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Azolla and *Salvinia* species (Azollaceae and Salviniaceae, Pteridophyta), from the Caenozoic of Belgium

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Résumé

L'inventaire d'organes reproducteurs d'Azollacées et de Salviniacées, découverts dans des dépôts cénozoïques belges, est établi. La description détaillée de l'appareil mégasporique ainsi que des microsporanges et des microspores, s'accompagne de micrographies prises au microscope photonique et électronique à balayage ainsi qu'à transmission. La position stratigraphique est précisée et commentée. Une nouvelle variété de l'espèce *Salvinia natans* (L.) ALL. 1785, appelée *tuberculata*, est fondée pour des mégaspores de l'Argile de Campine (Pléistocène Inférieur), plus grandes que celles de l'espèce actuelle et caractérisées surtout par la présence de tubercules et de boursouflures allongées bien marqués sur la surface extérieure de la périne. Elles se distinguent nettement des mégaspores du Pléistocène Moyen dont la surface extérieure plus lisse ressemble davantage à celle de l'espèce actuelle.

Mots-clefs: *Azolla*, *Salvinia*, Pteridophyta, organes reproducteurs, Cénozoïque, Belgique

Abstract

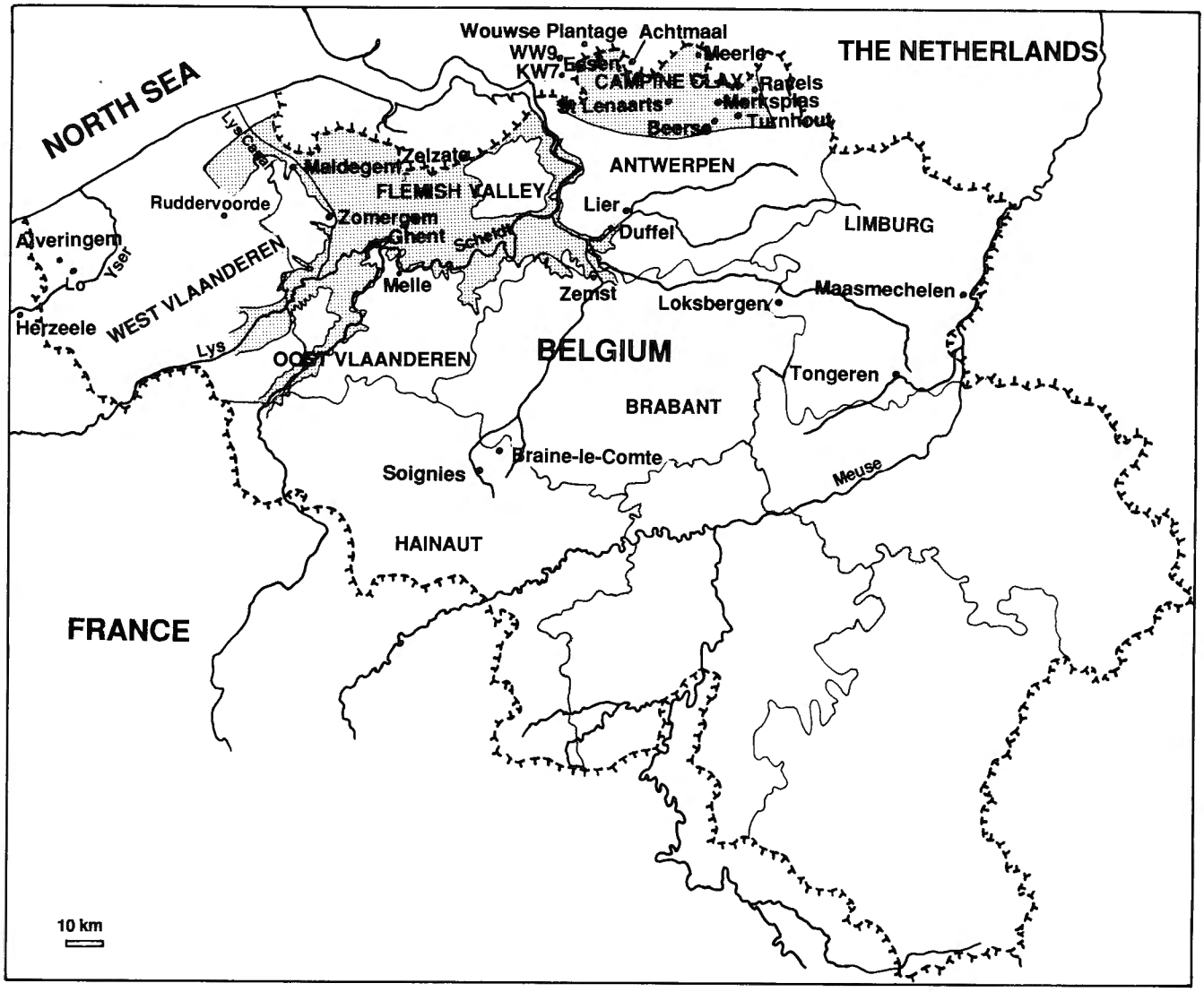
The reproductive organs of the Azollaceae and the Salviniaceae found in Caenozoic deposits of Belgium are recorded and their stratigraphic position elucidated. The megasporangia, the megaspores, the microsporangia and the microspores are described in detail and illustrated by micrographs taken with LM, SEM and TEM. A new variety of *Salvinia natans*, called *tuberculata*, is proposed for the Lower Pleistocene megaspores found in the Campine Clay. They are characterized by larger dimensions and especially by a well pronounced verrucate-rugulate sculpturing of the perine when compared to the smaller specimens discovered in the Middle Pleistocene, which also have a fairly smooth surface, resembling the megaspores of the Recent species.

Key-words: *Azolla*, *Salvinia*, Pteridophyta, reproductive organs, Caenozoic, Belgium.

Introduction

The occurrence in the Belgian Caenozoic of reproductive organs of Azollaceae and Salviniaceae has been recorded on several occasions. From the Tertiary some remnants of microsporangia containing spores of *Azolla* or *Salvinia* are reported in Upper Landenian deposits at Loksbergen (KRUTZSCH & VANHOORNE, 1977). The first discoveries in the Quaternary were confined to the Lower Pleistocene Campine Clay, where megasporangia of *Azolla tegeliensis* FLORSCH. are reported at Essen, St-Lenaarts, Beerse and Turnhout together with megaspores of *Salvinia* cf. *natans* ALL. (VANHOORNE, 1957; GREGUSS & VANHOORNE, 1961). In 1988 KASSE reported megasporangia of *Azolla tegeliensis* FLORSCH. in the Turnhout Clay, which is the upper member of the Campine Clay Formation, at Meerle, Ravels and Merksplas and also in the Netherlands near the Dutch- Belgian border at Achtmaal and in the Borings KW 7 and WW 9 (Korteven). This waterfern occurred together with *Salvinia* cf. *natans* ALL. except in the two borings where *Salvinia* cf. *natans* ALL. has not been found. On the other hand only megaspores of *Salvinia* cf. *natans* ALL. are recorded at Wouwse Plantages (Netherland). According to KASSE (1988) Meerle (Slikgat) is the only place where massulae of *Azolla tegeliensis* FLORSCH. have been discovered. Mid Pleistocene sediments yielded megasporangia and massulae of *Azolla filiculoides* LAM. at Lo (VANHOORNE, 1962 & 1968), at Melle (VANHOORNE, 1977, 1989; DE GROOTE, 1977) and Zomergem in boring B7 (PAEPE et al., 1981). In pollendiagrams massulae of the same water fern species are reported in Mid-Pleistocene deposits of the clay pit in Herzeele (Nord, France) at a few kilometers from the French-Belgian border (VANHOORNE, 1978) and at Maldegem in samples of the boring DB 6, MB 11 and MB 17 carried out in sediments filling the Flemish Valley, which according to HEYSE (1979) belong to the Eemian lithostratigraphic layer of Oostwinkel but are assigned by DE GROOTE (1977) to the Hoxnian on palynological grounds. Studying the boring BH 350 at Alveringen (formerly Stavele), PONNIAH (1977) found microsponrangia of *Salvinia* in peaty clay, considered to be deposited in the Holsteinian. The two megasporangia of *Azolla filiculoides* LAM. discovered in Eemian sediments at Zelzate (PAEPE & VANHOORNE, 1967) are probably reworked. Eemian peat layers deposited in the Flemish Valley at Ghent and Zemst yielded many magaspores of *Salvinia natans* ALL. (PAEPE & VANHOORNE, 1967; VANHOORNE, 1971).

Surprisingly the three recorded waterfern species are also found in Weichselian periglacial deposits. The finds



Text-fig. 1 — Map showing the Flemish Valley, the Campine Clay area and the localities where reproductive organs of Caenozoic Salviniales were found in Belgium and in close contiguous areas in Northern France and the Netherlands.

are located at Duffel and Lier, where megasporangia of *Azolla filiculoides* LAM. and megaspores of *Salvinia* cf. *natans* ALL. were found, at Ruddervoorde and Soignies (Neufvilles), where respectively only *Azolla filiculoides* LAM. and *Salvinia natans* ALL. were recorded and at Ghent and Duffel, where megasporangia of *Azolla tegeliensis* FLORSCH. were encountered. At Braine-le-Comte a megasporangium is assigned to *Azolla* sp. (VANHOORNE, 1957; PAEPE & VANHOORNE, 1967). Their presence is interpreted by reworking.

All these data appear in previously published plant lists but without any description nor illustration except for the Upper Landenian microsporangia of Loksbergen, which are represented by five pictures (KRUTZSCH & VANHOORNE, 1977 pl.9. figs.7-11), for the massulae of *Azolla filiculoides* LAM. from Herzeele, represented by two pictures (VANHOORNE, 1957, pl.3, figs.36-37), for a megasporangium of *A. filiculoides* from Duffel, represented in VANHOORNE, 1957, fig.8 on pl.3, and for a megasporangium of *A. tegeliensis* and a megaspore of *Salvinia* cf. *natans* both from Essen (VANHOORNE, 1957, pl.3, figs.9 & 10). New discoveries and the opportunity of using the TEM and SEM led to this paper which gives an illustrated account of the different taxa of Azollaceae and Salviniaceae found so far in Caenozoic deposits of Belgium and some limitrophe areas of France and the Netherlands very close to the Belgian border.

Taxonomy

Division Pteridophyta
Order Salviniales
Family Azollaceae

Genus *Azolla* LAMARCK 1783

Section *Azolla*
— *Azolla filiculoides* LAM. 1783
— *Azolla filiculoides* LAM. var. *rubra* (R. BR.) STRASBURGER 1873
Section *Rhizosperma*
— *Azolla nikitinii* DOROFEEV 1955 emend. FRIIS 1977
— *Azolla tegeliensis* FLORSCHÜTZ 1938 emend. BERTELSEN 1972

Family Salviniaceae

Genus *Salvinia* ADANSON 1763
Section *Salvinia*
— *Salvinia natans* (LINNAEUS 1753) ALLIONI 1785
— *Salvinia natans* (LINNAEUS 1753) ALLIONI 1785 var. *tuberculata* nov. var.
Section *Cerebrata*
— *Salvinia cerebrata* NIKITIN 1948 ex DOROFEEV 1955

Genus **Azolla**

In the genus *Azolla*, the fossil female reproductive structures have been referred to megasporangia because they contain all the components of a megasporangium. Indeed these female reproductive organs are composed of the functional and abortive megaspores, the perine and the homologous pseudocellular mass of the floats, both of tapetal origin, and a membrane covering the apex of the float apparatus, which is a remnant of the sporangial wall. Only that part of the sporangial wall covering the rest of the float apparatus and the perine of the megaspore is lacking. In my opinion there is no objection in palaeobotany in using the name of the complete organ if part of a component is missing. In this way it was possible to avoid the term megaspore apparatus used in the literature, which is an unwieldy word especially when it is used in the plural form.

