

Pollen morphology and aperture evolution in *Agave* Linn.*

K. Ambwani & Madhav Kumar

Birbal Sahni Institute of Palaeobotany, 53 University Road, Lucknow 226007, India

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Aperture types in the pollen grains are the most important characters frequently used for the taxonomic and phylogenetical studies. In Agavaceae, the tribe Agavae is known to represent monosulcate, bisulcate as well as pont-operculate type of apertures. SEM studies confirm the inclusion of anazonosulcate aperture in the above series exhibited by the pollen of *Agave*. The characteristic progressive reduction of the exine leading to the formation of anazonosulcate is discussed here. Variation in the exine architecture is also recorded.

Key-words—Pollen morphology, aperture evolution, Agavaceae.

INTRODUCTION

LILIACEAE is one of the largest families of monocotyledonae, widely distributed in warm, temperate and tropical regions. Bentham and Hooker (1883) transferred various taxa from Liliaceae and a new family Agavaceae was established by merging the tribe Dracaenae and the genus *Sensevieria* (Sensu Krause, 1930 in Engler and

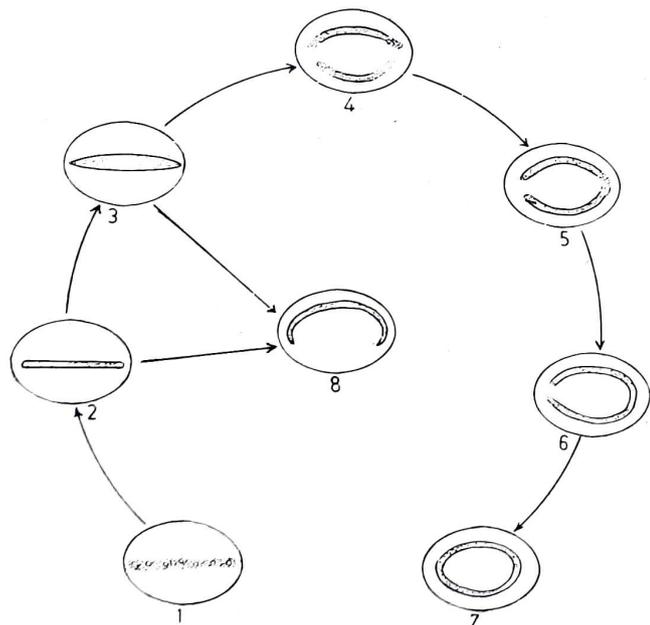
Prantle). Hutchinson (1959, 1973) placed Xanthorrhoeaceae and Agavaceae under the order Agavales. Cronquist (1968) treated Agavaceae under subclass Lilidae, whereas Dahalgren and Clifford (1982) considered Agavoidae as subfamily of Agavaceae.

Palynological studies of Agavaceae has been carried out by Alvarez (1985), Gentry (1972), Ludlow-Wiechers and Ojeda (1983), Ojeda *et al.* (1984), Palacios-Chavez (1978) and Zavada (1983) using light and scanning electron microscope. Alvarez and Kohler (1987) studied 16 genera of this family. They recorded monosulcate, disulcate and pont-operculate types of apertures and suggested the exclusion of *Hosta*, *Hesperocallis* and *Leucocrinum* from Agavaceae.

In the present work different species of *Agave* were studied under light and scanning electron microscope. It is important to note that in addition to monosulcate, bisulcate and pont-operculate apertures, the anazonosulcate type has also been recorded, which indicates an evolutionary sequence of aperture development in this genus (Pl.1, figs 1-9; Pl.2, figs 1-13; Text-fig.A).

MATERIAL AND METHOD

The polliniferous material of *Agave americana* and *A. wightii* was acetolysed; a part of the pollen material was utilised in the preparation of permanent slides, whereas the remaining part used for SEM studies. The pollen were mounted on a clean glass piece and allowed to dry at 30°C which then mounted on the metallic stubs



Text-figure A. Aperture variation in *Agave* Linn. 1-3, Monosulcate, 4, Bisulcate, 5-6, Pont-operculate, 7, Anazonosulcate, 8, extended monosulcate.

