

CONTRIBUTIONS TO THE KNOWLEDGE OF THE CAYTONIALES

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ABSTRACT

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Some additional features of the caytonialean capsule are described and the conventional interpretation of the “mouth” is challenged. The *Caytonanthus* pollen grains examined in the light and scanning electron microscope show a bilobed equatorial saccus sculptured with endosexinous ridges. The caytonialean seeds and androclads (*Caytonanthus tyrmensis* sp. nov.) from the uppermost Jurassic—lowermost Cretaceous Tyrma locality (Far East of the U.S.S.R.) are closely comparable with the corresponding organs of their Middle Jurassic predecessors showing striking evolutionary conservatism. However, the evolutionary potentials of the Caytoniales must not be underestimated. The caytonialean monandra and monogyna are considered as the nearest approach to angiosperm stamens and pistils.

INTRODUCTION

The Caytoniales have thrived for about 100 million years, from the Late Triassic to the Maastrichtian. In other words, they appeared and perished together with the Mesozoic world, and were a peculiar part of it, cosmopolitan and rather common in the Mesozoic plant communities, though never attaining a dominant status. They entered the textbooks on palaeobotany and plant morphology as the only Jurassic plants acquiring functional angiospermy. Thomas (1925) considered them if not immediate predecessors of the angiosperms, then a side branch of their ancestral stalk. Harris (1933, 1951, 1964) described the first Liassic *Caytonia* from Greenland and made important contributions to knowledge of the Yorkshire Middle Jurassic Caytoniales. Most of his emendations of the original reconstruction were against the idea of the angiosperm affinities. Both Thomas and Harris designated the *Caytonia* ovuliferous trusses as megasporophylls.

Subsequent contributions were made by Edwards (1929), Townrow (1962) and recently by Reymanowna (1973, etc.) who studied the vascular anatomy of *Caytonia* and clarified the position of ovules within the capsules. She also discussed the caytonialean mode of pollination and dehiscence. Millay and Eggert (1970) compared the *Caytonanthus* pollen organs to the

Pennsylvanian *Idanothekion* (Callistospermaceae) producing pollen grains of the *Vesicaspora* type, and Reymanowna suggested the derivation of the Caytoniales from the callistospermaceous pteridosperms.

Structurally preserved caytonialean fossils were recently collected from the Tithonian—Berriasian beds of the Tyrma River (Far East of the U.S.S.R.). They are about 20 m. y. younger than the European records and, thus, allow us to estimate the amount of evolutionary change. A few capsules of the type species *Caytonia seawardii* were macerated for comparison with the Tyrmanian fossils.

TERMINOLOGY

Male and female organs of the Caytoniales have been described as sporophylls bearing synangia or cupules. I avoided this terminology because it suggested a questionable homology with spore-bearing organs or those of pteridosperms. Such terms as stamen, anther or fruit are more applicable, though it is still better to use non-committal descriptive terms, e.g., monandron and monogynon (a basic polliniferous or ovuliferous unit, see Meeuse, 1974, etc.), androclad and gynoclad (a branching organ bearing monandra or monogyna). Sporophyll derivation of the *Caytonia* spicate gynoclad was supported by slight dorsiventrality of the axis cuticle (Thomas, 1925), though this might be merely preservational. R. Melville's term "gonophyll", i.e., epiphyllous gynoclad, appears in the new interpretation of caytonialean monogyna tentatively suggested here as a matter for consideration.

Caytonia seawardii H. Thomas from Yorkshire (Plate I, 1—7; Plate II, 1—2; Plate III, 1—6; Plate IV, 1—4; Plate V, 1—5).

A complete description of *Caytonia seawardii* was given by Thomas, Harris and Reymanowna (loc. cit.). I am describing here only those features which are relevant to the interpretation presented below.

The globose capsule is composed essentially of two cutinised sacs — the outer fleshy sac and the inner thinly cutinised sac with ovules. The thick cuticle of the outer sac is marked with conspicuous ribs radiating from the stalk and occasionally anastomosing. The scar-like opening ("mouth") is situated close to the stalk and protected by a valve, or "lip". Plate II, 1 shows the lip about 0.5 mm off the stalk, pointing away from it and bulging over the mouth on its outer side. Other capsules show slightly raised mouths, their edges stiff and protruding, and never continuous with the stalk. Transverse "bars" on the lip correspond to the wall ribs. The surface of the mouth region is scabrate due to the bulging and occasionally hair-like epidermal cells.

On the inner side of the capsule wall, the mouth is bordered by the prominent ridge or swell about 0.25 mm high, also showing transverse "bars" (Plate II, 2).

The inner sac occupies about two thirds of the capsule volume. It is connected with the mouth by a short tube which is attached to the ridge on

the inner side of the mouth. The tube is more heavily cutinised than the rest of the inner sac. The tube wall is sharply plicated, forming a series of grooves or "channels" (Plate III, 2, 5). The cells are nearly isodiametric or transversely stretched in the grooves, slightly elongated between them, with clearly marked walls, about 18–21 μm long. A number of pollen grains was observed arrested in the grooves; they are mostly distorted but some are fairly well preserved showing distinctive features of the *Caytonanthus* pollen (Plate III, 4).

The inner sac is filled with closely packed imbricate ovules, their micropyles facing the mouth. Plate IV, 2 shows micropyles of two seeds, their bulging cells are nearly contiguous.

The ovules are pressed against the inner sac wall, their integuments adnate to the inner sac membrane leaving conspicuous sutures (Plate IV, 4). The inner sac cuticle is delicately striated, showing indistinct rectanguloid cells arranged in longitudinal files.

Discussion

It was suggested that the *Caytonia* ovules were embedded singly in a flesh of large cells. This interpretation was in accordance with the supposed megasporophyll derivation of the caytonialean capsules. Reymanowna (1973) has proposed a new reconstruction of the capsule interior with ovules gathered in a packet covered by a cutinised membrane. My observations essentially agree with her conclusions. I macerated inner sac membranes enveloping undistorted ovules, their integuments adhered to the membrane and to each other, forming a honeycomb of locules for loosely attached nuclei. It was possible to trace the extension of the inner sac membrane into the more heavily cutinised tube connecting the locule with the mouth. The details of this pollen-transferring, style-like structure came to light and the pollen grains arrested within the tube confirmed the function of the "channels".

The previously held idea of the mouth as a gap between the stalk and the involuted megasporophyll apex (the lip) does not appeal to me, since I observed the mouth on the distal edge of the lip, that is outside the lip-stalk space. Thus, I believe that the mouth was independent from the stalk though situated close to it. An alternative interpretation of the *Caytonia* capsule is represented in Fig.1. The mouth and the pollen-transferring tube correspond to the point of attachment and the stalk of the epiphyllous cupule. The facts behind this morphological speculation are (1) the resemblance of the juvenile capsules to involute *Sagenopteris* leaflets (Harris, 1951) and (2) the similarity between *Sagenopteris* and *Glossopteris* as well as between the pollen grains and seeds of the Caytoniales and Glossopteridales (Harris, 1954; Pant and Nautiyal, 1960; Townrow, 1962). These similarities are in favour of the glossopteridalean ancestry of the Caytoniales. Pollen-bearing organs comparable to *Caytonanthus* occur not only in the lyginopteridalean pteridosperms but also in the Glossopteridales (Surange and Maheswari, 1974). One may argue against the leaf comparisons because the leaf characters are

