A RHAETO-LIASSIC FLORA FROM AIREL, NORTHERN FRANCE

by M. MUIR *and* J. H. A. van KONIJNENBURG-van CITTERT

ABSTRACT. An assemblage of fossil plants from the Upper Triassic/Liassic of Airel (Manche), Northern France, is recorded, and two new species, *Hirmerella airelensis* sp. nov. and *Classopollis harrisii* sp. nov., are described and figured. *In situ* and dispersed pollen is compared and a lycopod megaspore and microspore described. The assemblage is compared with others from France and Wales.

THE plant material described in this paper was recovered from some sandy, light-grey clay collected from Airel in the Carentan basin, near Caen, France. Various suggestions have been made about the age of the deposit (Larsonneur 1962, 1963) ranging from Norian to Hettangian. The assemblage is limited, but is generally comparable with the assemblages described by Levet-Carette (1964) and Briche, Danzé-Corsin, and Laveine (1963) from deposits in the neighbourhood of the Boulonnais. Their material came from fissure-fillings in the Carboniferous, while our material appears to be lacustrine, the plants being associated with ostracods and charophytes (Larsonneur 1963).

The macrofossils are in a remarkably good state of preservation; they are almost uncompressed, and the spiral leaf arrangement is evident. Leafy shoots, fragments of leaves, female cone-scales, male cone axes, fragments of microsporophylls, and separate pollen masses were recovered and are here described. Dispersed megaspores, microspores, and pollen from the clay were also examined.

Methods of study. Selected macrofossils were treated by maceration in Schulze's solution followed by dilute ammonia. The male cone fragments were recovered by bulk maceration of the clay, which was disintegrated in water, and then treated with Schulze's solution. Specimens were then mounted in glycerine, and examined and photographed with a Leitz Ortholux microscope. Some of the macrofossil cuticles, pollen masses, and megaspores (both macerated and unmacerated) were mounted on Durofix, coated with gold/palladium and examined on a Cambridge Instrument Company 'Stereoscan' scanning electron microscope.

The microfossils were recovered by a standard method, i.e. disintegration of the clay in H_2O_2, followed by HCl, HF, and HCl treatment. The residue was then macerated in concentrated nitric acid and washed in distilled water. The microspores were then mounted in glycerine jelly and examined and photographed in a Zeiss photomicroscope.

SYSTEMATIC DESCRIPTIONS

Genus HIRMERELLA Hoerhammer emend. Jung

Type species. H. (*Cheirolepis*) *muensteri* (Hoerhammer) Jung.

Hirmerella airelensis sp. nov.

Plate 78, figs. 1–5; Plate 79, fig. 2; Plate 80, fig. 1; text-fig. 1A

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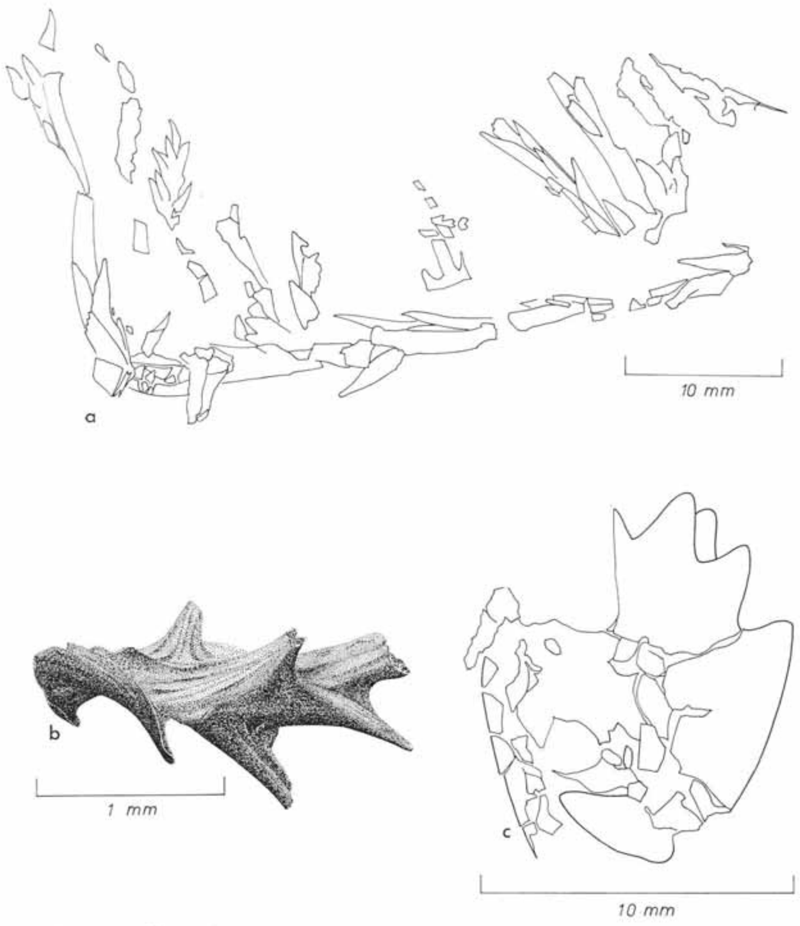