Azolla nikitinii DOROFEEV 1955 emend. FRIIS 1977
Pl. 1, Figs. 2-6; Pl. 2, Figs 1-7; Pl. 3, Figs. 1-8

LOCALITY AND STRATIGRAPHYY
Almost six thousand megasporangia were isolated from a thin lignite layer intercalated in the clay of the clay pit "Our Lady" of the tile works Francart, situated to the north of the city of Tongeren (Limburg). The samples were collected in 1955 at a depth of about 2 to 3 m below the surface. The lignite horizon occurred as a thin seam separating the underlying lignite sands from the upper compact clay. This clay was overlain by loam, deposited in the Weichsel Pleniglacial. The lignitic sands overlie blue-green compact clay, which lies on sands belonging to the Sands of Neerrepen. The whole complex between the surface loam and the sands of Neerrepen is assigned to the Henis Clay, which is considered to represent the lower part of the uppermost Tongrian (Pl.1, Fig.1). A review of the stratigraphy of the Tongrian is given by ROCHE & SCHULER (1976), who made a palynological study of the same lignite sampled in 1966 and 1970 in the same clay pit. They conclude that the lignite contained a typical Oligocene flora with subtropical character. VAN DER BURGH (1971) described some pieces of silicified wood in the same clay pit as *Taxodioxylon gypsaceum* (GÖPPERT) KRÄUSEL, which is known in Belgium from the Eocene to the Upper Tertiary.

Eighty megasporangia were also found by washing a lignitic sample of the boring nr 204, sheet Opoeteren of the topographic map of Belgium, located at Maasmechelen (Limburg). The sample stored at the Belgian Geological Survey, was taken in the lagoon facies of the uppermost Tongrian at 191 m depth. The description and stratigraphical interpretation of the part of the boring between 190 and 196 m by M. GULINCK is available for consultation in the archives of the Belgian Geological Survey.

DESCRIPTION OF THE MEGASPORANGIA
The megasporangia have a broad ovoid shape. They are composed of a semi-globular, tubercular, basal part, which contains the megaspore and a rounded, broadly conical, apical part, composed of nine floats, which is called the swimming apparatus (Pl.1, Fig.2).

Total length inclusive floats
The polar axis was measured on eighty specimens. The average length was 369 μm, the extreme values being 238 μm and 442 μm.

Diameter
The mean diameter of seventy nine specimens was 270 μm, ranging from 215 μm to 330 μm.

Colour
Megasporangia display a dark brown colour, while the floats are lighter brown. The membrane on the top of the floats, which is the remaining part of the sporangial wall, is also dark brown.

Megaspore wall
The megaspore wall is composed of an inner exine and an outer perine, connected to each other by hairs, which are considered to represent the endoperine (Pl.1, Fig.3). The exine is often separated from the perine proximally (Pl.2, Fig.7). Thickness: average of fourteen measurements: 14 μm, the minimum being 11 μm and the maximum 17 μm.

Exine
Observed in LM the exine appears to be radially striped (Pl.1, Fig.4). This is also the case by examination in TEM at low magnification (Pl.1, Fig.5), but at high

magnification it looks porous with minute cavities of irregular shape, the longest of which attains 1,4 μm (Pl.1, Fig.6). This means that the tubes are radially orientated but very sinuous.

Perine

The perine consists of an inner zone, the endoperine which is composed of a tangle of small threads (Pl.2, Fig.1). In this mass of threads arise centrifugally circular to oblong alveoles, which become greater outwards (Pl.2, Fig.2). This alveolate zone may be considered as the mesoperine, which can be divided into an inner mesoperine **a** with small alveoles and an outer mesoperine **b** with large alveoles, although there is no sharp boundary between both (Pl.2, Fig.3). The length of the alveoles varies between 0,8 μm and 13 μm. The mesoperine is covered by a homogeneous, solid substance, which occurs as a thin layer from which arise columns or baculae, which support irregular, dome-shaped, flattened knobs arranged in a tectum perforated with irregular, round and oblong openings in the grooves separating the knobs (exoperine) (Pl.2, Figs.3 & 4). The surface of the tectum is verrucate to rugulate (Pl.2, Fig.4). The diameter of the verrucae varies between 0,2 μm and 0.4 μm. The tectum displays in section small cavities and bigger alveoles, which may be part of the openings at the surface of the tectum (Pl.2, Fig.3). Large protuberances of different shape develop from the tectum, especially at the distal side of the megaspore (average diameter at the base of the protuberance: 31.3 μm; minimum: 14.5 μm; maximum: 47.9 μm) (nine measurements) (Pl.1, Fig.4 & Pl.2, Fig.5). The average height of the protuberances is 17.5 μm (minimum: 10 μm; maximum: 26 μm) (Pl.2, Fig.6).

Apex of the megaspore

The apex of the megaspore consists of a collar and a column (Pl.3, Fig.1).

The collar is a ring-like structure formed at the proximal part of the megaspore by extension of the perine. It is separated from the adjacent floats and the megaspore by a groove. Because this groove is filled with hairs (Pl.3, Fig.2) and other exoperine material (Pl.3, Fig.3), the collar is externally invisible under incident light. The collar is an extension of the perine (Pl.3, Fig.4), in which the mesoperine has undergone a great development. It consists mainly of mesoperine **b**, in which the lacunae are much larger than in the mesoperine **b** of the megaspore wall and may attain a length of 12 μm (Pl.3, Fig.5). The mesoperine **b** is covered by the exoperine, to which belong also the hairs connecting the collar with the floats and the megaspore (Pl.3, Fig.4).

The column is the central projection of the apical, proximal part of the perine around the megaspore (Pl.3, Fig.1). It has a triradiate structure. Its base passes laterally into the collar (Pl.3, Fig.3). The column is composed of mesoperine **a** in the centre, surrounded by mesoperine **b**, which is covered by a layer of exoperine, from which arise the hairs, connecting the column with the floats (Pl.3, Fig.7). The column may attain one third to one half of the total height of the swimming apparatus (Pl.3, Fig.1).

The swimming apparatus

The swimming apparatus consists of nine floats, arranged in two tiers, an upper tier of three and a lower tier with six (Pl.1, Fig.2). The floats are mainly composed of mesoperine **b**, in which the alveoles are slightly larger than those in the collar (Pl.3, Fig.5). An opaque centre containing presumed remains of abortive megaspores is visible in the centre of each float (Pl.2, Fig.7 & Pl.3, Fig.8). The floats are connected by a dense mass of hairs to the column and the collar (Pl.2, Fig.7). The development of these hairs belonging to the exoperine, is very slight between the floats of the upper and lower tier and is almost absent between the adjacent surfaces of the floats of the lower tier (Pl.2, Fig.7). The apex is composed of a dense mass of hairs arising at the top of the uppermost floats and spreading down to connect with the column. Over the apex of the float apparatus there is a dark brown shining membrane (Pl.3, Fig.6).

The characteristics of the megasporium correspond to those described by DOROFEEV (1955) and FRIIS (1977), but all the measured data are larger.

Azolla tegeliensis FLORSCHÜTZ 1938 emend. BERTELSEN 1972, Pl. 4., Figs. 1-6

LOCALITY AND STRATIGRAPHY

A great number of megasporangia of *Azolla tegeliensis* FLORSCH. have been found in peaty horizons occurring at the top and the base of clay deposits belonging to the Campine Clay located in the north of Belgium. Only in the east can two clay layers be clearly distinguished because they are separated by a sand deposit, displaying cryoturbation phenomena. The lowermost clay, the Rijkevorsel Clay, has been correlated with the Tiglian; the uppermost clay, the Turnhout Clay, with the Waalian, whereas the intermediate sand, the Sand of Beerse, is believed to have been deposited in the Eburonian (PAEPE & VANHOORNE, 1970). Another stratigraphic interpretation is given by KASSE (1988), who assigned both clay members to the Tiglian, respectively to the TC3 and the TC6, and the intermediate sand to the TC4 interstadial of the Tiglian. In the clay pits located more to the west only one unit of clay can be observed so that it is difficult to determine if the clay belongs to the lowermost or uppermost member, especially as the clay is generally lacking fossils.

DESCRIPTION OF THE MEGASPORANGIA

The megasporangia have an elongate, ovoid form and are composed of a subspherical, basal part containing the megaspore, and a conical swimming apparatus,

rounded at the top. The swimming apparatus consists of nine floats arranged in three groups each with three floats (Pl.4, Fig.1).

Total length inclusive floats
Measurements carried out on eighty specimens gave a mean length of the polar axis of 554 μm, ranging from 442 to 624 μm.

Diameter
The mean diameter obtained from the same set of eighty specimens amounts to 376 μm with extreme values of 237 μm and 426 μm.

Colour
Megasporangia display a brown colour

Perine
The surface of the perine displays a semi-tectum composed of rugulate, verrucate elements in which sporadically small pits occur (Pl.4, Fig.2). The semi-tectum is dotted by evenly distributed, round or oval protuberances, which seem to be formed by local excrescence and fusion of some sculpturing elements (Pl.4, Figs. 2 & 3). Their diameter or length is 3 μm to 7 μm and the breadth 2 μm to 4 μm. Their surface is smooth but the contour of the fused, sculpturing elements is still discernible (Pl.4, Fig.2). No collar separates the floats from the basal part of the megasporangium.

The swimming apparatus
The swimming apparatus is composed of a central, triradial column, which arises from the proximal part of the megaspore and to which the discoidal floats are attached in three groups by hairs. Each group comprises two lower floats and an upper float. The surface of the floats is foveolate. The pits of irregular shape have a diameter of 1 μm to 4 μm (Pl.4, Figs.4 & 5). A dark brown, shining membrane considered by KEMPF (1969) as a remain of the sporangiodermis (sporangial wall) covers the top of the swimming apparatus. The hairs are clearly visible on the surface in the wedges situated between the three groups of floats (Pl.4, Fig.5). These hairs spread downwards over the megaspore body and some have coiled ends (Pl.4, Fig.6). No massulae have been found attached to the megasporium.

Azolla filiculoides LAM. 1783, Pl. 5, Figs. 1-6

LOCALITY AND STRATIGRAPHY
In Belgium megasporangia and massulae of the extant species *Azolla filiculoides* LAM. were first discovered at Lo in the Pleistocene Yser Estuary, where they were isolated from a peat layer of Middle Pleistocene age, occurring at the base of a marine shell crag (VANHOORNE, 1962). Later on the same reproductive organs were encountered in the Pleistocene Flemish Valley at Melle in two superposed peat deposits separated by a clay layer (VANHOORNE, 1987) and in cores of several borings carried out prior to the broadening of the Lys canal (PAEPE *et al*, 1981). A Holsteinian age may be assigned to these finds except perhaps at Lo, where a Cromerian age cannot be exluded on palynological grounds and at Melle, where *A. filiculoides* LAM., occurring in the lowermost peat of Holsteinian age, reappeared in the uppermost peat, probably deposited at the beginning of the Wacken Interstadial belonging to the Saalian Glacial.

In Northern France near the French-Belgian border massulae of *Azolla filiculoides* LAM. were found in pollen slides from the Formation of Herzeele at Herzeele probably covering a timespan from the Cromerian to the end of the Holsteinian (VANHOORNE, 1978; VANHOORNE & DENYS, 1987).

DESCRIPTION OF THE MEGASPORANGIA
The megasporangia of *Azolla filiculoides* LAM. consist of a globular basal part, which contains the megaspore, and a rounded, conical, apical part, composed of three floats, which is known as the swimming apparatus (Pl.5, Fig.1).

Total length inclusive of the swimming apparatus
The measurements of the polar axis of ten specimens from Melle result in a mean length of 277 μm, the extreme values being 240 μm and 365 μm. By measuring sixty specimens isolated from the peat and the superposed loamy layer at Lo, an average of 255 μm was obtained with extreme values fluctuating between 190 μm and 310 μm.

Diameter
The measurements of the same set of sixty specimens from Lo yield a mean maximum breadth of 199 μm with as extreme values 170 μm and 230 μm. On the other hand the measurements of the same ten specimens originating from Melle, already used for the measuring of the length, result in an average of 211 μm, the extreme values being 170 μm and 230 μm.

Colour
The megasporangia are pale grey but the apex of the swimming apparatus is covered by a dark brown cap.