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and coated by evaporating gold palladium up to 300 Å. The samples were then observed under scanning electron microscope (Philips 505). The accelerating voltage for image analysis varied from 15 Kev to 30 Kev. The observation thus recorded by LM and SEM are as follows.

DESCRIPTION

Agave wightii Linn.

Pl. 1, figs 1,2,5,7-9; Pl. 2, figs 1-4,6,8,10,11

Pollen elliptical, subcircular to oval, 80-120 µm long, 60-90 µm broad, monosulcate, bisulcate, pont-operculate as well as anazonosulcate; exine 2-3 µm thick, tectate, coarsely reticulate; lumina circular to polygonal, 5-22 µm broad, luminal area filled with nexinal bacula/grana/pila (0.5 µm - 1 µm); muri 3.5 µm thick. In SEM exine reticulate-retipilate, muri with pendent columellae, fine lumina also visible on smooth muri. The pendent columellae fused and proliferate at the nexinal contact.

Agave americana Linn.

Pl. 1, figs 3,4,6; Pl. 2, figs 5,7,9,12,13

Pollen oval to subcircular, 55-110 µm long, 25-75 µm broad; monosulcate, bisulcate, pont-operculate as well as anazonosulcate. Exine distinctly reticulate, retipilate to microreticulate, tectate; lumina up to 15 µm, muri generally thick, thin near the sulcus margin. In SEM exine distinctly reticulate, thin along the sulcus margin, pila/bacula and gemmae sometimes less than 1 µm.

Aperture

The aperture in *Agave* is monosulcate, bisulcate, pont-operculate as well as anazonosulcate; sulcus extend up to poles, 70-80 µm long. Initially a monosulcate condition is achieved by dissolution of reticulum at a particular place and leads to a meridionally placed sulcus (Pl. 1, fig. 1; Pl. 2, fig. 8; Text-fig. A). The bisulcate pollen are frequent in the samples. The second sulcus is smaller

than the first (Pl. 1, fig. 5). The pont-operculate condition can be visualized with two sulculi fused at one pole (Pl. 1, fig. 8; Pl. 2, fig. 4). The union of two sulculi at both the ends leads to the formation of an operculum. Thus the pollen becomes anazonosulcate and a transition from monosulcate to anazonosulcate is observed (Pl. 1, fig. 6; Pl. 2, fig. 6).

Exine

Exine in *Agave* is generally characterized by reticulate ornamentation, the reticulum is supraaxial, perforated, heterobrochate, muri raised and frilled (Pl. 2, figs 1-11). The reticulum provided with pendent columellae hanging from the underside of the network, subsequently fused with the nexine (Pl. 2, figs 9, 12). Notably this reticulum becomes very fine along the sulcus margin (Pl. 1, figs 5, 7). Nexine profusely ornamented with grana/bacula/pila as well as gemmae (Pl. 2, fig. 11). The lumina vary from oval to angular in shape.

DISCUSSION

Alvarez and Kohler (1984) studied pollen morphology of *Agave*, *Yucca*, *Furcraea*, *Hosta*, *Manfreda*, etc. and observed monosulcate, bisulcate and pont-operculate types of apertures. In the present study, the authors observed the transitional stages of the aperture development from monosulcate to anazonosulcate. The course of aperture development is gradually followed with the formation of one more aperture parallel to the equator (Pl. 1 fig. 5; Pl. 2, fig. 2). Subsequently, two sulculi fused at one end giving rise to pont-operculate condition, which further extends due to the dissolution of the reticulum and forms an anazonosulcate aperture parallel to the equator (Pl. 1, figs 6, 9).