TEXT-FIG. 1. *Hirmerella airelensis* sp. nov. *a*, Holotype; ×2·5. *b*, Isolated male cone axis; ×30. *c*, Partly broken female cone scale, ×5.

Holotype. Specimen 2845: division of Palaeobotany and Pollen-morphology, Museum and Herbarium of the State University of Utrecht.

Diagnosis. Leaves spirally arranged; rather variable; free part 2–5 mm. long, 2–4 mm. wide, leaf-base cushion 2–3 mm. long, 2–4 mm. wide. Cuticle from 1 to 8 μ thick, usually about 4–6 μ; margin scarious, especially near the apex. Upper cuticle: stomata mostly arranged in short longitudinal rows, but some irregularly scattered; rows separated laterally by 3–10 epidermal cells in thin cuticles, 2–6 in thick ones; stomata within rows separated longitudinally by 2–10 epidermal cells in thin cuticles, 1–6 in thick ones; guard cells sunken, not usually visible; 4–6 subsidiary cells forming a thick, raised ring around the guard cells, often striated and, especially in the thick cuticles, papillate; encircling cells present but not clear; normal epidermal cells in rows, papillate, varying from rectangular with thin walls, to almost square with thick walls; thick walls often pitted. Lower cuticle similar to the upper, but with more stomata, and with few papillae on the epidermal cells.

Description. The material consists of a large number of well-preserved small shoots, usually not more than 2 cm. long. Most of the material is uncompressed and shows the spiral arrangement of the leaves very well.

The leaves vary considerably in size and proportions, from rather long narrow ones, with a large free part, and a rather thin cuticle, to broader ones with a short free part and a rather thick cuticle. All kinds of intermediates between these two extremes have been found. We believe that the long narrow leaves are immature, whilst the broader ones are older, although they may represent sun and shade leaves. It is known that the young and old leaves of recent conifers commonly differ considerably in cuticle thickness and size of the epidermal cells (Napp-Zinn 1966). We very often find *Classopollis harrisii* sp. nov. pollen grains sticking to the thicker cuticles, which reinforces our opinion that they are older leaves.

Discussion and comparison. These shoots can certainly be placed within the genus *Hirmerella*, but they differ in some respects from the type species *Hirmerella muensteri*.

In *H. muensteri*, the cells of the upper cuticle do not have papillae, while in our species, these are prominent. There are more, and longer, rows of stomata, and the stomata are more closely crowded together within rows in *H. muensteri* than *H. airelensis* (Plate 78, fig. 6); the stomata appear to be indistinguishable in the two species.

The presence of male and female cone-scales and of pollen grains which resemble those of *H. muensteri* confirm the placing of the new species within the genus *Hirmerella*.