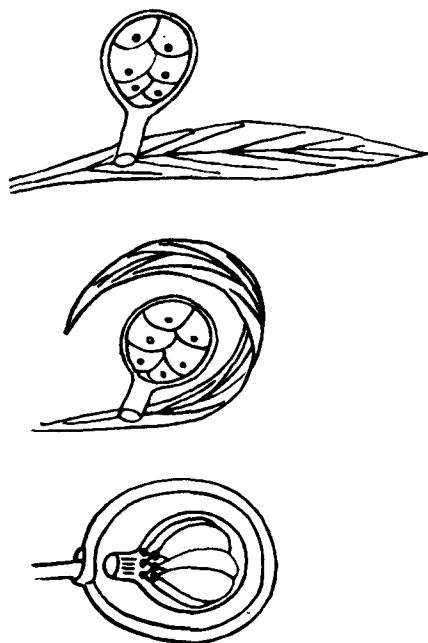


Fig.1. Hypothetical derivation of the caytonian capsule by involution of a glossopterid gonophyll.

especially liable to convergence. However, the evolutionary mechanism responsible for supposed convergence of the qualitative leaf characters was never explained. The foliar identity of the Cretaceous and modern angiosperms, despite considerable character displacement in floral organs, the retention of the *Nilssonia* leaf type in both the Beaniaceae and more advanced Dirhoplostachiaceae (Krassilov, 1975) and many other examples, illustrate the striking conservatism of the leaf characters. The resemblance of *Sagenopteris* to *Glossopteris* is, thus, of no minor importance in demonstrating affinities. The caytonian capsule might evolve by involution of a stegophyll enclosing a *Cistella*-like cupule followed by transformation of the cupule stalk into a pollen-transferring device.

CAYTONIALEAN PLANTS FROM THE TYRMA RIVER

The Tyrma plant locality is among the richest in Asia. Plant megafossils came from the tuffites of latest Jurassic or Berriasian age outcropping on the right bank of the Tyrma River, a tributary of the Bureya. They have been described by Seward (1912), Novopokrovsky (1912), and other authors (see Krassilov, 1973 for references and floristic list). This locality (latitude 50° N) yielded remains of *Khukia*, *Cyathea* and *Araucaria* — the thermophilous plants not represented or extremely rare in the Bureya localities, about 200 km to the north.

Sagenopteris leaves and isolated leaflets are rather common in the Tyrma locality. They are essentially like *S. phillipsii* (Brongniart) Presl in gross morphology and cuticular characters. Other caytonialean fossils are the *Caytonia* seeds and *Caytonanthus* staminate fructifications described below. The fragments of *Caytonanthus* are associated with *Sagenopteris* on the same hand-specimens. The seeds were obtained by bulk maceration of the *Caytonanthus*-bearing rock.

Seeds (Plate VI, 1–7)

Of the two seeds obtained by bulk maceration from the *Caytonanthus*-bearing rock, one is narrow ovate, 1.6 mm long, 0.8 mm broad, smooth, orthotropous with chalazal end slightly truncate; the hilum is proportionally large and the micropylar end bluntly pointed (Plate VI, 1). The micropyle is sunken. The outer cuticle is very delicate showing fine striation and obscure outlines of rectanguloid cells, about $37\text{--}50 \times 18 \mu\text{m}$. The stone is thick, the outer stone layer composed of palisade-like cells about $50\text{--}62 \times 31 \mu\text{m}$ (Plate VI, 2). The nucellus is elongate, $144 \mu\text{m}$ long, $400 \mu\text{m}$ broad, gradually tapering to the top, nucellar beak scarcely differentiated, widely open (Plate VI, 3, 4). The nucellar cuticle is thick and durable, longitudinally ridged, showing elongate cells about $60 \times 18.6 \mu\text{m}$, with very thin, slightly undulate, indistinctly marked walls. The beak cells are small, about $17 \times 12 \mu\text{m}$, polygonal, with thick, well-defined walls. No pollen grains were found within the beak. There are no indications of a cutinised megaspore membrane. Another seed is ovate, 2 mm long, 1.3 mm broad, bulky, not flattened, with a proportionally very narrow nucellus, only $160 \mu\text{m}$ broad. The nucellus tapers to both ends, with a dark central body occupying about one half of its width (Plate VI, 5–7). The nucellus appears shrunk and is probably exhausted by the developing embryo. However, the details of the central body are not discernable.

Remarks: The main reason for attributing these seeds to *Caytonia* is their close correspondance to the *Caytonia sewardii* seeds in external morphology and nucellar characters. The nucelli prepared from the Yorkshire specimens (Plate V, 1–5) are elongate, 1.2–1.5 mm long, 0.4–0.6 mm broad. The chalazal end is rounded or shortly stalked, the nucellar beak is open or occasionally collapsed. The cuticle ridges are somewhat less developed and the cell outlines are more distinct than in the Tyrmanian nucelli.

Caytonanthus tyrmensis Krassilov sp. nov. (Plate VII, 1–6; Plate VIII, 1–7; Plate IX, 1–12; Plate X, 1–4; Plate XI, 1–4; Plate XII, 1–5; Plate XIII, 1–4).

Diagnosis: Anther 3.5–5 mm long, 4-loculed, terminal on a short filament, pollen sacs dorsally carinate. Cuticle thin, longitudinally ridged, cells rectanguloid ca. $31 \mu\text{m}$ long. Pollen grains ca. $25 \mu\text{m}$ wide.

Holotype: 550-235, Museum of the Institute of Biology and Pedology, Vladivostok (Plate VIII, 3, 4).

Locality: Tyрма River, Late Jurassic—earliest Cretaceous (Tithonian—Berriasian).

Several isolated stamens were found on the rock surface and obtained by bulk maceration. There are also two androclad branches, one of them 6 mm long, bearing five stamens, all on the same (presumably basiscopic) side (Plate VII, 3, 4). Detached stamens on the same rock slab apparently belong in the same branch. Another branch (Plate VII, 1) is 2 mm long and bears six stamens, their arrangement on the rock surface suggesting radial attachment. Transfer preparations were made from the counterparts of these specimens (Plate VII, 2). The stamen consist of a stalk about 0.6 mm long and an elongate anther 3.5–5 mm long. The mode of dehiscence was the same as in *Caytonanthus arberi* Harris (1951, etc.): the ripe pollen sacs dehiscence inwardly by the ventral slit. Inrolling of the slit margins presumably caused separation of the pollen sacs, which remained joined at the base and apex (Plate VIII, 4, 5).

The pollen sac shows a prominent dorsal keel constantly retaining pollen grains. The pollen sac wall consists of an epidermis and a subepidermal layer of parenchymous tissue.

The cuticle of the pollen sac is moderately thick and longitudinally ribbed. The cell outlines are rather obscure, the cells arranged in longitudinal files, rectanguloid or irregular, about $31 \times 18.6 \mu\text{m}$, anticlinal walls thin, straight or slightly waved.

The anthers normally have radial symmetry, but a single specimen from the bulk maceration which is about half as large as the rest shows bilateral symmetry with two pollen sacs on one side 1.3 times longer than those on the other side (Plate VII, 1–3).

Pollen grains appear bisaccate when examined under the light microscope, the bladders are hemispherical or occasionally pear-shaped, showing an irregular reticulum and transverse folds radiating from the bladder roots. The lateral walls of the corpus which form the bladder roots are seen through the saccus on the distal face (Plate IX, 4, 5). The sulcus appears as a narrow slit with wavy margins. The dimensions are fairly constant: the total grain width (equatorial diameter of the saccus) ca. $25 \mu\text{m}$ (range $21\text{--}29 \mu\text{m}$), the height (polar axis) ca. $13\text{--}15 \mu\text{m}$.