Perine
The perine has a verrucate surface, the diameter of the individual verrucae varying between 20 μm and 30 μm. Hairs arising from these tubercles form a weft uniting the verrucae laterally and covering the whole basal part. These hairs extend to the lowermost edge of the collar (Pl.5, Fig.2) but are not so abundant as on a modern specimen of the variety *rubra* STRASB. illustrated by MARTIN (1976).

Swimming apparatus
The swimming apparatus consists of a central triradial column and a collar, to which the three floats are attached by hairs. The space between the floats is also filled with hairs, which are 0.3 μm to 0.7 μm broad and intertwined (Pl.5, Fig.3). Their surface is slightly wrinkled (Pl.5, Fig.4). The rugged surface of the floats displays scattered perforations, the diameter of which varies between 0.1 μm and 1 μm. The apex of the swimming apparatus is covered by a membrane, which is considered by BERTELSEN (1972) as a part of the indusium. MARTIN (1976), however, claims that it is formed from cells of the sporangial wall. It is attached to the apex of the floats by a dense mass of hairs, which spread down to connect with the column.

DESCRIPTION OF THE MASSULAE AND THE MICROSPORES
The massulae found in slides from Melle prepared by acetolysis for pollen analysis have an irregular oval outline. The major axis measured in LM has a mean length of 288 μm and the minor axis 233 μm. The extreme values are 161 μm and 345 μm for the major axis and 147 μm and 303 μm for the minor axis (20 measurements). A specimen from Lo measured in SEM was smaller, its major axis being only 153 μm (Pl.5, Fig.5). In most cases the massulae contain, embedded in a pseudocellular mass, microspores which are laevigate, trilete and have a circular amb. Their mean diameter is 35 μm with extreme values of 23 μm and 58 μm (99 measurements). The attached anchor-shaped glochidia (Pl.5, Fig.5) have an average length of 73 μm with extreme values of 46 μm and 100 μm (10 measurements), whereas the maximum breadth averages 10 μm with extreme values varying from 7 μm to 15 μm. They catch in the hairs of the perine of the megasporangium (Pl.5, Fig.6). Some glochidia do not display any septation but others have at least four septa. This leads to the conclusion that also the variety *rubra* thrived in the Mid Pleistocene marshes of Belgium.

Genus **Salvinia**

Salvinia cerebrata NIKITIN 1948 ex DOROFEEV, 1955
Pl. 6, Figs. 1-9, Pl. 7, Figs. 1-6

LOCALITY AND STRATIGRAPHY
Besides *Azolla nikitinii* more than fifteen hundred megaspores and a great number of microsporangia of *Salvinia cerebrata* have been found in the lignite encountered in the tile works Francart at Tongeren (see p.233). From the lignitic core at 191 m depth of the boring 204 situated at Maasmechelen (p.230) one hundred and eleven megaspores and a large number of microsporangia of *Salvinia cerebrata* have also been isolated.

DESCRIPTION OF THE MEGASPORES
The megaspores are egg-shaped, often flattened to tetrahedral with four convex planes. The perine of the proximal part is transformed into three, initially closed, valves, which open at germination. Then the triradiate column can be seen through the open valves. The sutures, looking like a trilete scar correspond to the edges between three sides of the tetrahedron (Pl.6, Fig.1). Often they are not conspicuous. At the surface the perine developed as a foamy mass, organized in pronounced, irregular ridges, similar to the rugulate structure of some pollen grains such as *Ulmus* (Pl.6, Fig.2). In some specimens the rugulate perine is missing on some parts of the surface.

Total length (Polar axis)
Measurements carried out on thirty specimens result in an average length of the polar axis of 337 μm, the extreme values being 237 μm and 395 μm.

Diameter
The mean diameter obtained from measurements on the same thirty megaspores is 313 μm but ranging from 268 μm to 355 μm.

Colour
White to brown.

Ray length of the trilete scar of the perine
Measurements on twenty specimens give a mean length of 13,5 μm, the extreme values being 7.5 μm and 22.5 μm.

Wall
The megaspore wall is composed of an inner exine and an outer perine (Pl.6, Fig.3). Sometimes some remnants of the intine are preserved (Pl.6, Fig.4). The megaspore wall is surrounded by remains of the sporangial wall, which is best preserved in the grooves between the winding ridges (Pl.6, Fig.3). The total thickness ranges from 24 μm to 117 μm (Pl.6, Fig.5).

Exine
The dense exine displays a multitude of small, more or less radially oriented tubules of 0.02 μm diameter, the concentration of which is the highest in the middle part of the exine (Pl.6, Fig.6). Larger perforations of irregular shape, the diameter of which ranges between 0.17 μm and 1 μm (artefacts?), are much less frequent in the inner half of the exine (Pl.6, Figs.4 & 6). The mean thickness of the exine resulting from eighteen measurements amounts to 6.1 μm showing extreme values of 5.0 μm and 12.5 μm.

Perine
The perine can be subdivided into two zones: an inner zone, the endoperine and an outer zone, the mesoperine, which can be further subdivided into an inner mesope-

rine **a** and an outer mesoperine **b**. The total thickness ranges between 27.5 μm and 97.5 μm (Pl.6, Fig.3).

Endoperine
The endoperine consists of densely intertwined threads with a diameter of 0.1 μm to 0.15 μm. The threads are attached to the exine. The average thickness resulting from twenty five measurements amounts to 3.6 μm but ranging from 1.6 μm to 6.5 μm (Pl.6, Fig.7).

Mesoperine
The mesoperine is composed of the same threads as the endoperine but they are partly fused together to produce a perforated membrane around the alveoles. These alveoles, small in the mesoperine **a**, have a diameter ranging between 0.3 μm and 5.3 μm. The thickness of the mesoperine **a** varies between 14 μm and 30 μm (Pl.6, Fig.8). The limit between mesoperine **a** and **b** is determined by the appearance in the outer part of the mesoperine of larger alveoles separated from one another by a mass of intensely coiled threads (Pl.6, Fig.9). The diameter of these alveoles, attaining exceptionally 19 μm does generally not exceed 11 μm. The thickness of the mesoperine **b** ranges between 6 μm and 23 μm.

The characteristics of these megaspores correspond with those described by DOROFEEV (1955) and FRIIS (1977). However all the comparable measurements are smaller. This is also the case when a comparison is made with the figures in KEMPF (1971).

DESCRIPTION OF THE MICROSPORANGIA AND THE MICROSPORES
The microsporangia are spheroidal, mostly ellipsoidal and sometimes discoidal due to flattening. The outline is slightly angular (Pl.7, Fig.1).

Diameter
The mean diameter of the major axis of fifty microsporangia measured with a dissecting microscope is 212 μm, the extreme values being 160 μm and 260 μm. In addition twenty three microsporangia found in a slide prepared by acetolysis for pollen analysis (Pl.7, Fig.2) were measured in LM. The average major axis is 264 μmm, varying between 151 μm and 383 μm, the average minor axis is 213 μm, while fluctuating between 127 μm and 350 μm.

Perine
The rugged outer surface of the microsporangial wall is foveolate with perforations ca 0.8 μm to 1.3 μm in diameter (Pl.7, Fig.3), which connect with the alveoles of the underlying pseudocellular mass, considered by KEMPF (1971) to be the equivalent of the megasporial perine. This pseudocellular mass is characterized by a honeycombed structure, the alveoles of which have a diameter varying between 1 μm and 8 μm (Pl.7, Fig.4). Within the pseudocellular mass bigger cavities occur, some of them containing a microspore, the others being empty.

Microspores
The microspores are laevigate, trilete with circular amb (Pl.7, Figs. 5 & 6). Measurements in LM of the equatorial diameter of twenty specimens yield a mean value of 32 μm, while fluctuating between 28 μm and 35 μm. Comparison with the figure of 25 μm recorded by FRIIS (1977) might suggest that the microspores had swollen as a result of the acetolysis treatment of the material. Each arm of the trilete mark has an average length of 13 μm, the extreme values being 6 μm and 23 μm (24 measurements). The exine is composed of an ectexine and an endexine, both 0.5 μm thick.

Salvinia natans (LINNAEUS 1753) ALLIONI 1785, Pl. 8, Figs. 1-7; Pl. 9, Figs. 1-4

LOCALITY AND STRATIGRAPHY
Megaspores of *Salvinia natans* have been found in the Lower Pleistocene Campine Clay situated in the northern part of the province Antwerpen, together with megasporangia of *Azolla tegeliensis*. Concerning the stratigraphic position of the Campine Clay, the reader is referred to the discussion under *Azolla tegeliensis* (p.232).

Megaspores and microsporangia of *Salvina natans* occurred also in Mid Pleistocene deposits at Lo and Melle and in Eemian peat at Ghent (Oost-Vlaanderen) and Zemst (Brabant). The stratigraphic position of the Mid Pleistocene specimens is made clear on p.233.

Finally some megaspores of *Salvinia natans* were discovered in Weichselian glacial deposits in the Nethe valley at Duffel and Lier (Antwerpen) and in the Clypot quarry at Neufvilles (Soignies, Hainaut). The occurrence of *Salvinia natans* in Weichselian sediments would appear to be due to reworking.

DESCRIPTION OF THE MEGASPORES
The megaspores of *Salvinia natans* are oval in outline with a rounded distal part and a more acute, proximal part carrying the three valves surrounding the triradiate column developped on the exine of the megaspore (Pl.8, Fig.1). The apex corresponding to about 1/3 of the total length of the megaspore is clearly discernible from the rest of the megaspore (Pl.8, Fig.2).

The surface of the megaspore is sculptured with closely spaced verrucae or rugulae, separated from one another by pits and grooves. This ornamentation is more pronounced on the megaspores originating from the Lower Pleistocene Campine Clay (Pl.8, Fig.2) than on those extracted from Mid-Pleistocene sediments (Pl.8, Fig.3). Exceptionally remains of the sporangial wall may be preserved in the pits and grooves.

Total length
Measurements of fifty megaspores collected in the Middle Pleistocene sediments at Melle give an average length of 490 μm, while ranging from 350 μm to 590 μm.

Fifty megaspores from the Lower Pleistocene Campine Clay at Essen have an average length of 590 μm, fluctuating between the extreme values of 440 μm and 730 μm.

Diameter
The average equatorial diameter of the same fifty megaspores amounts to 410 μm, oscillating between the extreme values of 320 μm and 530 μm for the Middle Pleistocene specimens and 480 μm with extreme values of 350 μm and 620 μm for the Lower Pleistocene specimens.

Colour
The megaspores of Mid-Pleistocene age are white grey, whereas the Lower Pleistocene specimens seem to be a little more yellowish. This impression is perhaps due to the occurrence of black material in the pits and grooves.

Exine
The exine is composed of a dense mass of threads disposed in various directions and in close apposition at the inner rough surface but still displaying some pores (Pl.8, Fig.4). At a lower magnification the threads appear more radially orientated (Pl.8. Fig.5). Thickness: 2 to 2.5 μm (Mid-Pleistocene megaspores from Melle), 2 to 4.1 μm (Lower Pleistocene megaspores from Essen).

Perine
The total mean thickness of the perine is 43.2 μm, varying between 30.5 μm and 72.4 μm for the Lower Pleistocene specimens from Essen and 35.6 μm, varying between 29.1 μm and 41.0 μm for the Mid Pleistocene megaspores from Melle.

The perine can be subdivided into an inner zone, the endoperine and an outer zone, the mesoperine (Pl.8, Fig.7).

Endoperine
The endoperine consists of intertwined threads connecting the outer surface of the exine with the mesoperine.

The diameter of these threads varies approximately between 0.05 μm and 0.2 μm for the Lower and Middle Pleistocene specimens (Pl.8, Fig.6).

Mesoperine
The mesoperine is divisible into an inner mesoperine **a** (Pl.8, Fig.6) and an outer mesoperine **b** (Pl.8, Fig.7).

The mesoperine **a** consists of the same threads as the endoperine but they are less dense and surround, like a membrane, irregular cavities, the diameter of which ranges between 0.3 μm and 1.2 μm for the Lower Pleistocene megaspores from Essen and between 0.2 μm and 1.0 μm for the Mid-Pleistocene specimens from Melle. The thickness of the mesoperine **a** of the Lower Pleistocene megaspores from Essen varies between 0.5 μm and 10 μm. The mesoperine **a** of the Mid-Pleistocene megaspores from Melle has a thickness ranging from 1.2 μm to 5.5 μm (Pl.8, Fig.7).