This material resembles very closely that described by Lewarne and Pallot (1957) and Harris (1957) from the Rhaeto-Liassic of Cnap Twt, South Wales, although these authors did not mention papillae on the upper cuticle, but thickenings. Re-examination of the material shows the 'central thickenings' to be papillae, and the stomata are rather widely spaced in short rows. Although the Welsh material agrees more in morphology with our species, it was referred to *Cheirolepis* (now *Hirmerella*) *muensteri*. Lemoigne (1967) has described some leafy shoots from Saint Fromond (Manche) in the same region of the Carentan Basin as Airel. Although they were referred to the 'Cupressales', in their over-all morphology and cuticular detail, they appear to be identical with our material. The stomata are very similar, and papillae are present as well. There seems to be no basis for their assignation to the 'Cupressales', and we believe that they should be placed in *Hirmerella airelensis* sp. nov.

Our material is closely comparable with that described by Chaloner (1962) from the Henfield borehole. He found that the isolated leaves are similar in all respects with those from Cnap Twt described by Lewarne and Pallot (1957) and Harris (1957). He mentions the papillae on the epidermal cells, but refers his material to *Cheirolepis muensteri*. We believe that these leaves, although fragmentary could be referred to *Hirmerella airelensis*.

Wood (1961) describes *Cheirolepis muensteri* from Lyme Regis, Dorset, England. While his material is similar to ours, it differs in having very thick cuticles (15–20 μ) and not showing papillae on the walls of the epidermal cells.

Isolated female cone-scales. About ten isolated female cone-scales were found (text-fig. 1C). Among them are a few isolated bract scales which yield good cuticles. The cuticles are like those of *Hirmerella muensteri* as described by Hirmer and Hoerhammer (1934) except that they show papillae on the upper (outer) sides of the cells, which are the same as those occurring on the vegetative shoots.

Some ovuliferous scales were found too, showing a clear five-fold division (see text-fig. 1C). In one case, a six-fold division was observed, the middle appendage being split. No complete seeds were discovered, but one megaspore membrane (7 mm. long) was found in a bulk maceration.

The female cone-scales agree closely with those of *Hirmerella muensteri* except for the papillae on the cuticle of the bract scale, and demonstrate that this new fossil conifer must be placed within the genus *Hirmerella*. Harris (1957) stated that he had found female cone-scales like those of *Hirmerella muensteri*, but he does not give any description or drawing. There are no preparations of female cone-scales in his material kept at

EXPLANATION OF PLATE 78

All transmitted light photographs of macerated cuticles.

Figs. 1–5. *Hirmerella airelensis* sp. nov. 1, Upper cuticle, showing papillae in the cells; ×250. 2, Thin lower cuticle, showing stomata; ×250. 3, Stoma, showing striations on the subsidiary cells; ×750. 4, Detail of epidermal cells showing pitting of walls; ×750. 5, Cell outlines and stomatal arrangement at edge of upper and lower cuticle; ×250.

Fig. 6. *Hirmerella muensteri* (Schenk) Jung. Cell outlines and arrangement of stomata, for comparison with fig. 5; note absence of papillae; ×250.

EXPLANATION OF PLATE 79

Figs. 1, 3. Stereoscan photographs of pollen mass of *Classopollis harrisii* sp. nov. 1, General morphology of the whole mass; ×300. 3, Morphology of single grain (centre), with series of pustules on surface representing collapse of outer surface of wall over the coarse bacula; ×1500.

Fig. 2. Stereoscan photograph of edge of cuticle of *Hirmerella airelensis* sp. nov., showing the papillae, and three stomata arranged in a row; ×250.

Fig. 4. Pollen mass of *Classopollis harrisii* sp. nov. showing an immature grain with a thin wall and tetrad mark; ×1000.

Figs. 5–8. *Classopollis harrisii* sp. nov.; ×1000. 5. Very immature grain showing prominent triradiate mark, and weakly developed wall structure. 6, Smooth inner body, isolated by pressing the cover slip. 7, Co-type of dispersed pollen species, showing all general features. 8, Holotype of dispersed pollen species, showing coarse baculae clearly.

EXPLANATION OF PLATE 80

Fig. 1. *Hirmerella airelensis* sp. nov., slightly compressed shoot showing leaf arrangement; Stereoscan photograph, ×25.