The equatorial outline of the pollen grains (viewed from the poles) is crescent-shaped, reniform or fiddle-shaped, showing two hemispherical bladders which occupy most of the distal face and which are separated by a narrow sulcus. In small and probably immature pollen grains, the bladders are contiguous in the middle of the distal face, diverging slightly towards the periphery. In the fully developed grains, the sulcus intersects the whole depth of the distal face extending as a narrow infolding on one of the lateral faces. The sulcus shows granulate slopes and well-defined leptoma.

The proximal face shows a prominent cappus with a slightly depressed central portion. This depression, seen in Plate X, 2 and Plate XI, 1, 4–5, probably represents a vestigial haptotypic feature. In some grains, the bladders are clearly delimited from the cappus while in the others the cappus—bladder

boundary is rather indistinct (Plate XII, 1, 4). In the lateral aspect, the cappus is strongly arched and protruding and nearly conical, the sulcus region is depressed and the bladders are inclined distally, though in some cases they are spread in the axial plane. The corpus is elongate-elliptical. Its lateral walls, forming the floors of the bladders, are slightly arched or straight and appear thick and rigid. The more delicate distal wall is moderately convex or depressed between the rigid lateral walls (Plate XII, 2; Plate XIII, 1, 2).

Several grains viewed from the proximal pole show the corpus completely surrounded by an equatorial saccus with the lateral connections between the lobes rather well developed, though the sexinous layer is usually infolded on one of the lateral sides (Plate X, 2; Plate XII, 1, 3). These connections are evident also in some of the lateral aspects: the lateral face is traversed by folds of the sexinous layer, forming bladders (Plate XIII, 2). However, the folded saccus wall is often collapsed between the rigid lateral walls of the corpus.

The smooth surface of the corpus is visible when the saccus is broken (Plate XIII, 4). The saccus is externally smooth or indistinctly granular and internally ornamented by endosexinous ridges forming an irregular reticulum. The folded saccus wall appears extremely fragile. The free portions of the bladders are usually perforated. These perforations are described as pits when observed with the light microscope. They are inconstant and cannot be used as a diagnostic character.

DISCUSSION

Meeuse (1974) has considered the caytonialean polliniferous organ as pinnate monandron. However, it appears more likely that this organ is androclad or polyandron, bearing stalked monandra or stamens. Harris (1951) has emphasized the radial symmetry of the *Caytonanthus* synangium as the most significant difference from the bilateral angiosperm anther. The underdeveloped anther with two large sacs on one side and two smaller sacs on the other is of some interest in this respect since it suggests bilateral symmetry with two unequal thecae in the early developmental stage, while the radial symmetry was achieved later.

The morphology of the Tyrmanian *Caytonanthus* agrees closely with the Yorkshire Middle Jurassic species. The anthers are longer than those of *C. oncodes* (2.5 mm) and *C. arberi* (3 mm); the average pollen grain size slightly exceeds that of *C. arberi*, but is less than *C. oncodes*. It is especially fascinating from the evolutionary point of view that the peculiar mode of the anther dehiscence adopted by the caytonialean plants remained unaltered through at least 20 m. y. The basiscopic attachment of the stamens on the longer branches and their radial disposition on the short appendages as well as the terminal position of the anthers, which are erect and not pendulous as in *C. arberi*, might have been of some evolutionary significance.

The *Caytonanthus* pollen grains are essentially like the Middle Pennsylvanian *Vesicaspora* occurring in the *Idanothekion* polliniferous organs (Millay and

Taylor, 1970, 1974), though much smaller. It is evident now that at least in one of the *Caytonanthus* species the corpus is surrounded by equatorial saccus except for a narrow sulcus. However, these pollen grains may well be described as bisaccate because of pronounced lateral constrictions of the saccus.

CONCLUSIONS

The comparison of the Tyrmanian Caythoniales with their Middle Jurassic predecessors suggests amazing evolutionary conservatism somehow related to considerable complexity and unique characters of their fructifications. The reproductive biology of the caytonialean plants was unchallenged in the Jurassic world. However, the evolutionary potentials of the Caytoniales must not be underestimated. They had no true pistils, but closed, many-seeded capsules; no stigma but a protostigmatic "mouth"; no style but a channeled pollen-transferring tube; no anthers but four-loculed protoantherae forming two protothecae in the early developmental stages. In other words, the caytonialean monogyna and monandra are the nearest approach to the angiosperm pistils and stamens and the final quantum step might have been made in response to the rapidly changing environment in Cretaceous time.

PLATE EXPLANATIONS

PLATE I (p.163)

Caytonia seawardii H. Thomas from Yorkshire.

1. Capsule showing the stalk base and the mouth, $\times 15$.
- 2, 3. Mouth region of the same capsule viewed from outside (2) and from inside (3), $\times 20$.
4. Cleared capsule showing inner sac with ovules, $\times 15$.
5. The same capsule, part of the wall removed, $\times 15$.
6. Packet of ovules from the same capsule, $\times 15$.
7. Cleared mouth region, $\times 30$.

PLATE II (p.164)

Caytonia seawardii H. Thomas from Yorkshire, SEM micrographs.

1. The base of the capsule shown in Plate I, 1. Note the lip bulging over the mouth on its distal edge, $\times 100$ (*m* = mouth; *l* = lip; *s* = stalk).
2. The same structure seen from within, $\times 100$.

PLATE III (p.165)

Caytonia seawardii H. Thomas from Yorkshire.

- 1, 2. Pollen-transferring tube attached to the mouth (1) and leading to the ovules (2), $\times 60$.
3. Cells of the tube; note transversely stretched cells forming the groove floor, $\times 395$.
4. Pollen grain arrested in the groove, $\times 395$.
5. Grooves of the pollen-transferring tube, $\times 166$.
6. Ovule base with funicle adnate to the inner sac cuticle, $\times 200$.

PLATE I

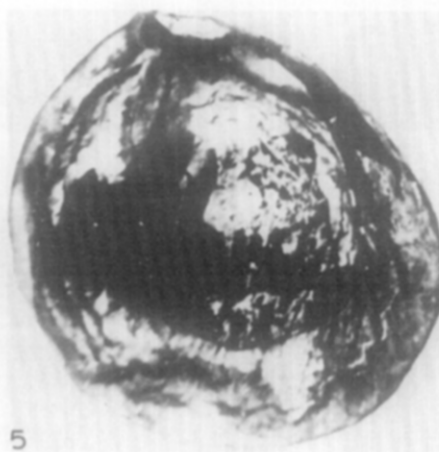
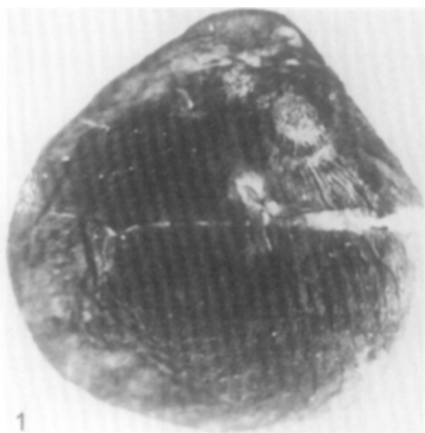