In the mesoperine **b** larger, irregular oblong and circular cavities appear and they are surrounded by a membrane which is formed by threads as this is the case for the membrane around the cavities of the mesoperine **a**. This membrane is foveolate with many small openings of about 0.1 μm in diameter and between them lie scattered, larger perforations with a diameter of 0.8 μm (Pl.9, Fig.1). The oblong alveoles display a length varying between 1.2 μm and 33 μmm and a breadth oscillating between 0.8 μm and 16 μm, whereas the diameter of the circular holes ranges between 3 μm and 5 μm in the Lower Pleistocene megaspores of Essen (Pl.9, Fig.1). The Mid-Pleistocene megaspores from Melle display oblong cavities with a length fluctuating between 1 μm and 18 μm and a breadth between 0.8 μm and 11 μm as well as circular cavities, the diameter of which ranges between 2 μm and 6 μm (Pl.8, Fig.7). Four measurements of the largest alveoles in the megaspores of Lower Pleistocene age from Essen give a mean length of 18.2 μm, while ranging from 9.6 μm to 33.1 μm, whereas the mean breadth is 8,5 μm, oscillating between 5.6 μm and 15.7 μm. The smallest have a mean length of 1.8 μm

Table 1
Recapitulation of the in text mentioned numerical data obtained by measuring cavities of mesoperine **a** and **b** in Lower and Middle Pleistocene megaspores of *Salvinia natans* from Essen and Melle.

	mesoperine **a**		mesoperine **b**							
	diameter of cavities in μm	thickness in μm	oblong alveoles		diameter of circular cavities in μm	largest alveoles		smallest alveoles		mean thickness in μm
			length in μm	breadth in μm		mean length in μm	mean breadth in μm	mean length in μm	mean breadth in μm	
Lower Pleistocene megaspores from Essen	0.3-1.2	0.5-10.0	1.2-33.0	0.8-16.0	3-5	18.2	8.5	1.8	1.5	40.8
Middle Pleistocene megaspores from Melle	0.2-1.0	1.2-5.5	1.0-18.0	0.8-11.0	2-6	14.8	7.1	2.0	1.2	34.5

although they fluctuate between 0.8 μm and 2.1 μm. Six measurements of the largest alveoles in the Mid Pleistocene megaspores from Melle show a mean length of 14.8 μm, ranging from 13.1 μm to 18.4 μm and a mean breadth of 7.1 μm varying between 3.0 μm and 11.5 μm. The smallest alveoles have a mean length of 2.0 μm varying between 1.2 μm and 3.0 μm and a mean breadth of 1.2 μm oscillating between 0.8 μm and 2.7 μm. The mean thickness of the mesoperine **b** is 40.8 μm, fluctuating between 22.5 μm and 69.8 μm for the Lower Pleistocene megaspores from Essen and 34.5 μm, oscillating between 25.5 μm and 41.0 μm for the Mid Pleistocene megaspores from Melle.

FLORSCHÜTZ & JONKER (1942, pl. 5, fig k) have already observed that the surface of Pleistocene megaspores of *Salvinia natans* was considerably rougher but they contented themselves to use the denomination cf. *natans*. KEMPF (1971) ascertained that there was a dissimilarity between the Lower and Middle Pleistocene megaspores of *Salvinia natans*. However he considered that it was unnecessary to introduce a new taxon because the anatomy was similar.

Nevertheless the creation of a new variety *tuberculata* for the Lower Pleistocene megaspores is opportune because:

— the megaspores are larger and more robust
— the outer wall surface is strikingly rougher due to the occurrence of a well pronounced verrucate-rugulate sculpturing on the perine allowing an easy determination. The verrucae are irregularly circular at the base with a mean diameter of 73 μm, oscillating between the extreme values of 60 μm and 96 μm (10 measurements on one megaspore). Sixteen measurements on five megaspores gave an average diameter of 61 μm with extreme values of 48 μm and 84 μm. The rugulae are sinuous, often anastomosing with one another. Their mean length reaches 125 μm, varying between 96 μm and 168 μm (10 measurements on the same megaspore where 10 verrucae were measured). On other megaspores the maximum length of a rugula may attain 312 μm.
— the thickness of the exine and the mesoperine are both thicker
— the alveoles of the mesoperine **a** and **b** are larger.

To date the variety *tuberculata* is confined to the Lower Pleistocene Campine Clay, whereas the smoother megaspores of *Salvinia natans* have only been recognized in the Mid-Pleistocene sediments of Belgium.

DESCRIPTION OF THE MICROSPORANGIA

Microsporangia of *Salvinia natans* have been found in the Mid-Pleistocene deposits of Melle. They have a length of approximately 432 μm and a breadth of approximately 360 μm. The outer surface is granular. The diameter of the verrucae reaches 88 μm (Pl.9, Fig.2). This surface is foveolate. The majority of the perforations have a diameter ranging from 0.15 μm to 0.04 μm. Between them larger openings with a diameter varying between 0.5 μm and 0.9 μm are scattered (Pl.9. Fig.3). Both dimensions are greater in another specimens. The small perforations range between 0.1 μm and 0.7 μm, whereas the axis of a large irregular oval opening is as much as 2.7 μm long (Pl.9, Fig.4).

Repository of material studied

The reproductive organs of the Azollaceae and Salviniaceae occurring in Caenozoic deposits of Belgium are part of the palaeobotanical collections kept in the Institut Royal des Sciences naturelles de Belgique, rue Vautier 29, B-1040 Brussels.

Acknowledgements

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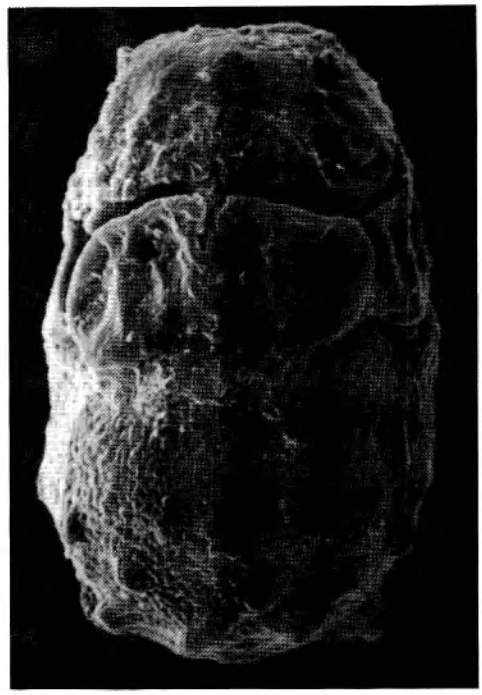
Abbreviations used on the plates

c : collar
cn : column
enp : endoperine
mp : mesoperine
exp : exoperine
ex : exine
f : float
oc : opaque centre
sp w : sporangial wall

1



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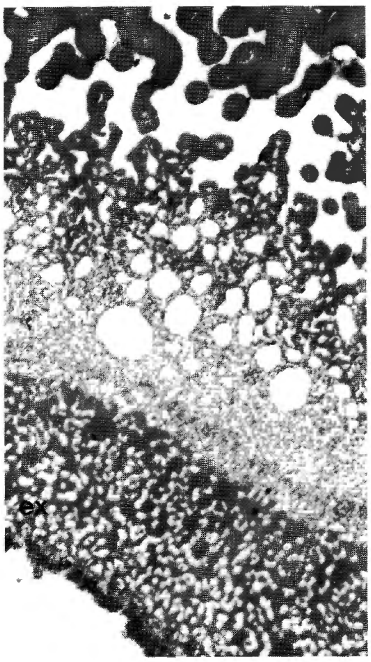

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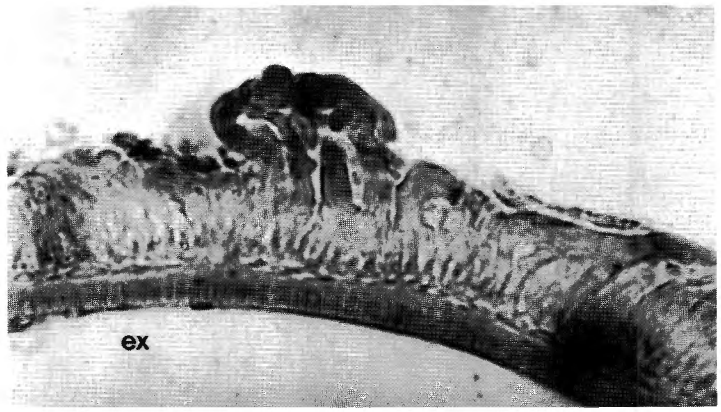

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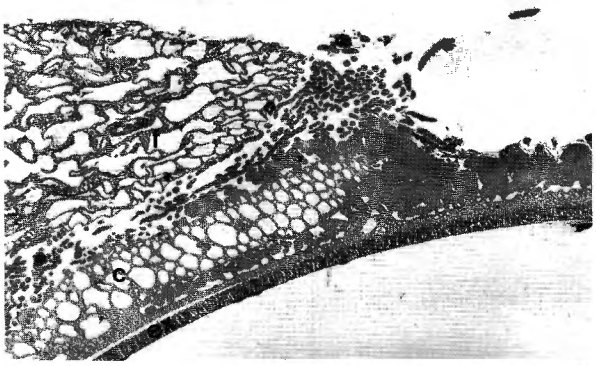

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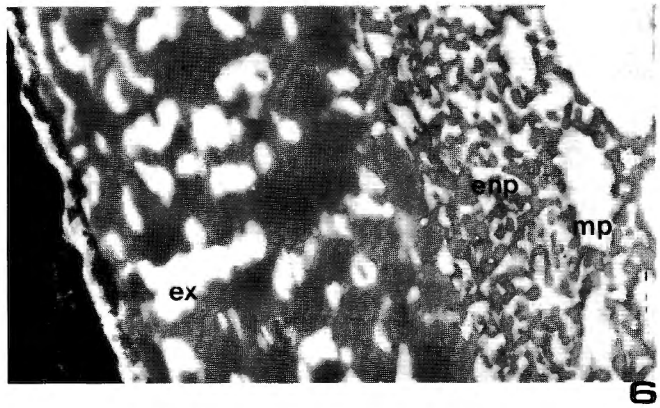

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PLATE 1

Azolla nikitinii (Provenance: Tongeren, Belgium)

Fig. 1 — section of the clay pit Francart at Tongeren in 1955.

Fig. 2 — megasporangium (SEM, 200x).

Fig. 3 — section of the megaspore wall showing the structure of the exine and the perine (TEM, 2500x).

Fig. 4 — section of the megaspore wall showing the striped character of the exine and a protuberance (LM, 1000x).

Fig. 5 — section of the megaspore wall, collar and float (TEM, 600x). Note the striped appearance of the exine.

Fig. 6 — section of the exine, endoperine and mesoperine (TEM, 100x). Note the cavities in the exine.

PLATE 2

Azolla nikitinii (Provenance: Tongeren)

Fig. 1 — section of the exine, endoperine and mesoperine (TEM, 10000x). Note the threads of the endoperine.

Fig. 2 — section of the exine, endoperine, mesoperine and exoperine (TEM, 10000x). Note the larger alveoles in the mesoperine **b**.

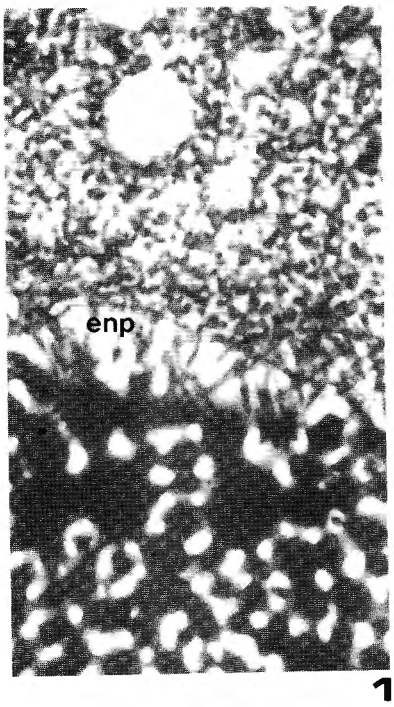
Fig. 3 — section of the megaspore wall (TEM, 3000x). Note the homogeneous layer covering the mesoperine **b**, the baculae arising from this layer and the tectum of the exoperine.