Fig. 2–5. *Bacutriletes tylotus* (Harris) Potonié. 2, Stereoscan photograph showing the general morphology and triradiate mark; ×200. 3, Transmitted light photograph of B.M. specimen V 32623 of Lewarne and Pallot, for comparison with fig. 2; ×200. 4, Detail of fig. 2; ×400. 5, Detail of fig. 3; ×400.

Figs. 6, 7. *Heliosporites reissingeri* (Harris) Chaloner 1969. 6, Detail of spine and surface; ×1000. 7, whole grain; ×600.

the British Museum (Natural History), where all the other Rhaeto-Liassic material is deposited, and so comparison with Harris's material is not possible.

The female cone-scales described by Lemoigne (1967) are papillate, but have eight appendages, and so appear to differ somewhat from the Airel specimens, but the illustrated specimens appear to be broken, and may, in fact, only have five or six appendages.

Isolated male cones. Fragments of male cones are common in the Airel material, but no complete cones have been found, here or elsewhere. There is one isolated male cone axis (3 mm. long), showing the spiral arrangement of the microsporophylls clearly, but there are no microsporophylls adhering (text-fig. 1B). Isolated microsporophylls are common, but none of them has the pollen sacs attached. Microsporophyll heads are almost peltate, the stalk being slightly tilted and attached nearer to the base. They are about 2 mm. long and 2·5 mm. wide. Just below the stalk, there are two regions (one on either side) which are very sunken and polished, indicating the places of attachment of the pollen sacs. The Cnap Twt material of Harris (1957) also had two attachment areas. In *Hirmerella muensteri* (Hoerhammer 1933, Hirmer and Hoerhammer 1934, Jung 1968), however, there are up to twelve pollen sacs on one microsporophyll. Barnard (1968) found a situation similar to this in his material from the Liassic of Iran.

Isolated pollen sacs are also found, usually about 1·5 mm. long, 0·5 mm. wide, and almost circular in section. The wall of the pollen sac is very thin (*c.* 0·5 μ) and composed of rectangular cells. They yield pollen grains in different stages of maturity which are described under *Classopollis harrisii* sp. nov.

These isolated male cone fragments can be assigned with reasonable certainty to *Hirmerella airelensis* sp. nov. since the leaves are the only macrofossils in this material. The evidence of association is thus strong. Harris (1957) also described male cone fragments from Cnap Twt which he attributed to *Cheirolepis muensteri*, by far the most common macrofossil in that assemblage, although he found some dispersed cuticles of other species as well.

We believe that those fragments can be attributed to *Hirmerella airelensis* instead of *H. muensteri* because of their association with the leaves. Both male cone fragments differ from *H. muensteri* in having probably only two pollen sacs in each microsporophyll, while *H. muensteri* has a ring of twelve on each microsporophyll.

Genus CLASSOPOLLIS Pflug 1953

Type species. C. classoides Pflug 1953.

Classopollis harrisii sp. nov.

Plate 79, figs. 1, 3–7

Holotype. Specimen 2845A: division of Palaeobotany and Pollen Morphology, Museum and Herbarium of the State University of Utrecht.

Dimensions. Maximum diameter 37·0 μ; minimum diameter 22·2 μ; average size 25·6 μ. Holotype: maximum diameter 37·0 μ; minimum thickness of wall 1 μ; maximum thickness of wall 6 μ.

Diagnosis. Pollen grains spherical; characterized by an equatorial thickening which is divided off from the distal polar area by a thin ring furrow; no striations visible; no distal pore seen; proximally triradiate, tetrad mark usually not distinct; exine two-layered; outer layer tegillate; inner layer thin, indistinct. Exine varies in thickness from 1 to 6 μ.

Description. These well-preserved grains can clearly be placed within the genus *Classopollis*, but are distinguished from previously described species by the absence of equatorial striations, and by the apparent absence of a distal pore (Plate 79, figs. 7, 8). The pollen grains have never been observed in tetrads, and this too is a distinctive feature. It can be separated from *Circulina meyeriana* Klaus 1960 by the prominent exine structure in *C. harrisii*.