PLATE II

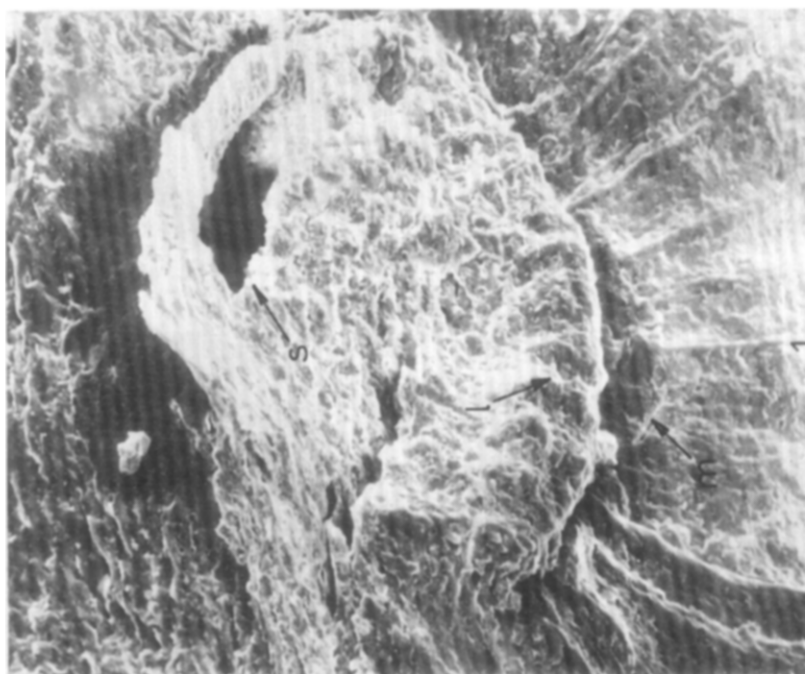
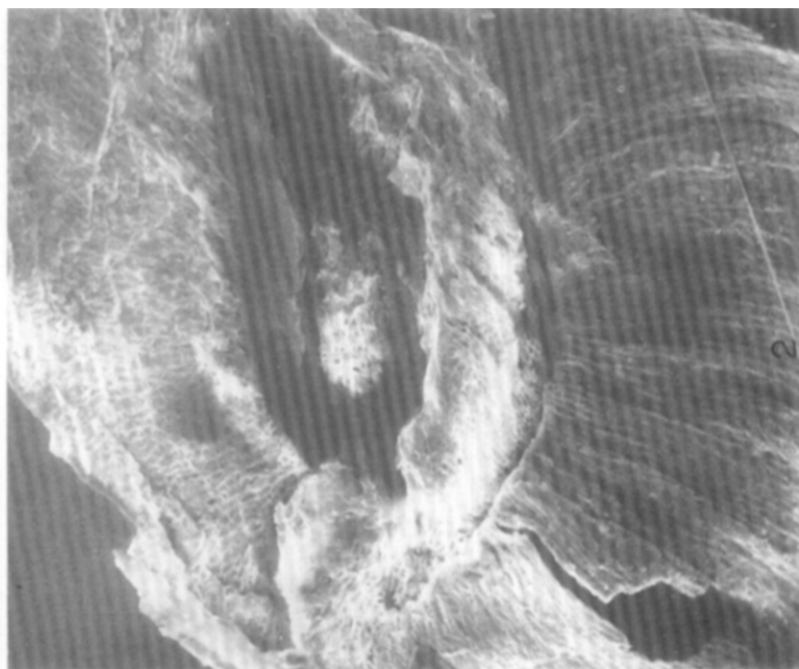


PLATE III

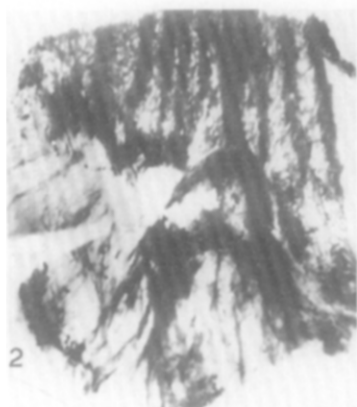
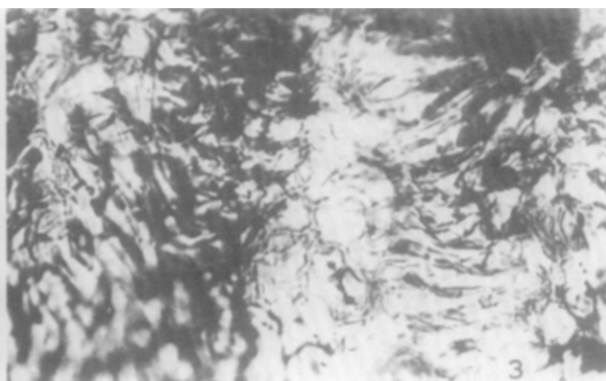
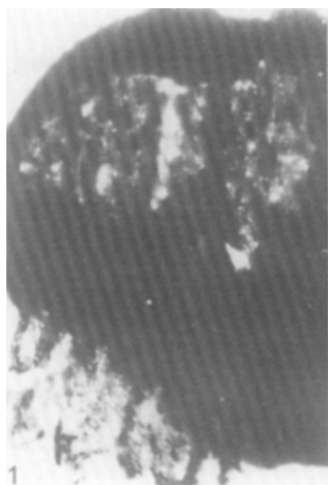


PLATE IV (p.167)

Caytonia seawardii H. Thomas from Yorkshire.

1. Micropyles of the ovules enclosed with longitudinally striated inner sac membrane, $\times 166$.
2. Contiguous micropyles of the tightly pressed ovules, $\times 395$.
3. Micropyle of another ovule from the preparation shown in 1, $\times 166$.
4. Ovule sutures on the inner sac membrane, $\times 166$.

PLATE V (p.168)

Caytonia seawardii H. Thomas from Yorkshire.

- 1—5. Nucelli showing the open (1, 3) and collapsed (2, 4) beaks and the stalked base (5), $\times 60$ and 166 .

PLATE VI (p.169)

Caytonia seeds from the Tyrma River.

1. Seed, $\times 35$.
2. Outer stone layer of palisade-like cells, $\times 166$.
3. Nucellus of the same seed, $\times 60$.
4. Nucellar beak, $\times 166$.
- 5—7. Shrunken nucellus showing dark central body, $\times 60$ and 166 .

PLATE VII (p.170)

Caytonanthus tyrmensis sp. nov. from the Tyrma River.

1. Short branch with radially arranged stamens, $\times 8$.
2. Transfer preparation of the same branch, $\times 8$.
- 3, 4. Longer branch bearing stamens on one side, $\times 4$ and 8 .
5. Valves of dehiscent anther shown in 2, $\times 16$.
6. Pollen sac, $\times 16$.

PLATE VIII (p. 171)

Caytonanthus tyrmensis sp. nov. from the Tyrma River.

1. Small anther with two unequal pairs of pollen sacs, $\times 30$.
2. The same anther, smaller pollen sacs in focus, $\times 30$.
3. The same anther showing larger pollen sac pair, $\times 30$.
- 4—7. Stamens with closed and dehiscent anthers, $\times 16$.