Fig. 4 — perine surface of the megaspore wall (SEM, 6000x). Note the verrucate to rugulate structure and the openings in the grooves.

Fig. 5 — perine surface of the megaspore wall (SEM, 1000x). Note the protuberance.

Fig. 6 — section of the megaspore wall (TEM, 1500x). Note the structure of the protuberance.

Fig. 7 — section of the swimming apparatus and the proximal part of the megaspore (TEM, 300x).



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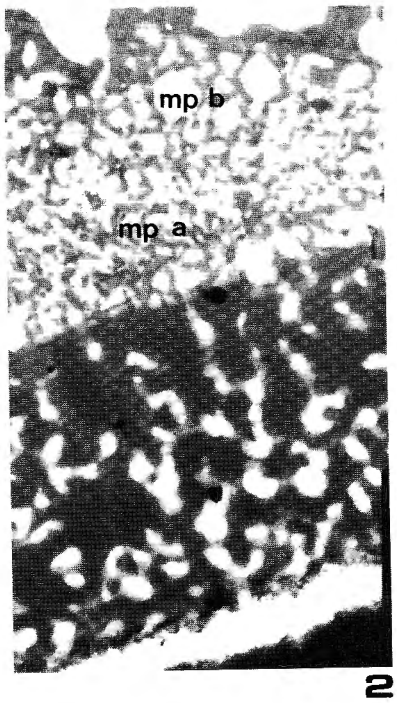

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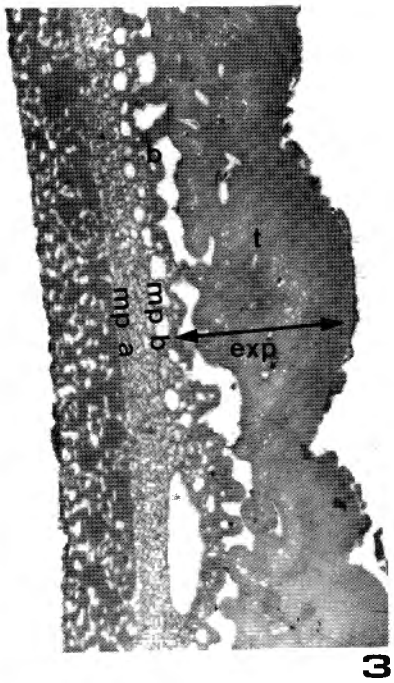

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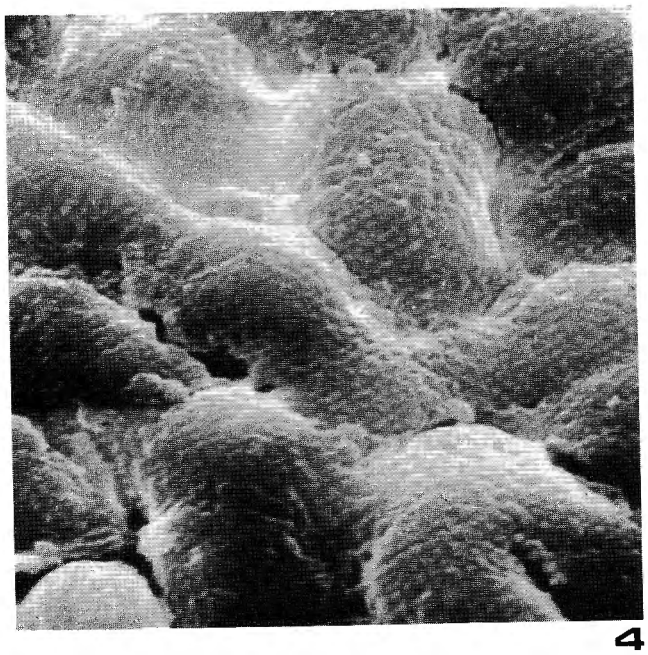

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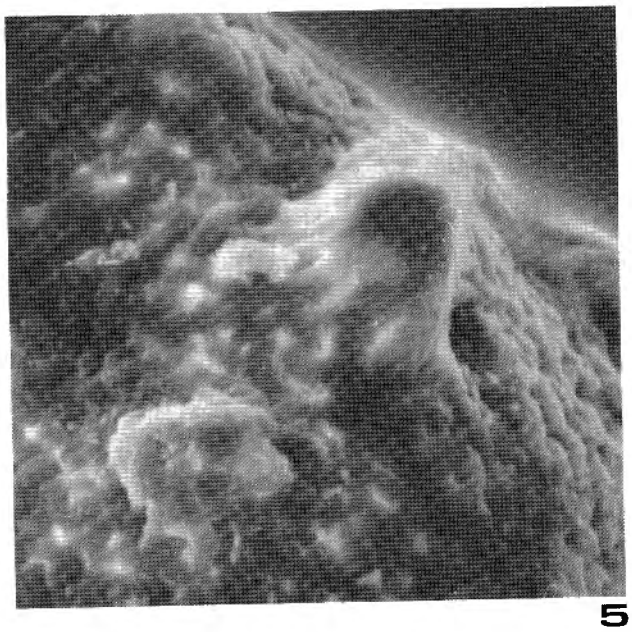

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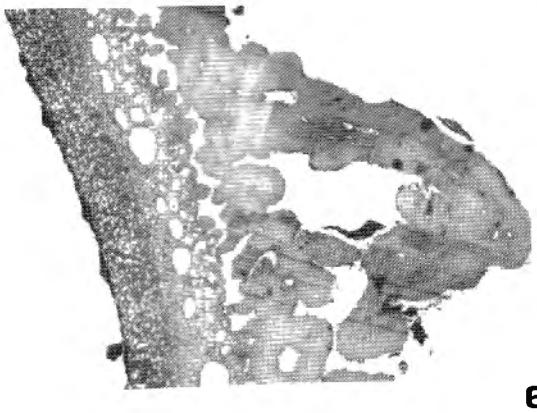

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PLATE 3

Azolla nikitinii (Provenance: Tongeren)

Fig. 1 — section of the megasporangium showing the megaspore and the swimming apparatus with collar, column and floats (TEM, 200x).

Fig. 2 — hairs between swimming apparatus and megaspore (SEM, 4500x).

Fig. 3 — section of the megaspore wall, collar and part of a float (TEM, 800x). Note the groove between the collar and the megaspore, filled with tectum material. Remark also the groove between the collar and a lower float filled with tectum material and hairs.

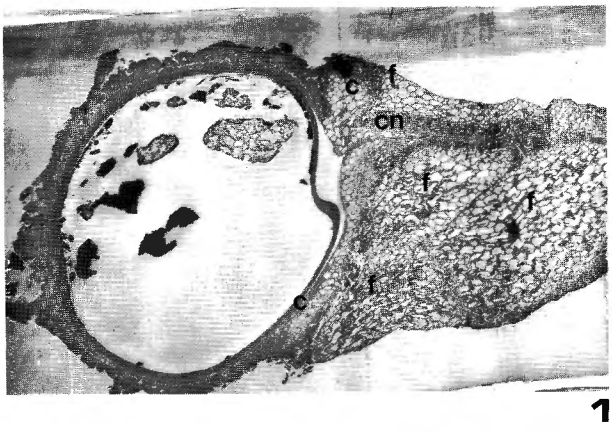
Fig. 4 — section through the collar and the megaspore wall (TEM, 1500x). Note the groove between the megaspore wall and the collar filled with tectum material and hairs as well as the transition of the megaspore wall into the mesoperine of the collar.

Fig. 5 — section of a float showing the large alveoles of the pseudocellular mass, corresponding to the mesoperine **b** in the collar and the megaspore wall (TEM, 3000x).

Fig. 6 — section of the upper part of the swimming apparatus, revealing the hairs at the top in connection with the hairs between the adjacent faces of the upper float and column (TEM, 300x).

Fig. 7 — section of a part of the column and the adjacent floats showing the mesoperine **a** in the centre of the column, surrounded by the mesoperine **b** with large alveoles and covered by the exoperine from which the hairs arise (TEM, 2500x).

Fig. 8 — section through a float revealing the opaque centre in the middle of the mesoperine (LM, 500x).



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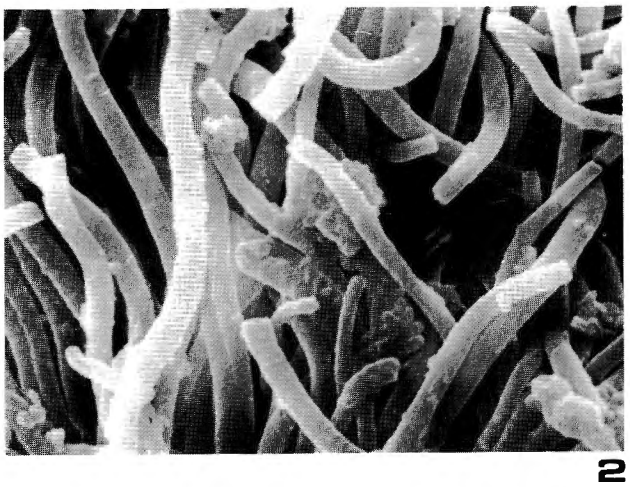

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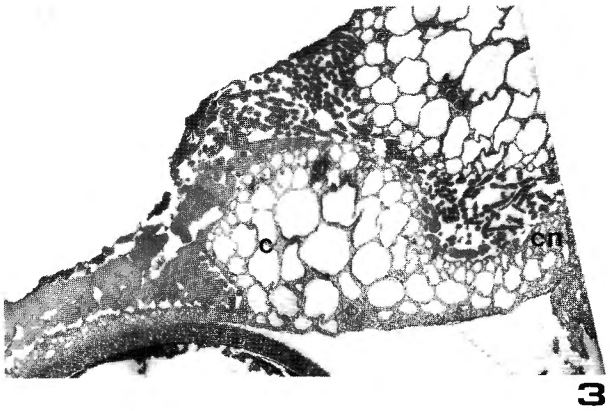

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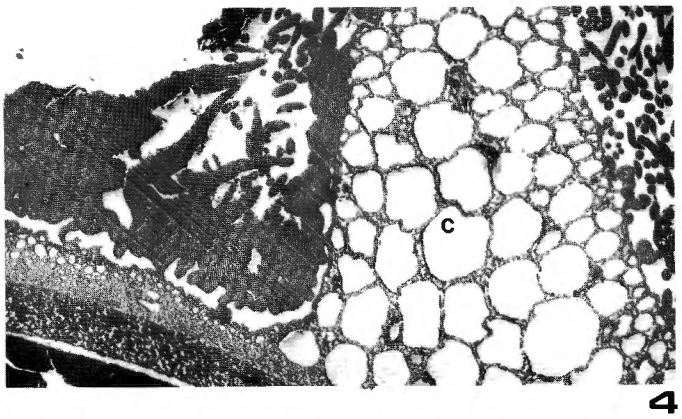

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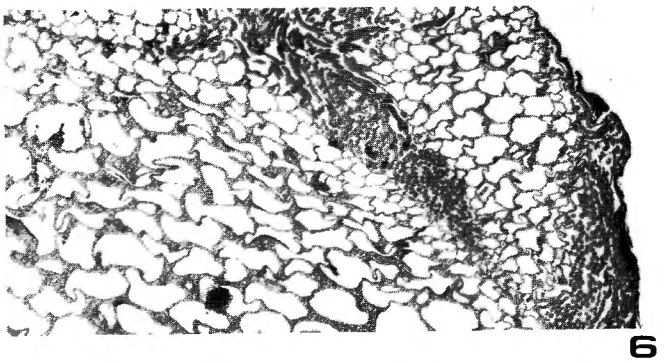

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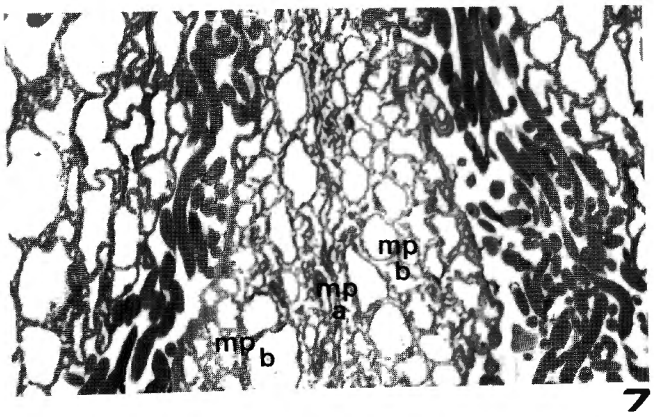

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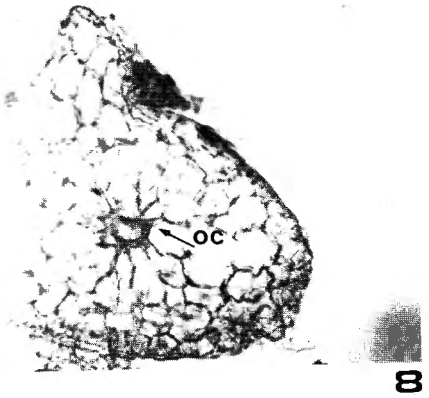

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PLATE 4

Azolla tegeliensis (Provenance: Essen)

Fig. 1 — megasporangium (SEM, 160x).