Discussion. Almost the entire assemblage of dispersed spores from this locality consists of *Classopollis harrisii* sp. nov. (over 99% of the entire assemblage). This is typical of Rhaeto-Liassic assemblages, and less common earlier, suggesting that the assemblage is more likely to be Rhaetian than Norian.

The dispersed pollen grains can be closely compared with most of the pollen *in situ* in the pollen sacs and pollen masses associated with *Hirmerella airelensis* sp. nov., but the *in situ* pollen shows considerable variation. This probably reflects different stages in the development of the pollen grains. None of the pollen found, whether *in situ*, or dispersed, occurs in tetrads. This suggests that the grains went through the stage of tetrad formation before sporopollenin was deposited, and only separated grains are preserved. This would also tend to explain why the tetrad mark is not well developed on many grains.

We have found *in situ* some very small grains (11·1 μ to 18·5 μ maximum diameter) which all possess very thick-walled, smooth inner bodies. The inner bodies are completely spherical and rarely show any sign of either a tetrad mark or distal pore; sometimes, they possess an equatorial thickening which has no internal structure, although it is occasionally delimited by a ring furrow. The wall structure of the outer body is poorly developed, and the wall material is rather thin (Plate 79, fig. 5).

In the same pollen mass are more mature grains which still possess an inner body, but this is rather thin-walled and has no equatorial thickening (Plate 79, fig. 6). The outer layer of the exine has become thicker and its tegillate structure has become much more obvious. The equatorial region of the outer wall is frequently detached from the inner body, and the furrow ring clearly developed. Occasional striated grains are found at this stage of development.

In sporangia with mature grains, the inner body is almost undetachable, either because it is very thin, or because it has become closely attached to the outer layer. No striations are visible, but the ring furrow is very distinct. The dispersed pollen recovered from the clay is exactly like this. Inner bodies are only occasionally visible.

Comparison. These spores agree well with those described by Harris (1957) from the Rhaeto-Liassic of Cnap Twt and Ewenny, South Wales. He described the inner body of the grains and commented that its variability of preservation may be due to preservation of the intine 'partly impregnated with oil'. The electron microscope studies of Pettitt and Chaloner (1964) on *Classopollis* from Cnap Twt, show the presence of an internal layer corresponding to the inner body, as well as the coarse inwardly pointing baculae of the outer wall. These baculae can be seen on the Stereoscan photographs of pollen in pollen masses (Plate 79, figs. 1, 3) standing up as positive projections with the external layers of the exine collapsed over them. Our pollen grains agree in size with those of Harris, and the only difference appears to be that Harris described thin areas on the inner bodies which he believed to represent the polar regions. However, we believe that our grains are similar to those described by Harris, if not identical; Harris did not name a species.

Classopollis harrisii sp. nov. differs from *C. belloyensis* Pocock and Jansonius 1961 in the lack of separation of the two layers of exine in the mature grains.

Rioult and Levet-Carette (1966) described three species of *Classopollis* under the generic name of *Classopollenites* from Cotentin, and assigned a Lower Lias age to the assemblage. In spite of the near geographical position, none of these species appear to be identical with *C. harrisii*: *Classopollenites tripartitus* is triangular in outline, and is ascribed by Rioult and Levet-Carette to the Pteridosperms, although not with any great certainty.

Classopollenites (*Classopollis*) *classoides* Pflug is equatorially striated and although the wall structure of *Classopollenites minor* is similar to that of *C. harrisii*, it is described as having a prominent tetrad mark, and distal pore.

Pollen associated with *Brachyphyllum scottii* Kendall 1948 resembles *C. harrisii* sp. nov. closely, being normally non-striate, but has much finer wall structure, and occasionally occurs in tetrads. The *Masculostrobus* pollen described by Barnard (1968) associated with *Brachyphyllum expansum* from Iran differs from ours in the large number of striations on the equatorial thickening.

Genus BACUTRILETES (van der Hammen 1954) Potonié 1956

Type species. B. (*Triletes*) *tylotus* (Harris 1935) Potonié (1956).