PLATE IV

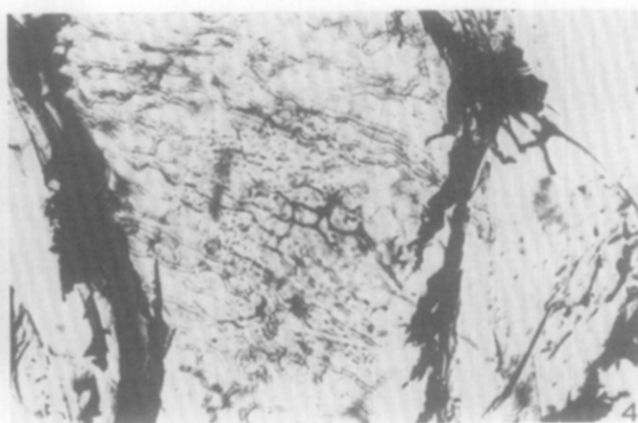
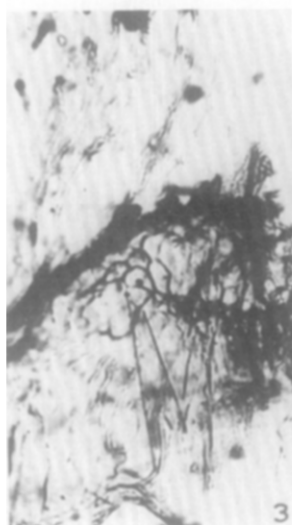
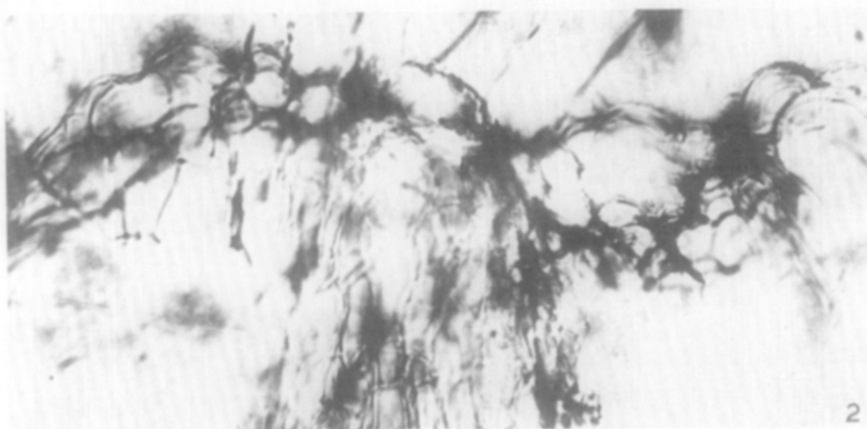
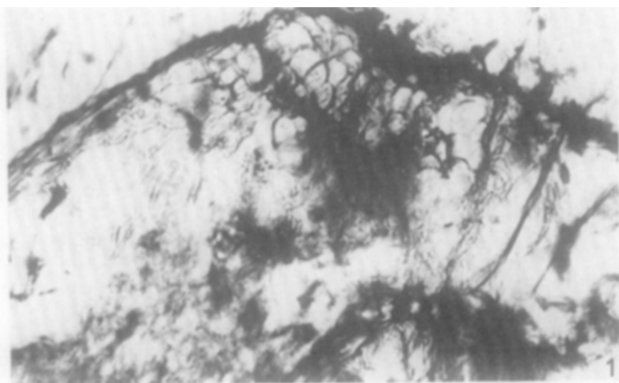


