

Investigations on a fossil agavaceous axis from Neyveli Lignite, Tamil Nadu, India

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(Received 10 November 1997; revised version accepted 9 November 1998)

ABSTRACT

Ambwani K 1999. Investigations on a fossil agavaceous axis from Neyveli Lignite, Tamil Nadu, India. *Palaeobotanist* 48(3) : 245-250.

Further anatomical observations on a fossil agavaceous axis from Neyveli lignite Mine-1, Neyveli, Tamil Nadu show the presence of anomalous secondary growth with amphivasal vascular bundles as well as other cell inclusions such as raphides. Simple perforation in the fossil vessel end plates suggests an advanced character of the plant. Association of monosulcate reticulate pollen (*cf. Liliacidites*) in the same axis further supports its affinities with Liliaceae.

Key-words—Fossil axis, Anomalous secondary growth, Raphide, Agavaceae, Neyveli Lignite, India.

सारांश

भारत के तमिलनाडु प्रान्त के नयवेली लुगुंडांगार (लिग्नाइट) से प्राप्त एगेवेशियस पादपाशम अक्ष पर अनुसन्धान

कृष्ण अम्बवानी

तमिलनाडु के नयवेली लुगुंडांगार (लिग्नाइट) खदान-1 से प्राप्त एक एगेवेशियस पादपाशम अक्ष के पुनः शरीर रचनात्मक प्रेक्षण करने पर फ्लोएमकेन्द्री संवहनी बण्डलों के साथ असंगत द्वितीयक वृद्धि की उपस्थिति प्रदर्शित हुई है, साथ ही अन्य कोशिकीय समावेशन, जैसे रैफाइड की उपस्थिति भी प्रदर्शित हुई है। पादपाशम वाहिका छोर प्लेट में सरल छिद्रों का होना पौधों के अग्रगामी अभिलक्षण को सूचित करता है। एक ही अक्ष में एकखांची जालिकारूपी परागकणों (तुलनात्मक रूप-लिलिएसिडाइटिस) का साहचर्य इसकी लिलिएसी के साथ सजातीयता को पुनः समर्थित करता है।

INTRODUCTION

THE family Liliaceae is one of the largest families of Monocotyledonae distributed widely in warm tropical regions. Some taxa of this family also grow in temperate climate. Bentham and Hooker (1883) established family Agavaceae in their classification system and merged Draceneae with Liliaceae. Engler (1892) included the family Liliaceae under the order Liliiflorae and treated Agavaceae as a subfamily. However, Wettstein (1901) preferred to classify

Agavaceae as a separate family in Liliiflorae. Hutchinson (1959) maintained Agavales as a separate group under which he accommodated Agavaceae and Xanthorrhoeaceae. Chmura (1956) preferred to merge Agavaceae under the order Liliales and Cronquist (1968) treated Agavaceae under subclass Liliidae. Dhalgren and Clifford (1982) in their revised classification for monocotyledons created Liliiflorae as a super order which included family Liliaceae under the order Liliales. According to them, the family Agavaceae is further subdivided into two subfamilies, viz., Agavoideae and Yuccoideae.

The Agavoideae contained the genera *Agave*, *Beschorneria*, *Bravoa*, *Furcraea*, *Littaea*, *Manfredra*, *Polianthes* and *Pseudobravoa*, whereas Yuccoideae includes *Clistoyucca*, *Hesperaloe*, *Hesperocallis*, *Hesperoyucca*, *Samulea* and *Yucca*. Nevertheless, family Agavaceae needs more attention to resolve its evolutionary status in the plant kingdom. The agavaceous fossils (pollen and wood) are known as early as Late Maastrichtian to Pliocene (Chmura, 1973; Suc, 1974; Van Campo & Sivak, 1976; Ambwani, 1982).

MATERIAL AND METHOD

The agavaceous fossil axis was collected by the author from the Neyveli lignite Mine-I, Neyveli, Tamil Nadu and preliminary observations were published (Ambwani, 1982). In the present paper detail anatomy has been carried out under SEM and some more significant observations have been studied.

For SEM observations transverse and longitudinal sections of the axis were prepared, and dried under controlled temperature between 30°-50°C. Then the sections were mounted on the metallic stub and conducted by applying silver paint. The specimens were then coated by evaporating gold/Palladium alloy and studied under scanning electron microscope (Phillips 505). The accelerating voltage for image analysis varied from 15 KV to 20 KV.