The pollen having colpus-like structure "sulcus" at the distal pole is the type found dominant in the super order Magnoliflorae as well as Nymphaeiflorae of the dicotyledons (Dahlgren & Clifford, 1982), while in the monocotyledons such types as well as ulcerate aperture

Plate 1

Figures 1-9. SEM microphotographs showing different views and aperture types of pollen in *Agave* Linn. →

1. *Agave wightii*, apertural view showing formation of sulcus, ca. x 900.
2. *A. wightii*, Showing formation of anazonosulcate aperture (note reduction in size of lumina along the sulcus margin), ca. x 1000.
3. *A. americana*, apertural view of monosulcate pollen showing coarsely reticulate exine with broad lumina (note the exinal baculae), ca. x 900.
4. *A. americana* - non apertural view, with variable lumina, ca. x 800.
5. *A. wightii*, bisulcate pollen, ca. x 850.
6. *A. americana*, anazonosulcate aperture, ca. x 580.
7. *A. wightii*, lateral view showing extended sulcus ca. x 900.
8. *A. wightii*, pont-operculate sulcus, ca. x 1050.
9. *A. wightii*, anazonosulcate pollen showing complete dissolution of exine around sulcus (note the similarity between the reticulum of the operculum and rest of pollen exine), ca. x 980.