PLATE V

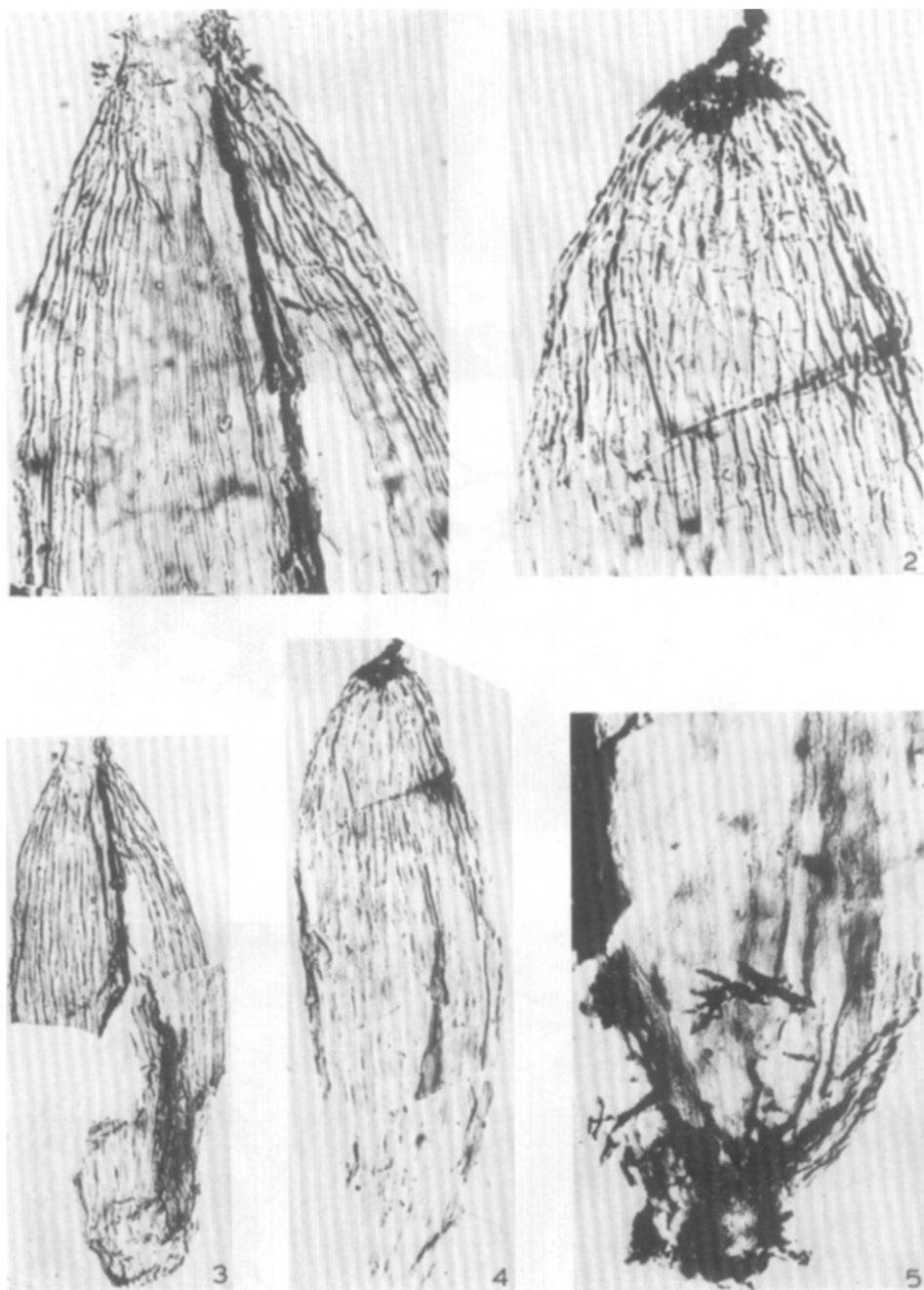


PLATE VI

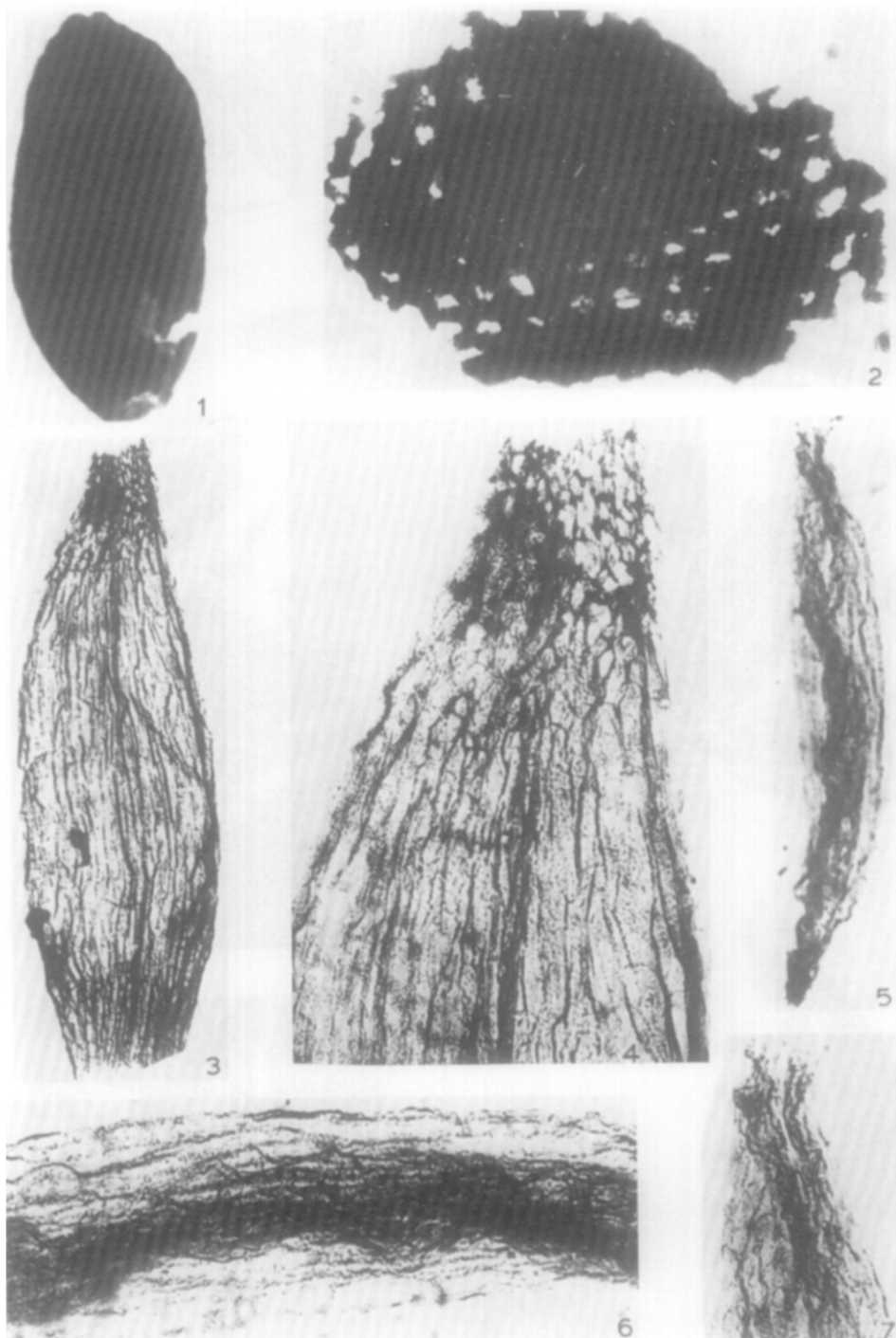


PLATE VII

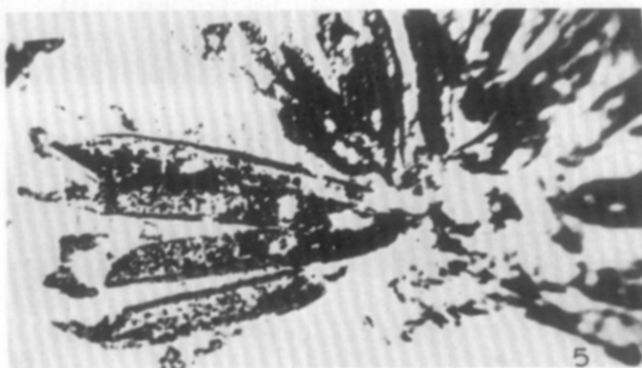
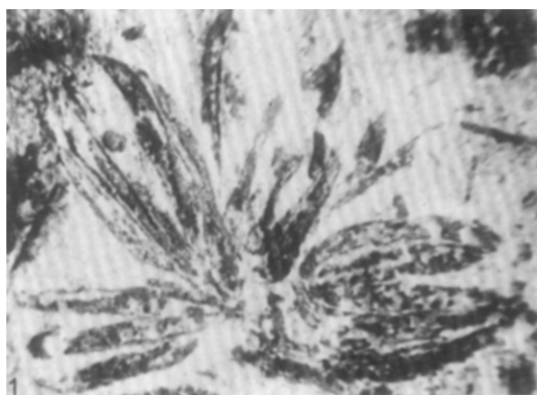


PLATE VIII



PLATE IX (p.173)

Caytonanthus tyrmensis sp. nov. from the Tyrma River.

1—3. Pollen sac cuticles, $\times 60$ and 166 .

4. Two pollen grains, distal (above) and lateral aspects, $\times 1000$.

5—12. Pollen grains, distal (5, 6) and lateral (7—12) aspects showing thick lateral walls of the corpus and the saccus ornamentation, $\times 1500$ and 2000 .

PLATE X (p.174)

Pollen grains of *Caytonanthus tyrmensis* sp. nov., SEM micrographs.

1. Lateral aspect, $\times 4000$.

2. Side view of the cappus, $\times 1000$.

3. Pollen on the pollen sac cuticle, $\times 600$.

4. Disintegrated tetrad, $\times 2000$.

PLATE XI (p.175)

Pollen grains of *Caytonanthus tyrmensis* sp. nov., SEM micrographs.

1—4. Distal face showing sulcus and leptoma, \times ca. 6000 (3) and 3500 (1, 2—4).

PLATE XII (p.176)

Pollen grains of *Caytonanthus tyrmensis* sp. nov., SEM micrographs, \times ca. 3500 .

1. Proximal face, cappus showing central depression.

2. Lateral aspect.

3. Proximal face showing corpus surrounded by equatorial saccus.

4. Proximal face showing well-defined cappus.

5. Side view of the pollen grain with folded saccus.

PLATE XIII (p.177)

Pollen grains of *Caytonanthus tyrmensis* sp. nov., SEM micrographs, \times ca. 3500 .