The fossil axis is dark brown in colour, measures about 4.5 cm long and 2-3 cm thick, cylindrical and surrounded by spirally arranged scars. These scars probably represent both leaf bases and flower pedicels indicating its being an apical part of the plant (possibly a part of inflorescence). The central conducting zone is also visible as a solid core in the axis (Pl. 1, fig. 1).

ANATOMY

Cortex—The cortical zone is well preserved and extends up to 2-3 mm in thickness. The cells of this zone are slightly thick-walled usually filled with some organic material, which are globular in shape and variable size ranging from 1-4 µm. At some places the parenchymatous cells also contain different cell inclusions of complex morphology of unknown nature (Pl. 2, figs 5, 6). The cortical zone bears radially running vascular strands (Pl. 1, fig. 2).

Cambium—A layer below the cortical zone probably belongs to cambium and does not extend more than 10-15 µm comprising elongated cells. This layer is responsible for the demarcation of primary tissue meristem (PTM) and the development of secondary tissue meristem (STM) in the stem. The STM generally helps to add the secondary vascular tissue in growing stems (Pl. 1, fig. 3).

Primary vascular bundle zone—Primary vascular zone consists of primary vascular bundles which are amphivasal in nature. They are irregularly scattered in the central ground parenchyma (Pl. 1, figs 2, 4). These bundles usually have peripherally arranged long overlapping tracheids and vessels surrounding the central phloem strand (Pl. 1, fig. 5). The xylem includes short parenchymatous cells.

The phloem cells are thin-walled and angular in shape. Each vascular bundle is surrounded by parenchymatous cells (Pl. 1, fig. 5). The size of the vascular bundles varies from 30-150 µm while the length of the tracheids may extend up to 70 µm or more and 10 µm wide. The vessel perforation measures 5 µm and the bordered pits 1-2 µm in diameter (Pl. 2, figs 2, 3). The ground parenchyma cells of this zone are thin-walled, but sometimes thick-walled cells may be observed, they invariably bear pits on the walls (Pl. 2, fig. 7).

Secondary vascular bundle zone—The secondary vascular bundles are more or less similar to that of primary vascular bundles which are responsible for growth in thickness in the stem. They are centripetally arranged and provide woody appearance to the axis. Thus more than 2/3 of the stem comprises secondary vascular system. The vascular bundles are amphivasal where xylem surrounds phloem (Pl. 1, fig. 6). The xylem tracheids are well preserved and show spiral, scalariform and reticulate thickenings (Pl. 2, fig. 1). However, vessels with simple perforation end plates are also present (Pl. 2, fig. 3), walls of the vessels have pitted thickenings, the pits on the outer side are simple but on the inner surface are slightly raised or bear thickening around them (Pl. 2, figs 2, 3). These pits are usually arranged in alternate fashion. Phloem in this zone is well preserved and seen in the central part of vascular bundles (Pl. 1, figs 5, 6).

Fibrous bundles—The fibrous bundles are present generally in the cortical zone measuring 6-8 µm and comprise 10-20 individual cells (Pl. 1, fig. 8).

Crystals—Needle-like crystals, probably calcium oxalate

PLATE 1



1. Fossil agavaceous axis showing leaf scars.
2. Cross section of the axis under low power (a part shows the arrangement of primary and secondary vascular bundles) x 25, x 50 respectively (Pv - Primary vascular bundles, Sv - Secondary vascular bundles, Lt - Leaf traces).
3. Part of the cortex showing cambium (cmb) cells (x 500).
4. Primary vascular bundles scattered in the central part of axis (x 300).
5. Vascular bundle in oblique section showing phloem cells (x 1000).
6. Single amphivasal vascular bundle showing phloem in the centre (x 1000).
7. Part of the vascular bundle enlarged to show vessels and xylem parenchyma (x 1200).
8. A part with fibre bundle in the cortex (x 750).