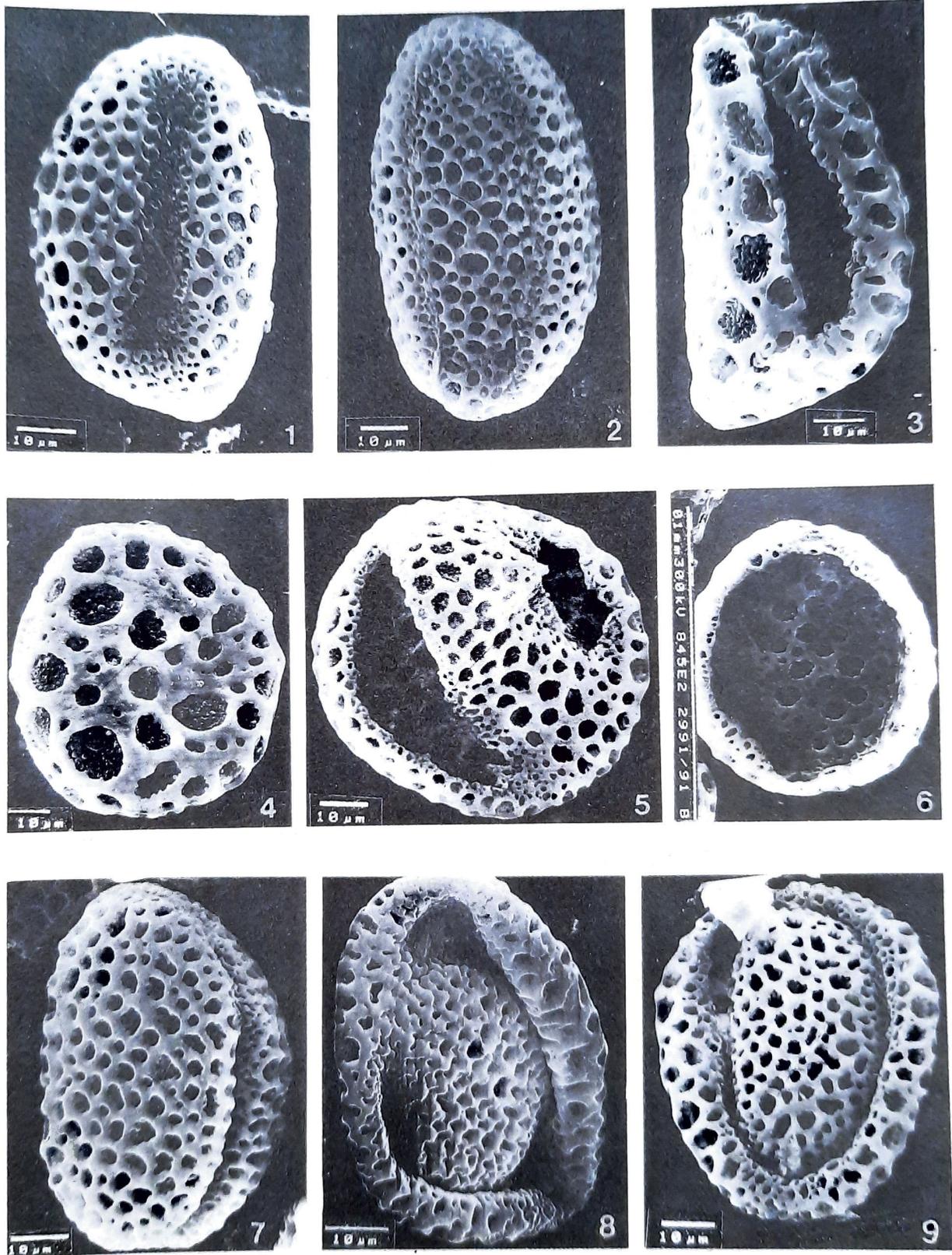


Plate 1

are most common. Whereas in the dicotyledons such types are nearly or almost absent (Walker, 1974, 1975, 1976, Dahalgren, 1977). Occurrence of sulcate pollen in the monocotyledons is common in the Liliiflorae and Areciflorae except Pandanales (Radulescu, 1973). In Areciflorae sulcate pollen occur up to 75% or more. Bisulcate pollen are mostly restricted to the order Arales (Ariflorae), Dioscoreales (Liliflorae) and a number of palms. This feature has no doubt been evolved independently in Agavaceae. The tectate, collumellate wall structure occurs even among ranalian taxa and appears to be an early phylogenetical development among dicotyledons (Doyle, 1969; Walker, 1976). Pollen with two furrow-like apertures parallel to the equator, are present in some members of the Ranales which represent a secondary fusion of two originally distinct "sulculi" (Walker, 1974,). The transition may be visualised as anasulcate-anazonosulcate through pont-operculate. Such progressive development of the sulcus transition is encountered in *Agave* (Text-fig.A).

Thus it is evident that the genus *Agave* has retained the ancestral primitive characters in the pollen. According to Huber (1977) this family shows much similarity with Magnoliales *Sensu lato* Discoriaceae-Asperagales line. However, it can be presumed that the extant Agavoidae provides missing links of the common ancestral characters through its pollen.

FOSSIL RECORDS

Fossil palynological records of Agavaceae are known from the Maastrichtian to Pliocene sediments. Chmura (1973) reported *Agave*-like pollen as *Liliacidites pollucibilis*, *L. creticus* and *L. varigatus*. Of these, the affinity of *Liliacidites pollucibilis* was suggested to *Agave virginica*. Suc (1974) reported agavaceous pollen assignable to *Yucca* and *Dracaena* from the Pliocene of Languedoc, France. *Dracaena*-type pollen, viz., *D. quinetti* and *D. saportae* were described by Van Campo and Sivak (1976)

from the Middle Miocene of Tunis and Czechoslovakia.

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Plate 2

Figures 1-4. *Agave wightii* LM, ca. x 500.

1. Non apertural view with reticulate exine.
2. Bisulcate pollen.
3. Non-apertural view showing lumina variable in size.
4. Pont-operculate type of sulcus.
5. *A. americana*, non-apertural view showing reticulate and retipilate nature of exine, LM ca. x 500.
6. *A. wightii*, pont-operculate (note attachment of operculum), LM x 1000.
7. *A. americana*, reticulate-retipilate exine (note the pila along the margin), LM ca. 1500.
8. *A. wightii*, a portion of sulcus magnified to show fine lumina

along the sulcus margin. SEM ca. x 1300.

9. *A. americana*, details of exine showing muri with pendent columellae, SEM ca x 2200.
10. *A. wightii*, apertural view showing foot layer, SEM ca. 1800.
11. *A. wightii*, a part of exine showing variable lumina. SEM ca. x 1700.
12. *A. americana*, Lumina showing pendent columellae and branched gammae at the base (note the fine pore on the muri), SEM ca. x 3800.
13. *A. americana*, a part of sulcus showing interspersed pila, bacula and grana (note fusion of pendent columellae with nexine), SEM ca. x 4200.