1. Lateral aspect showing straight corpus walls.

2. Lateral aspect showing folds of the saccus traversing the corpus.

3. Broken grain showing internal ornamentation of the saccus.

4. Proximal face with saccus partially broken, exposing smooth surface of the corpus.

PLATE IX

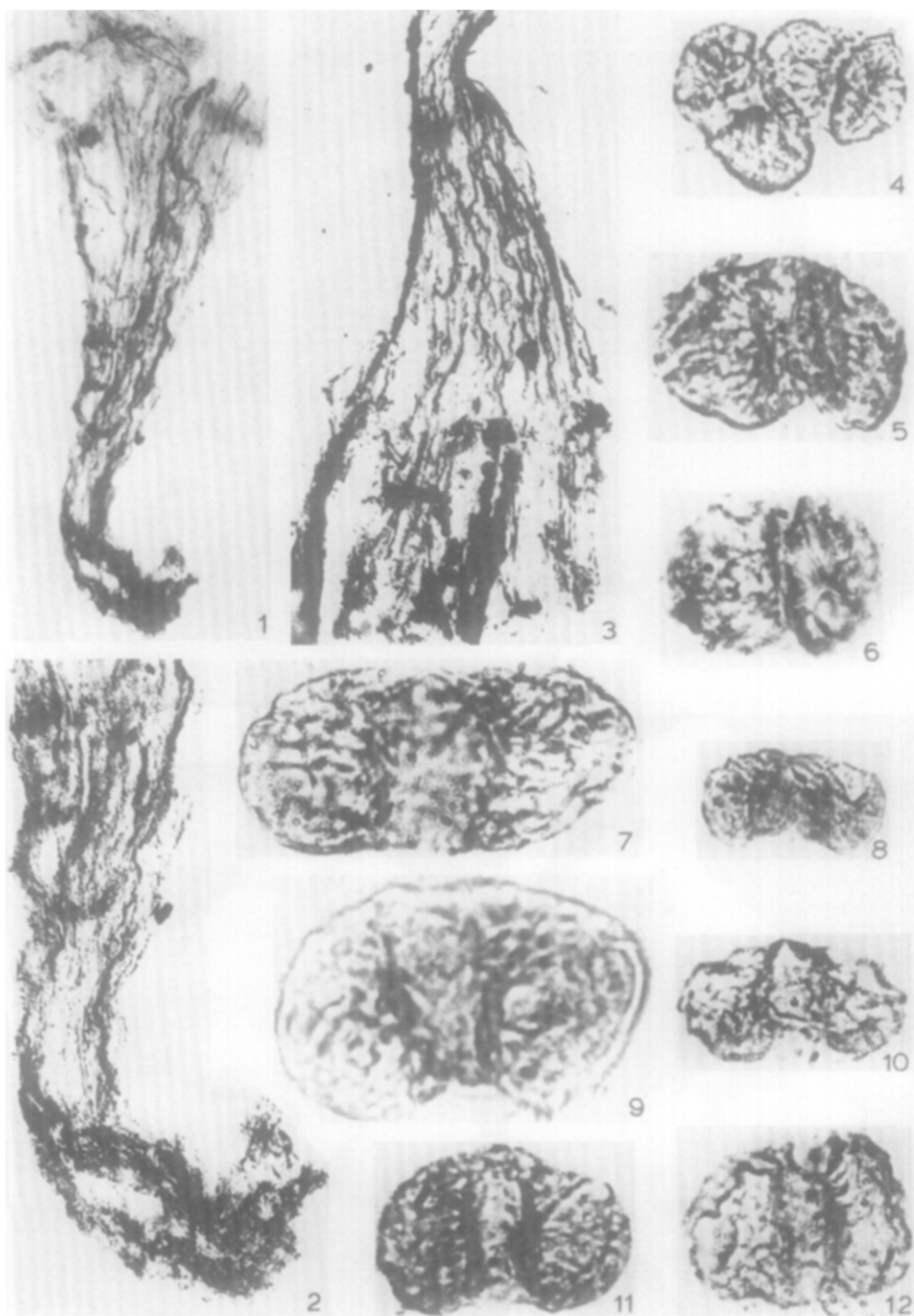


PLATE X

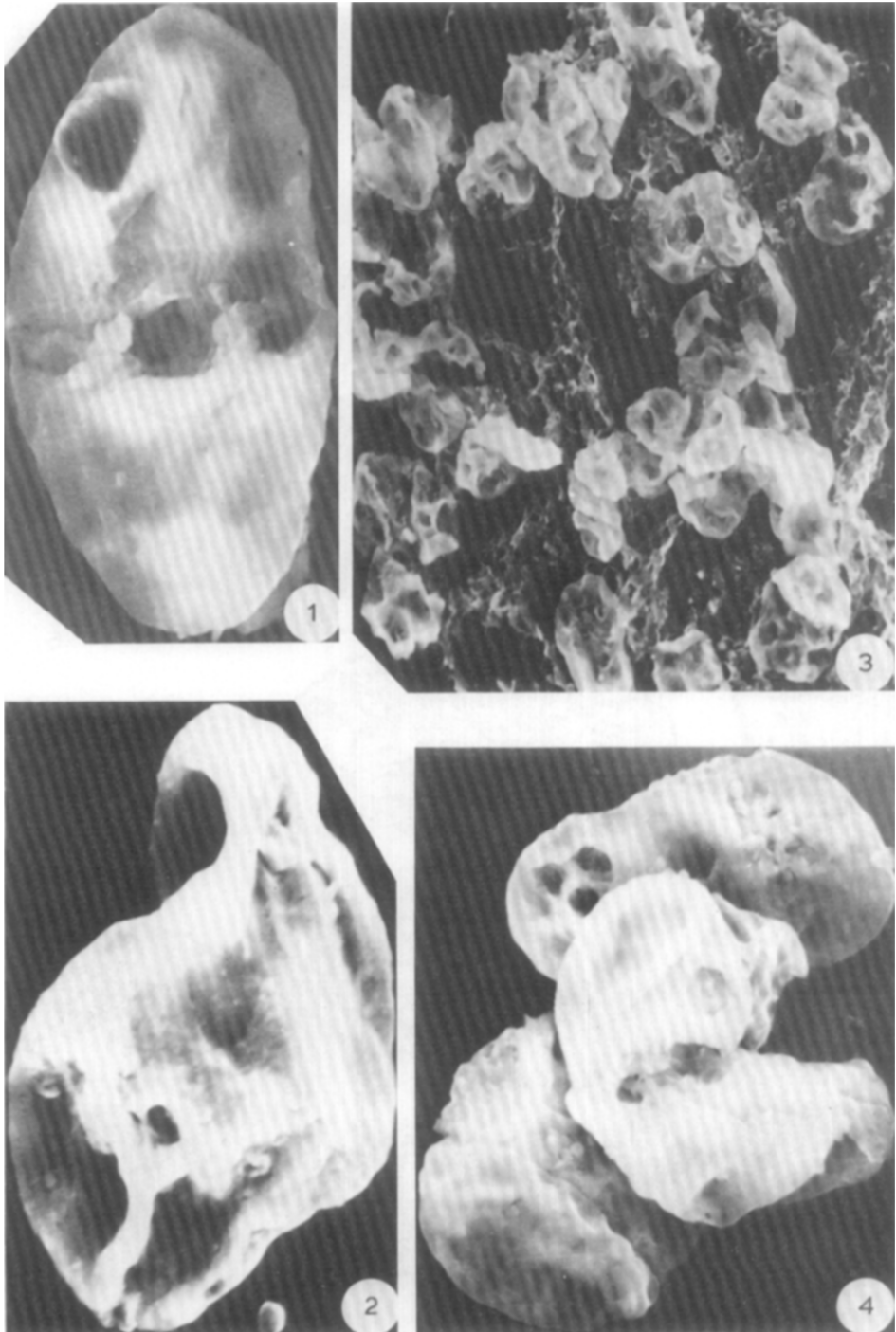


PLATE XI

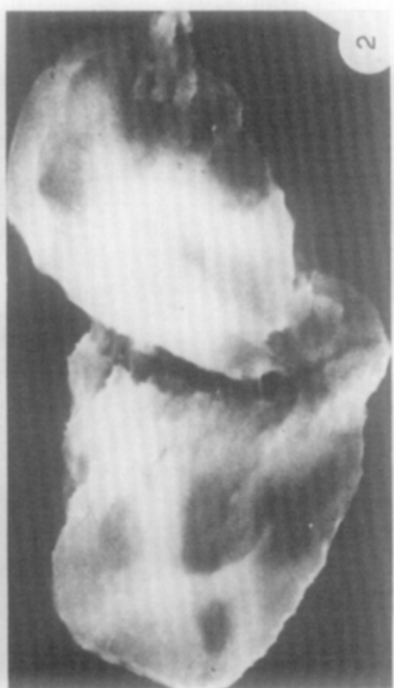