Fig. 2 — surface of the perine with protuberance (SEM, 5000x). Note the protuberance where the sutures of the fused sculpturing elements are still discernible.

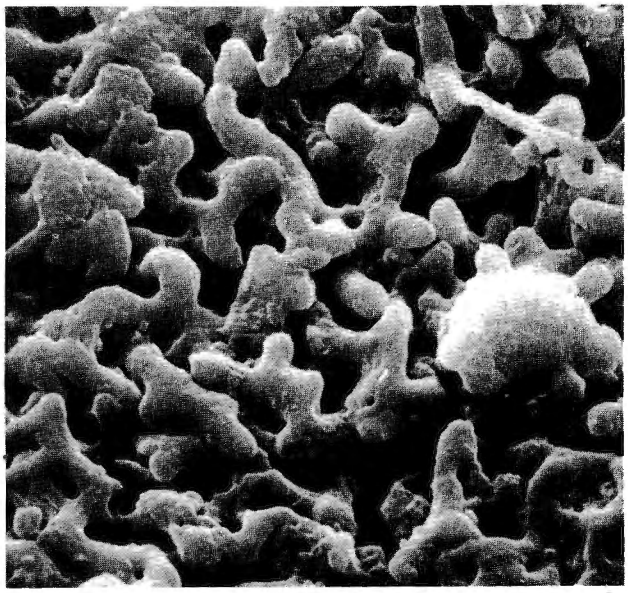
Fig. 3 — surface of the perine with protuberances (SEM, 1600).

Fig. 4 — foveolate surface of the float (SEM, 1500x).

Fig. 5 — hairs filling the wedge between two groups of three floats (SEM, 500x).

Fig. 6 — hairs with coiled ends occurring on the perine of the megaspore body (SEM, 5000x).

1



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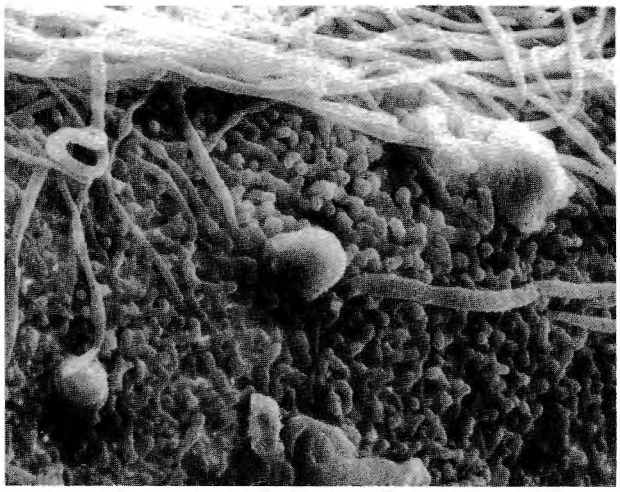

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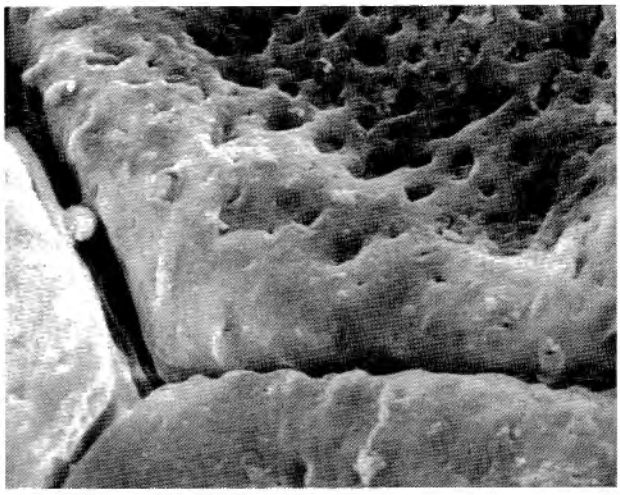

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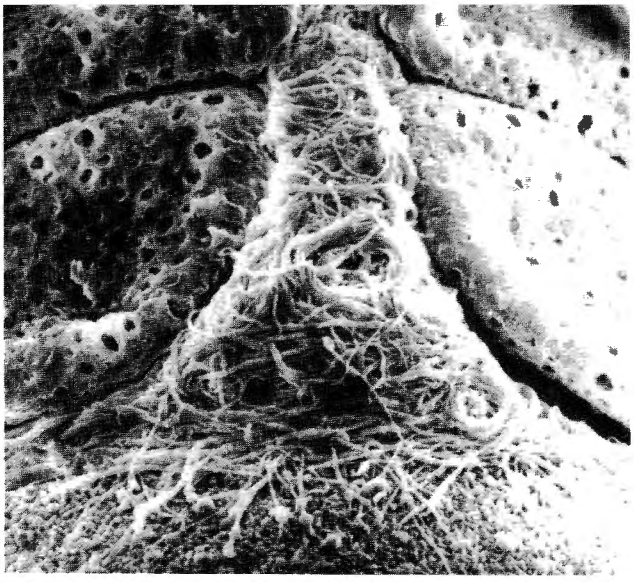

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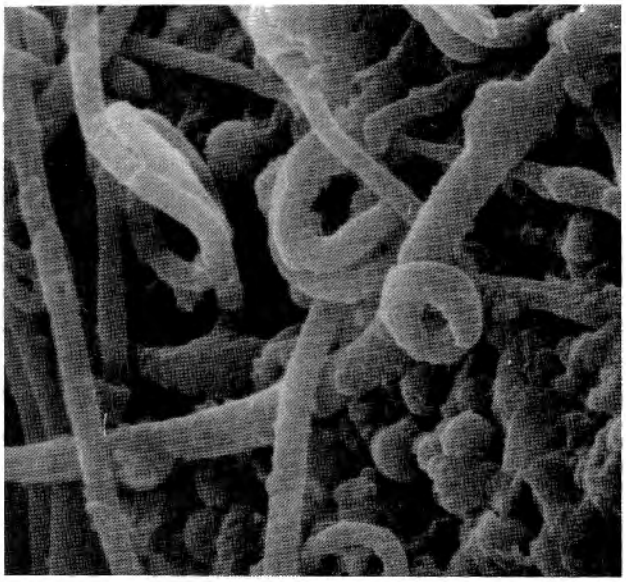

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PLATE 5

Azolla filiculoides (Provenance: Lo)

Fig. 1 — megasporangium (SEM, 200x).

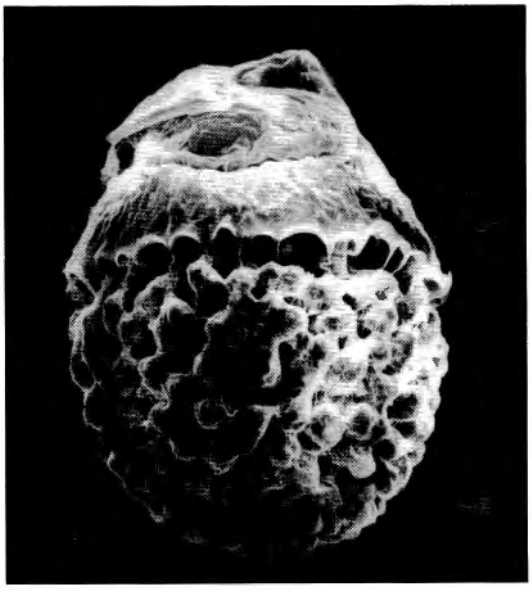
Fig. 2 — perine around the megaspore (SEM, 400x). Note the hairs connecting the perine around the megaspore with the lower edge of the collar.

Fig. 3 — hairs between two floats of the swimming apparatus (SEM, 3000x).

Fig. 4 — wrinkled aspect of the hairs (SEM, 10000x).

Fig. 5 — massula attached by anchor-shaped glochidia to the megasporangium (SEM, 600x).

Fig. 6 — anchor-shaped glochidium of the massula attached to a hair of the perine of the megasporangium (SEM, 6000x)



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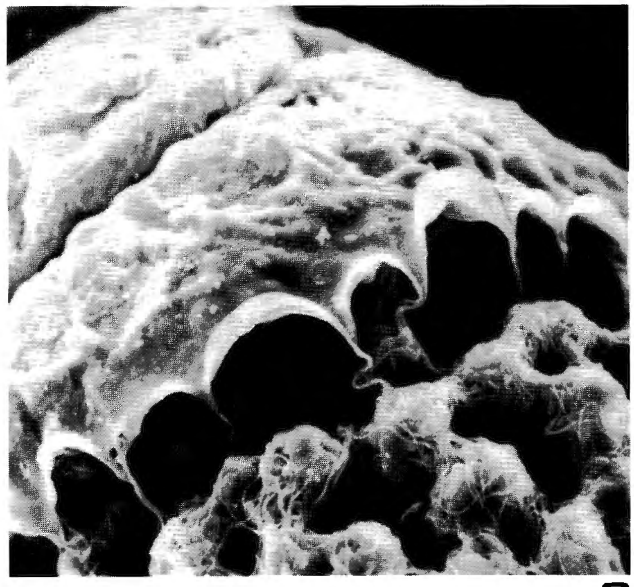

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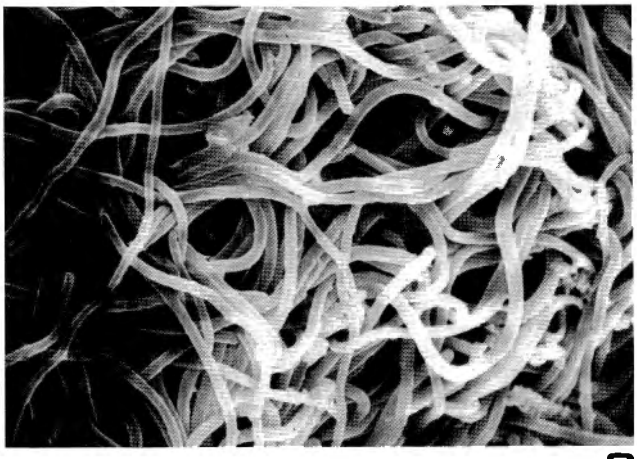

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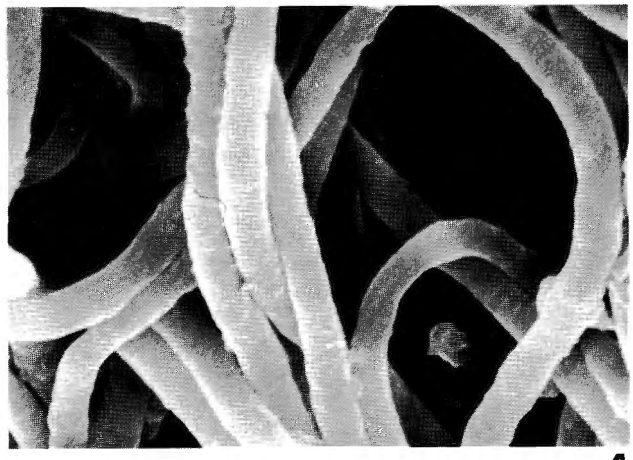

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PLATE 6

Salvinia cerebrata (Provenance: Tongeren)

Fig. 1 — megaspore with three open valves, through which the triradiate column is discernible (SEM).