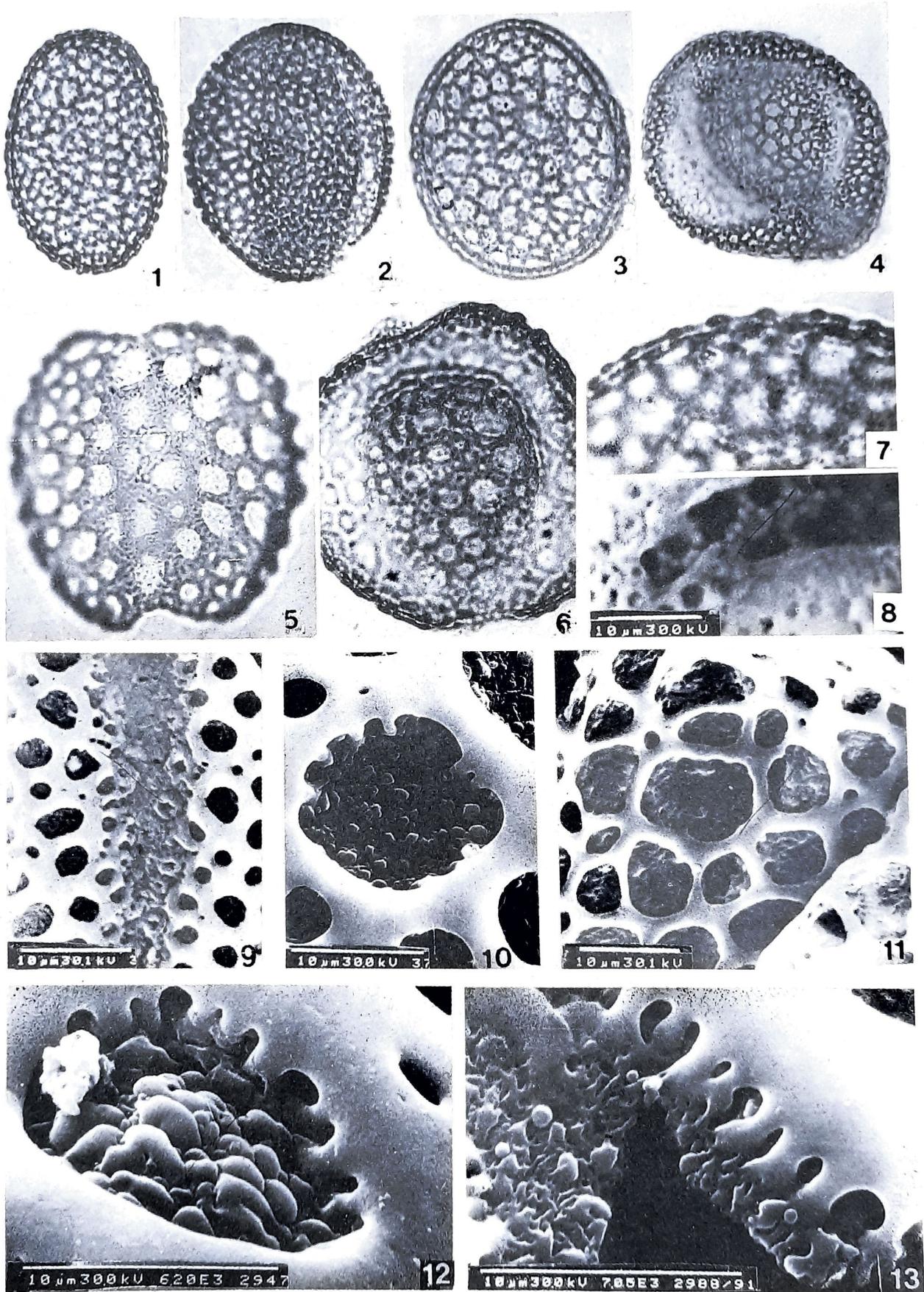


Plate 2

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