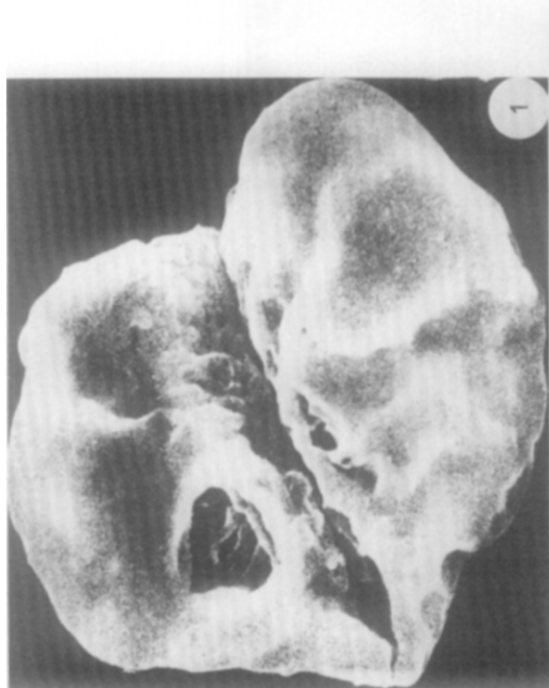


PLATE XII

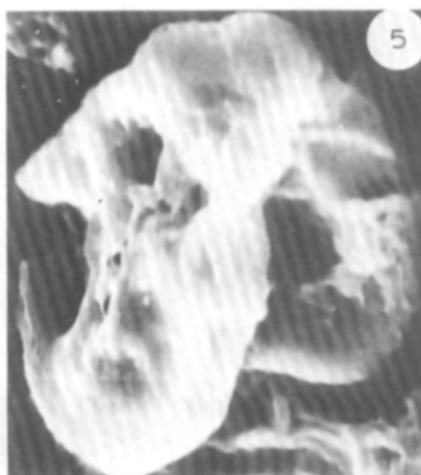
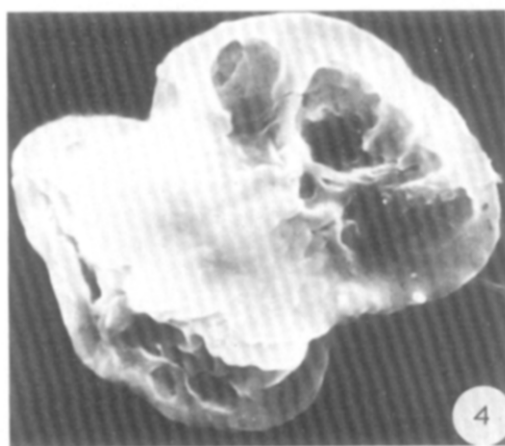
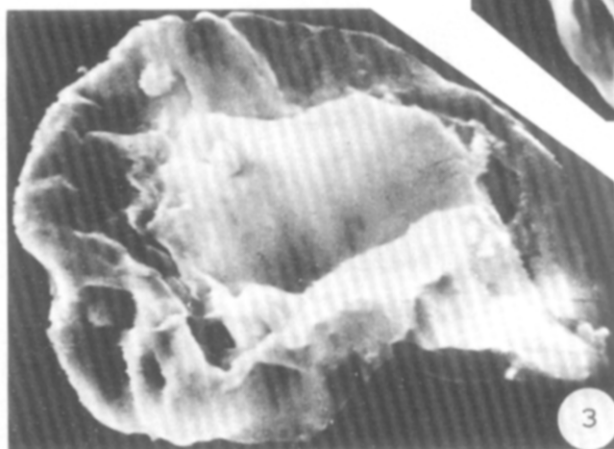
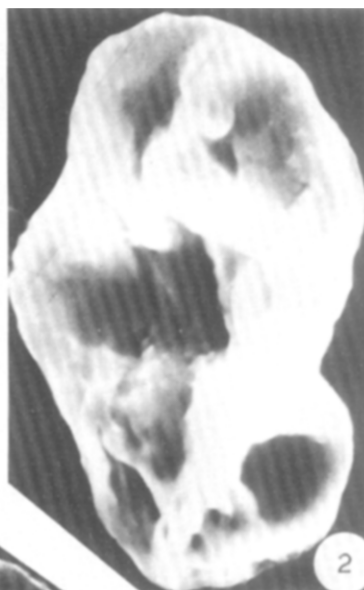
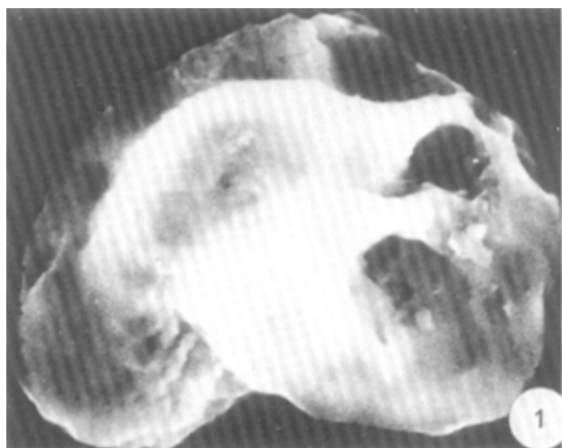
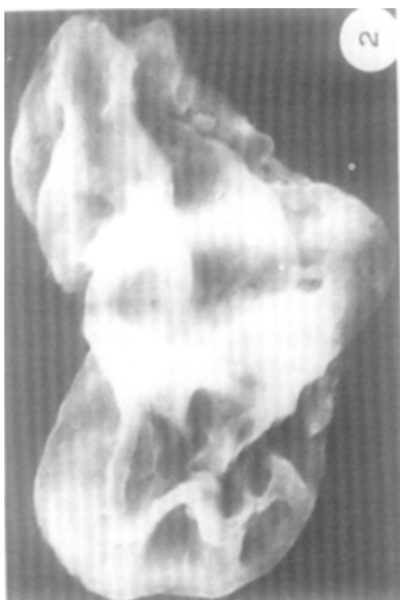
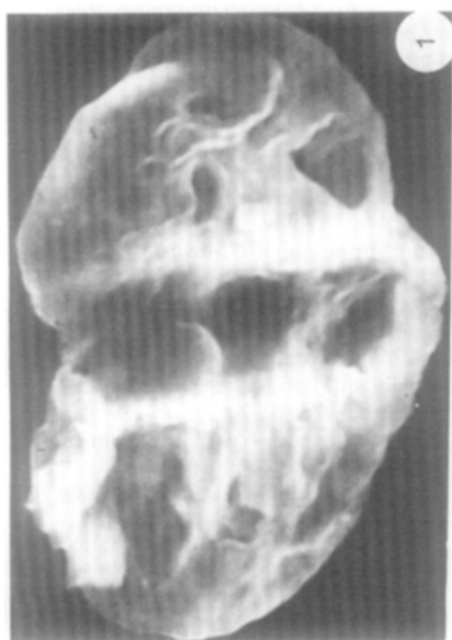


PLATE XIII



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