Fig. 2 — megaspore showing clearly the rugulate surface of the perine (SEM).

Fig. 3 — section of the megaspore wall (TEM, 1000x). Note the exine, endoperine, mesoperine **a** and **b** as well as the remains of the megasporangial wall.

Fig. 4 — section of the inner part of the megaspore wall (TEM, 3000x). Note the remnant of the intine.

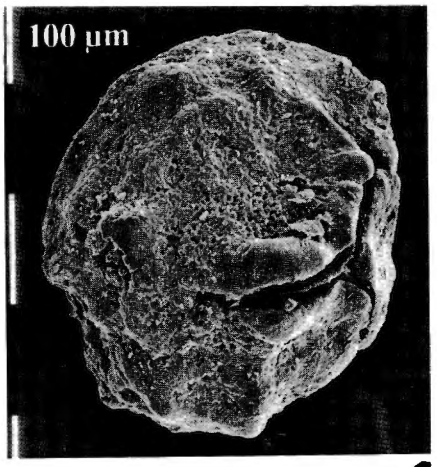
Fig. 5 — section of the outer part of the megaspore wall (TEM, 3000x). Note the layered structure of the remains of the sporangial wall.

Fig. 6 — section of a part of the exine and the endoperine (TEM, 8000x). Note the more or less radial orientated tubules in the middle part of the exine and the larger perforations (artefacts?).

Fig. 7 — section of the outer part of the exine and the innner part of the endoperine displaying the threads of the endoperine attached to the exine (TEM, 20000x).

Fig. 8 — section of the outer part of the exine, endoperine and the inner part of the mesoperine **a** (TEM, 8000x). Note the perforated structure of the membrane of the alveoles belonging to the mesoperine **a**.

Fig. 9 — section of the outer part of the mesoperine **a**, the mesoperine **b** and the remains of the sporangial wall (TEM, 3000x). Note the intensely coiled treads, forming the membrane around the large alveoles of the mesoperine **b**.



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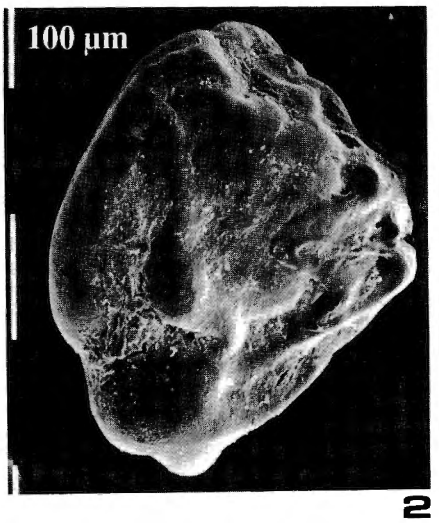

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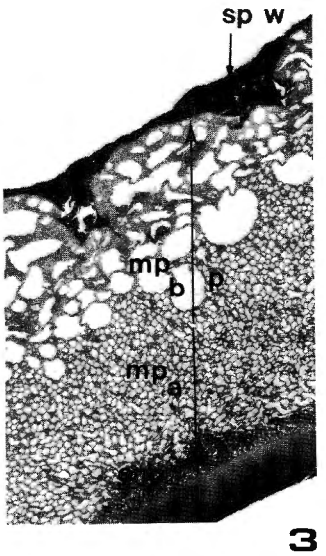

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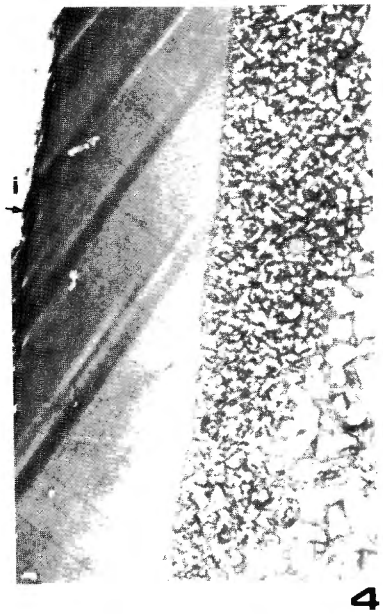

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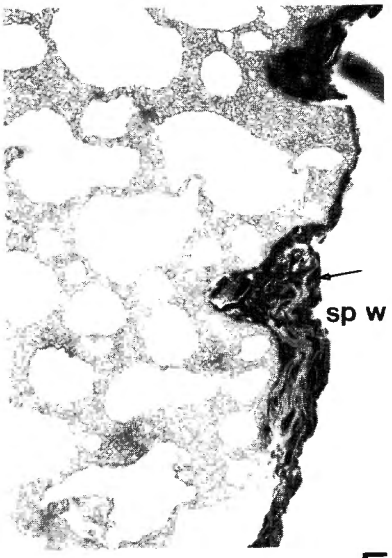

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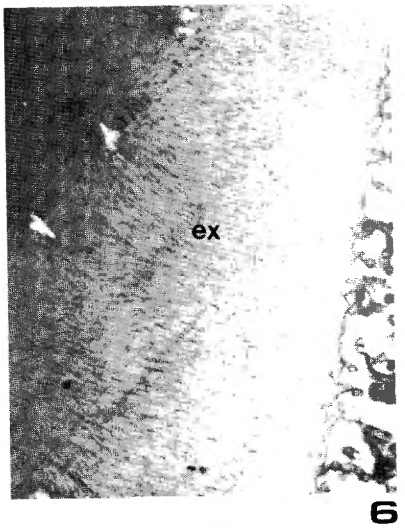

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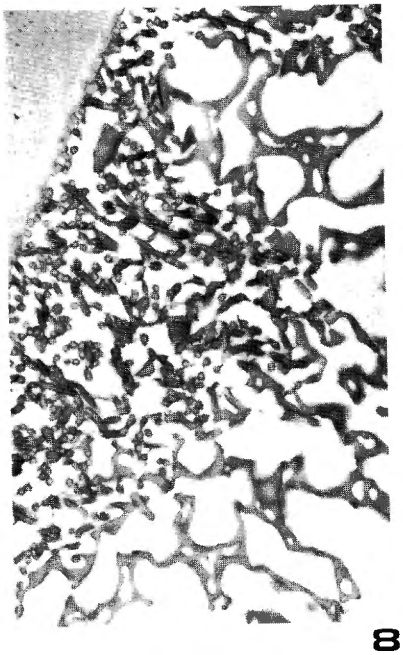

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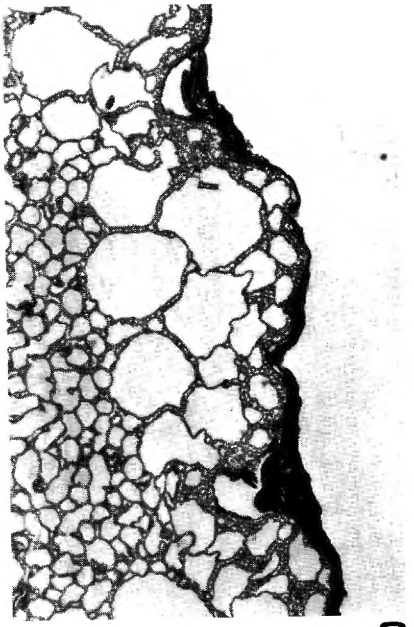

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PLATE 7

Salvinia cerebrata (Provenance: Tongeren)

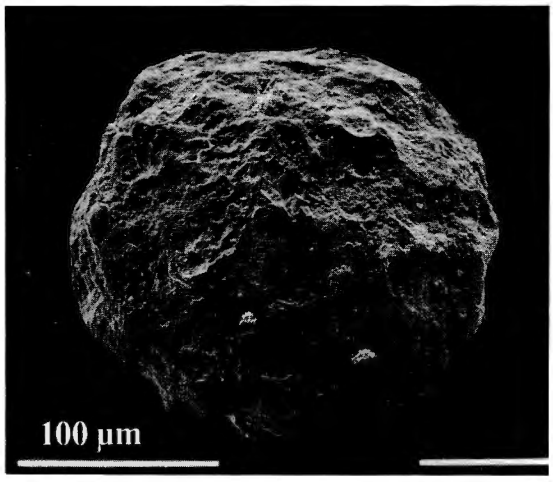
Fig. 1 — microsporangium (SEM).

Fig. 2 — microsporangium with microspores (LM, 190x).

Fig. 3 — rugged, foveolate surface of the microsporangium (SEM).

Fig. 4 — honeycombed structure of the pseudocellular mass of the microsporangium seen on fracture section (SEM).

Fig. 5 & 6 — microspores in microsporangium (LM, 600x).



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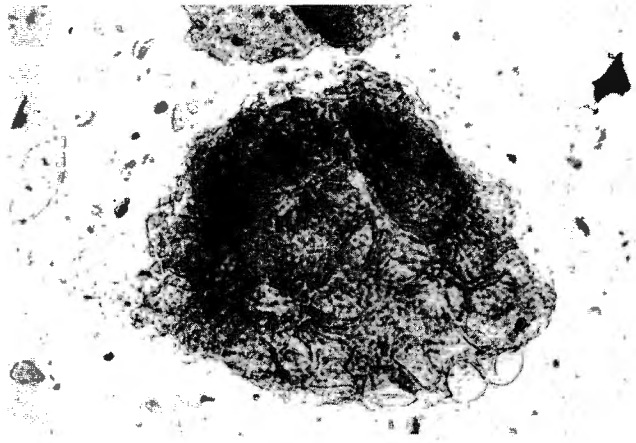

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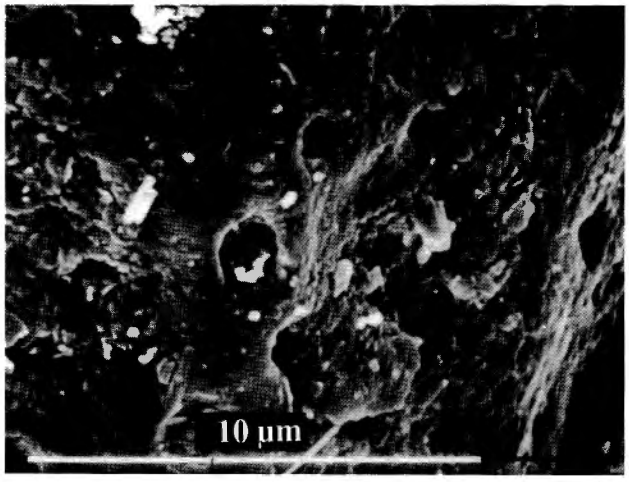

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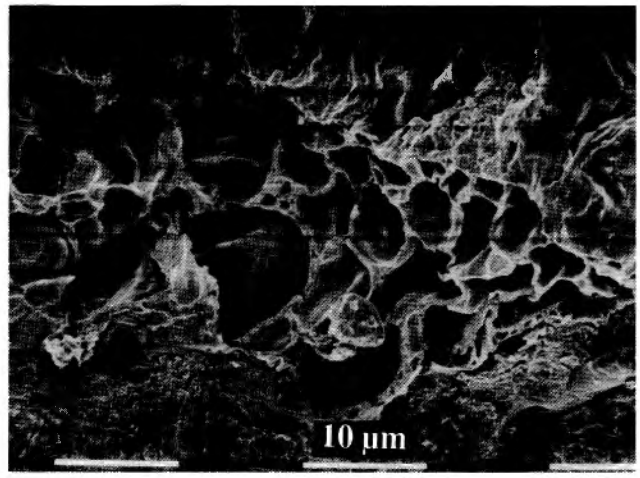

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PLATE 8

Salvinia natans (Provenance: Essen and Melle)

Fig. 1 — megaspore var. *tuberculata* from Lower Pleistocene (Provenance: Essen) (SEM).