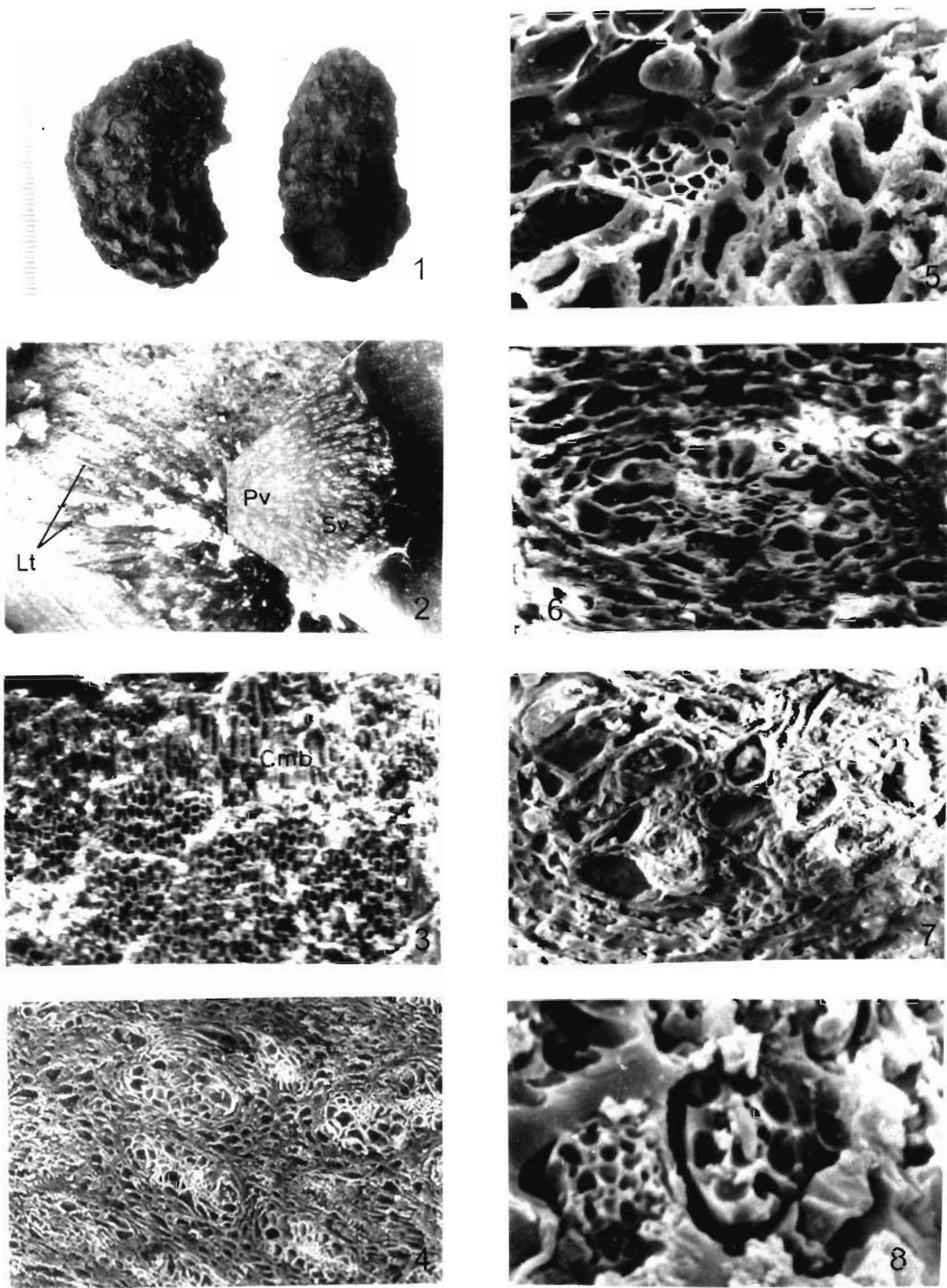


PLATE 1

in nature, are seen generally seated in parenchyma cells. However, they are profusely present in the suberised cells of the cortical zone. These calcium oxalate crystals are referred as pseudo-raphides. They may be branched or single. The thickness of crystals varies from 0.5-5.0 μm . The thicker crystals are broader at the base and become finer towards apex (Pl. 2, figs 8, 9).

