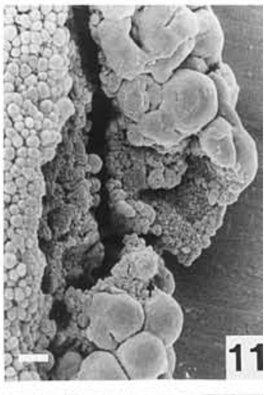
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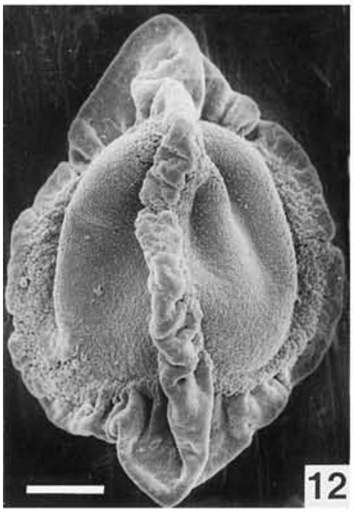
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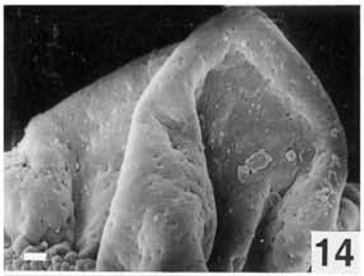
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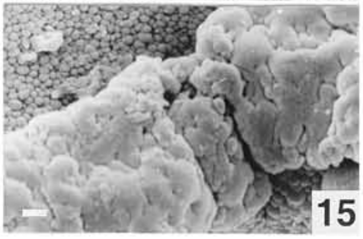
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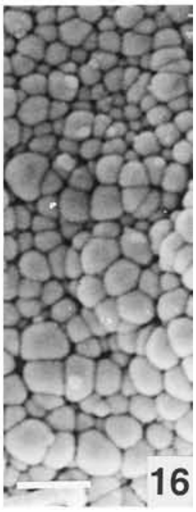
16

Plate 5

1–13. *Sporotrapoidites illingensis* Klaus
- 1, 2. Equatorial view, SEM, Badersdorf
- 3. Aberrant form with single crest, SEM, Badersdorf
- 4, 5. Equatorial view, SEM, Hausruck-Hinterschlagen
- 6. Fractured crest displaying elongated columellae, SEM, Hausruck-Hinterschlagen
- 7. Fractured exine demonstrating thick nexine and thin sexine, SEM, Hausruck-Hinterschlagen
- 8. Sculpture of crest in polar area, SEM, Hausruck-Hinterschlagen
- 9. Crest with germinal suture, SEM, Hausruck-Hinterschlagen
- 10. Fine sculpture of corpus (above) and coarser sculpture of transitional zone, SEM, Hausruck-Hinterschlagen
- 11. Fracture of pollen revealing exine stratification, SEM, Hausruck-Hinterschlagen
- 12. Fracture of transitional zone and crest, SEM, Hausruck-Hinterschlagen
- 13. Detail of transitional zone displaying spongy nexine, SEM, Hausruck-Hinterschlagen

14–17. *Trapa* cf. *quadrispinosa* Roxb.
- 14, 15. Equatorial view, SEM, Thimi
- 16. Detail of crest in polar area, SEM, Thimi
- 17. Sculpture of germinal area, SEM, Thimi

1–5, 14–15 Scale bar – 10 µm
6–13, 16–17 Scale bar – 1 µm

Plate 5