Fig. 2 — megaspore var. *tuberculata* from Lower Pleistocene (Provenance: Essen) (SEM).

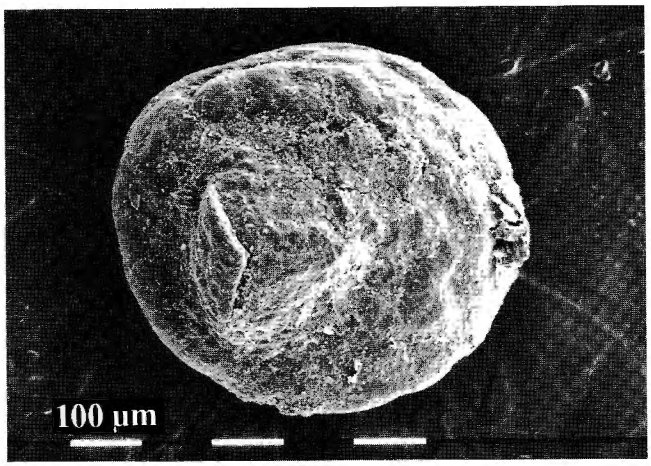
Fig. 3 — megaspore from Middle Pleistocene (Provenance: Melle).

Fig. 4 — inner face of the exine of a Middle Pleistocene megaspore (Provenance: Melle) (SEM).

Fig. 5 — fracture section of the megaspore wall from var. *tuberculata* (Lower Pleistocene) (Provenance: Essen) (SEM).

Fig. 6 — fracture section of the megaspore wall from var. *tuberculata* (Lower Pleistocene) (Provenance: Essen) (SEM).

Fig. 7 — fracture section of the megaspore wall (Middle Pleistocene) (Provenance: Melle) (SEM).



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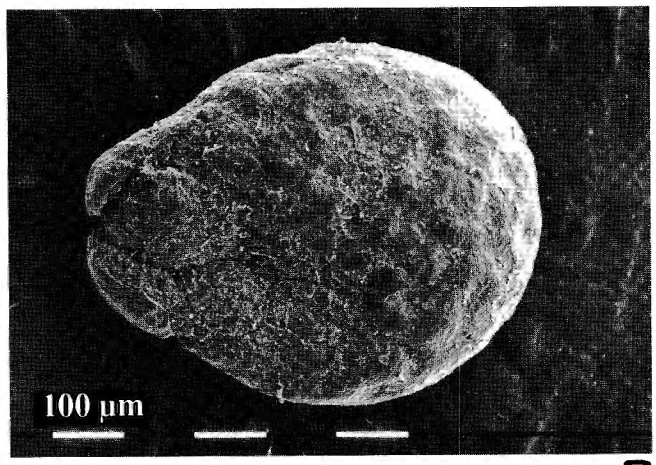

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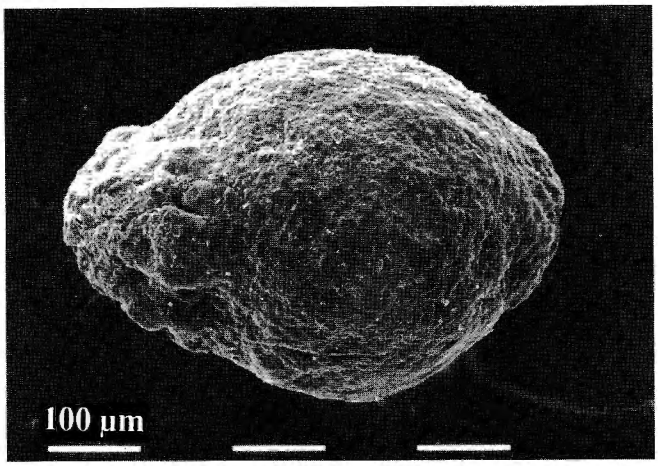

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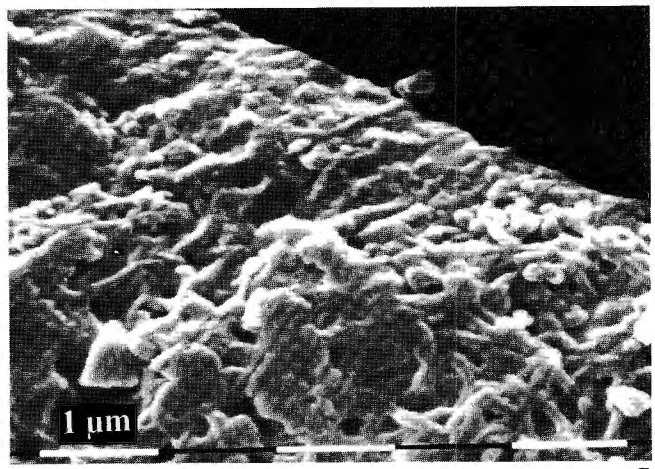

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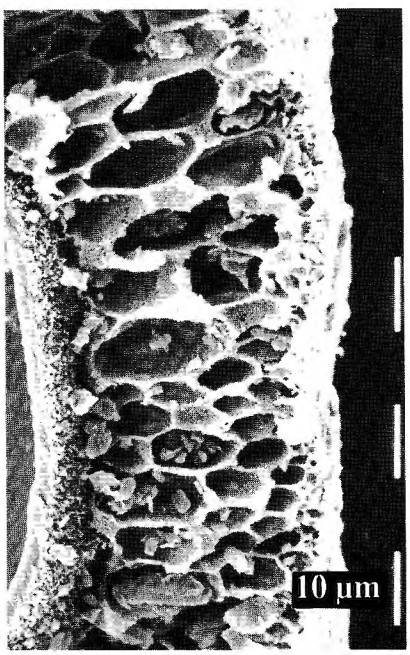

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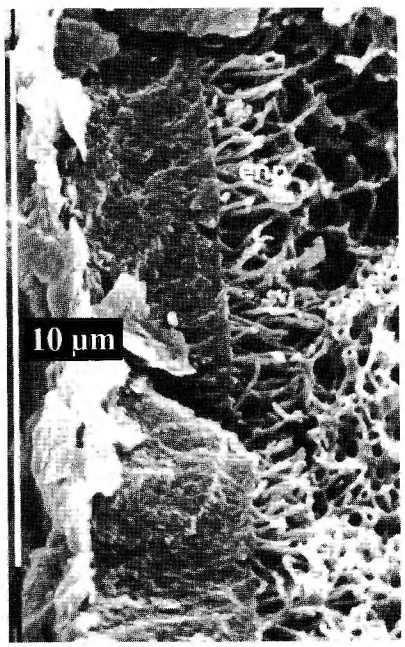

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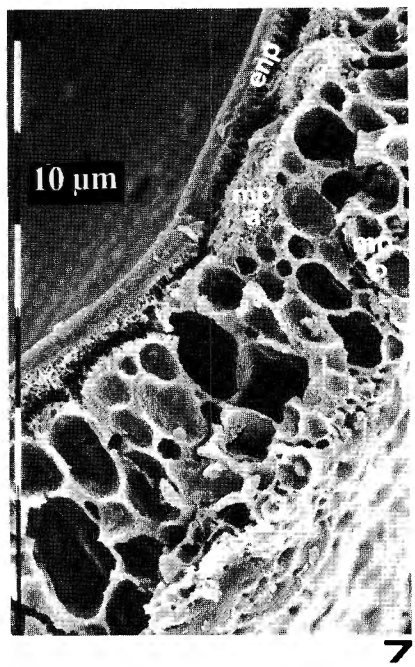

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PLATE 9

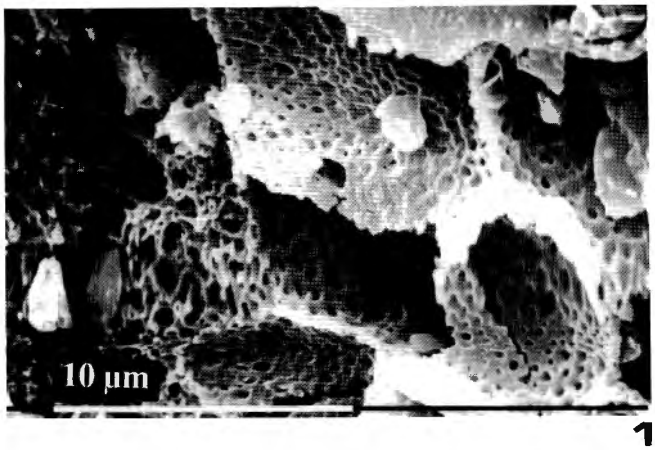
Salvinia natans (Provenance: Essen & Melle)

Fig. 1 — cavities of the mesoperine **b** of a Lower Pleistocene megaspore var. *tuberculata* (Provenance: Essen) (SEM). Note the foveolate membrane with large scattered perforations.

Fig. 2 — microsporangium (Provenance: Melle) (SEM).

Fig. 3 — outer surface of the previous microsporangium (Provenance: Melle) (SEM).

Fig.4 — outer surface of another microsporangium (Provenance: Melle) (SEM).



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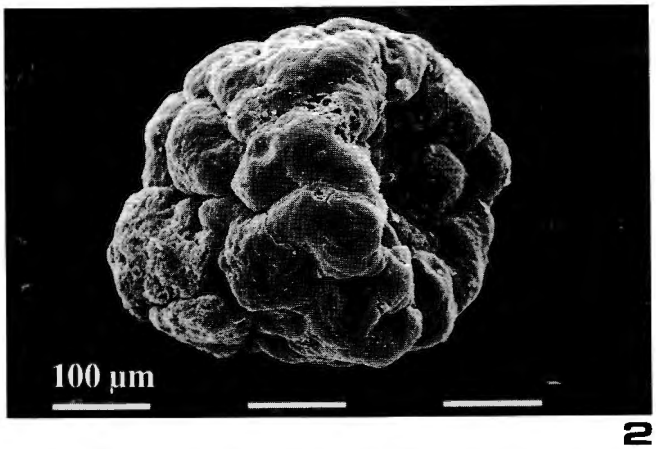

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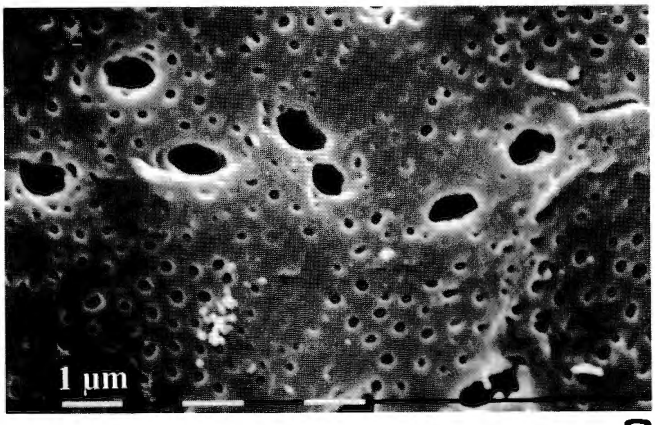

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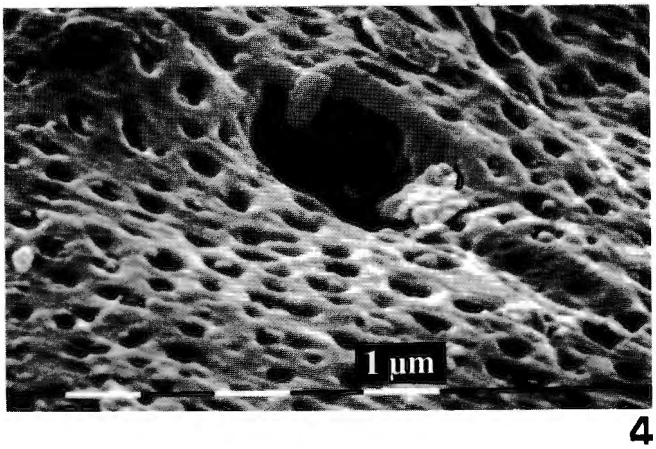

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