Other cell inclusions—In the parenchymatous cells of cortical zone, primary vascular zone as well as secondary vascular zone of the axis different cell inclusions have been observed. They vary from round to elongated bodies. A large number of sinuate bodies are also seen in the ground parenchymatous cells (Pl. 2, fig. 5). The size of these bodies varies from 1-5 μm (circular type), up to 10 μm (elongated type) and 10-20 μm (sinuate type). However, the exact nature of these bodies could not be ascertained.

DISCUSSION

Agavaceous plants are found usually as sub-shrub to shrubs sometimes large shrubs (e.g., *Dracena* and *Yucca*). In their herbaceous habitat the aerial stems develop from the underground rhizomatous stems and for this habitat they lost the cambial activity in their secondary vascular system as seen in most of the dicotyledonous plants. Such stems probably had adapted the atectostelic characteristic having two or more whorls of vascular strands. They probably had primitive vessels both in stem as well as root. These primitive vessels had generally oblique walls with scalariform perforation plates which, later, in more evolved taxa included vessels with simple perforation plates.

According to De Mason (1979) a number of monocotyledonous plants produce secondary growth by means of a special kind of cambium known by various names but Clowes (1961) termed it as secondary thickening meristem (STM). It is a characteristic of Agavaceae (Rudall, 1995), occurring in all the genera of the family (e.g., *Agave*, *Furcraea*, *Beucarnea*, *Dasyilirion*). The secondary tissue meristem (STM) differentiates from mature primary tissue. Anatomically the primary vascular bundles are colateral while the secondary ones are amphivasal in nature (see Tomlinson & Zimmermann, 1969). In the present fossil axis though collateral bundles could not be observed but the continuity of primary and secondary bundles is noticed (Pl. 1, fig. 2). Zimmermann and Tomlinson (1970) concluded that in *Dracaena fragrans* and *Yucca brevifolia* the primary vascular bundles are differentiated only when the shoot elongation is complete.

According to Cheadle and Kosakai (1971), the specialisation of tracheary elements in Agavaceae as a whole is at a relatively low level. Vessels of any kind seem to be absent in bulbs, rhizomes, inflorescence axes and leaves. The vessels identified by them in aerial stem are of only primitive nature. According to Ayensu (1972), Cheadle (1943) and Wagner (1977), the most primitive vessel types are considered with long, narrow and oblique wall perforations with scalariform perforation plates. Whilst the most advanced ones are short and broad with a single large circular perforation plate. However, vessels in the present specimen are comparatively short, scalariform and pitted with simple perforation plates. It therefore seems that the plant had already acquired an advanced anatomical character. It is also observed that the continuity with the primary vascular system is by means of short bridges which link with leaf traces; similar pattern in Agavaceae has been observed by Parthasarathy and Tomlinson (1967).

The monosulcate pollen recovered from the same specimen confirm that the axis is a part of an inflorescence and the sulcate nature indicates less advanced character (Pl. 2, fig. 10). Calcium oxalate accumulated in several types of cells in plants may be simple, short, crystals or needle-like ones (pseudo-raphides). They may also be druce type bundles or sometimes branched needles (Pl. 2, figs 8, 9). According to Dahlgren and Clifford (1982) and Gulliver (1864) the raphides are more common in monocotyledons than in dicotyledons which are of high taxonomic importance.

It can be presumed that monocotyledons have a close connection with particular group of dicotyledons and it is very likely that their ancestors far back were in common with the ancestors of dicotyledons. It is also evident from the primitive characters which are regarded as ancestral ones. The similarities are found between certain Liliales and Magnoliales of mono- and dicotyledonous groups respectively. However, Agavaceae exhibits a more stabilised organisation of typical characters in the stem, though has not been able to form a true wood.

Records of agavaceous fossils from the Maastrichtian lead to presume their origin in the Upper Cretaceous time. The present find of plant remain along with monosulcate pollen (cf. *Liliacidites*) (Pl. 2, fig. 10) further indicates that these plants were quite established in the Neyveli Formation as also reported by Ramanujam and Reddy (1984), Siddhanta (1986), Saxena (1992) and Thanikaimoni *et al.* (1984).

PLATE 2



- 1 Tracheids showing scalariform thickenings (x 2500).
- 2, 3. Section showing vascular pits and end perforation (x 4000).
4. Longitudinal section of vessel wall showing bordered pit with membrane (x 5000).
- 5, 6. Parenchymatous cells with cell inclusions (x 4000).
7. Parenchymatous cells showing pits on wall (with round bodies x 4500).
- 8, 9. Raphide crystals in the cortical zone (x 2000).
10. Monosulcate pollen (cf. *Liliacidites* sp.) (x 1200).

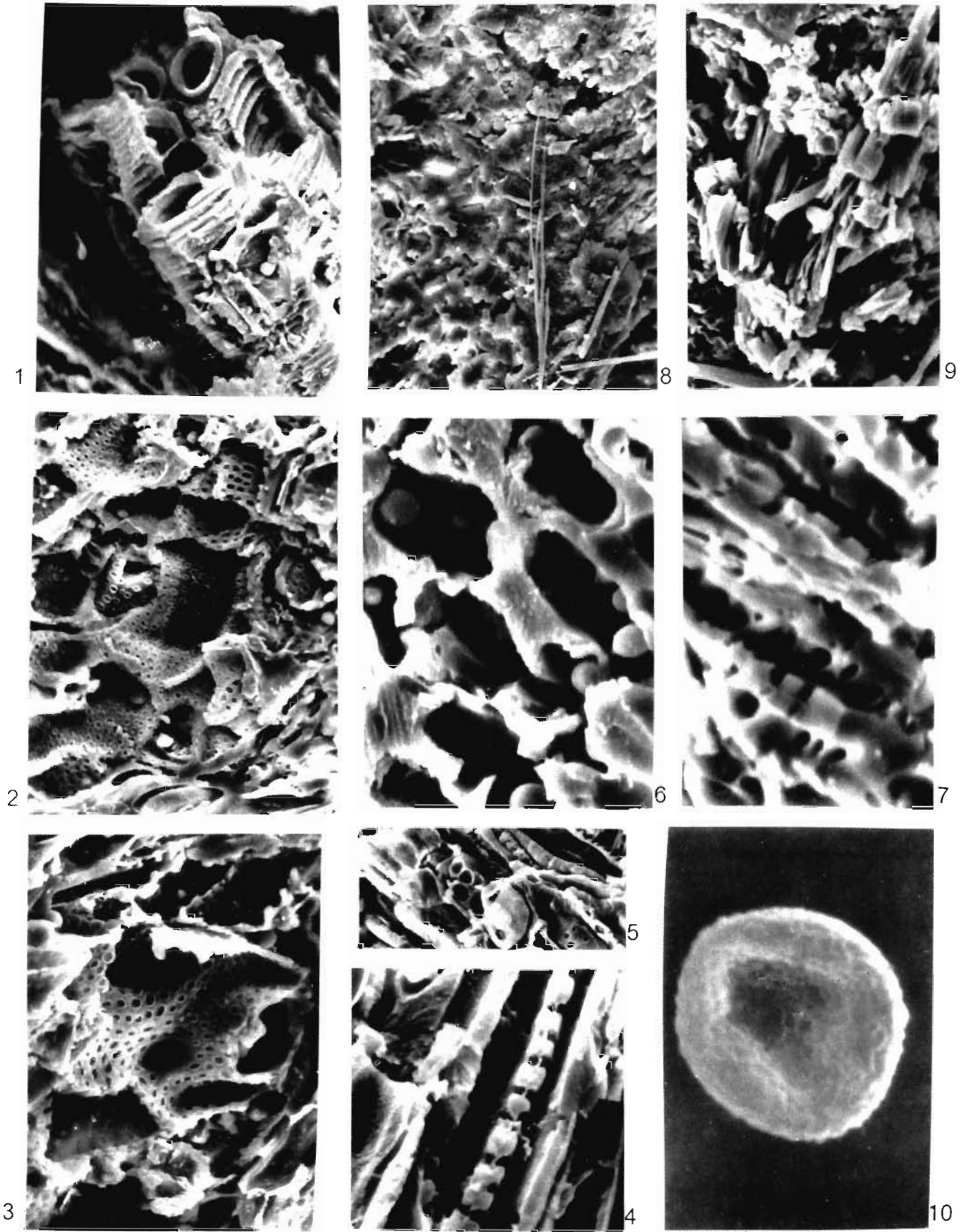


PLATE 2

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