Bacutriletes tylotus (Harris 1935) Potonié 1956

Plate 80, figs. 2–5

1935 *Triletes tylotus* Harris, p. 162.
1956 *Bacutriletes tylotus* (Harris) Potonié, p. 35.
1957 *Triletes tylotus* Harris; Lewarne and Pallot, p. 77, fig. 3 A, D.
1962 *Bacutriletes tylotus* (Harris) Potonié; Marcinkiewicz, p. 471.

Dimensions. Maximum diameter 475 μ; minimum diameter 350 μ (10 specimens); height of spines 20–5 μ; width of spines 6–12 μ; spines separated by distances of 5–10 μ.

Description. Our megaspores are very similar to those described by Lewarne and Pallot (1957). The triradiate mark is indistinct, but slightly elevated (illustrated fig. 3A of Lewarne and Pallot, but not described). The spines show a slight characteristic cross striation, also described from the Welsh material.

Discussion and comparison. The only megaspore comparable with this species is *Triletes sparassis* Murray 1939, from which it differs in the size and shape of the ornamentation. *Bacutriletes tylotus* has much more distinct spines.

Genus HELIOSPORITES Schulz 1965

Type species. H. altmarkensis Schulz 1965.

Heliosporites reissingeri (Harris 1957) Chaloner 1969

Plate 80, figs. 6, 7

1950 Cf. *Selaginella kraussiana* Reissinger, p. 104, pl. 12, fig. 28.
1957 *Lycospora reissingeri* Harris, p. 305, fig. 6, A, D.
1969 *Heliosporites reissingeri* (Harris 1957) Chaloner 1969.

Dimensions (10 specimens). Maximum over-all diameter, 49 μ; minimum over-all diameter, 35 μ; average width of cingulum, 10 μ; average length of spines, 10 μ.

Diagnosis. Harris (1957) gave a full diagnosis for this species, but the striations on the contact faces were not seen.

Description. The spores are clearly identical with those described by Harris (1957) as *Lycospora reissingeri*. A new combination of *Heliosporites reissingeri* (Harris 1957) has been proposed by Chaloner (1969).

CONCLUSIONS

The resemblance of this material to that described by Lewarne and Pallot (1957) and Harris (1957) and to the pollen studied by Pettitt and Chaloner (1964) from the fissure depths of Cnap Twt, Glamorgan, is remarkable. The cuticles of our material, with their distinctive stomatal arrangement and papillae are similar to those described from Wales. The male cones and pollen masses are also identical, and although our assemblage is rather restricted, the dispersed spores and pollen are also the same. We believe that the association of organs is so strong that the conclusion that the leafy shoots, female cone-scales, male cone fragments, and dispersed pollen grains come from one and the same plant is inescapable.

Unlike Lemoigne (1967) we do not believe that his (and our) material is Cupressalean. His assignment was based mainly on the wood fragments he found; Mr. van der Burgh studied some of our wood fragments and looked at Lemoigne's illustrations, and he believes that wood of this type may occur not only in the Cupressaceae, but probably also in other fossil conifer families such as the Voltziaceae and Cheirolepidaceae. The wood fragments described by Harris (1957) also look very like Lemoigne's and ours although our material was not fusainised. It does appear, therefore, on the evidence of association, that the wood fragments also belong to the same plant as the leaves, female cone-scales, male cone fragments, and pollen.

Heliosporites reissingeri and *Bacutriletes tylotus* have been found associated both at Airel and Cnap Twt, and this leads us to suggest that they represent the megaspores and microspores of one lycopodiaceous plant.

In our material we have evidence of a large amount of the *Hirmerella* conifer, which must have comprised almost a pure stand, and a lesser amount of the lycopod. The more varied assemblage found by Harris (1957) in the fissure fillings, which are comparable with those of the Boulonnais from which a plant assemblage was described by Briche *et al.* (1963) and Levet-Carette (1964), probably includes plant fragments washed in from some distance away, while our material, being lacustrine, is probably more or less local in origin.

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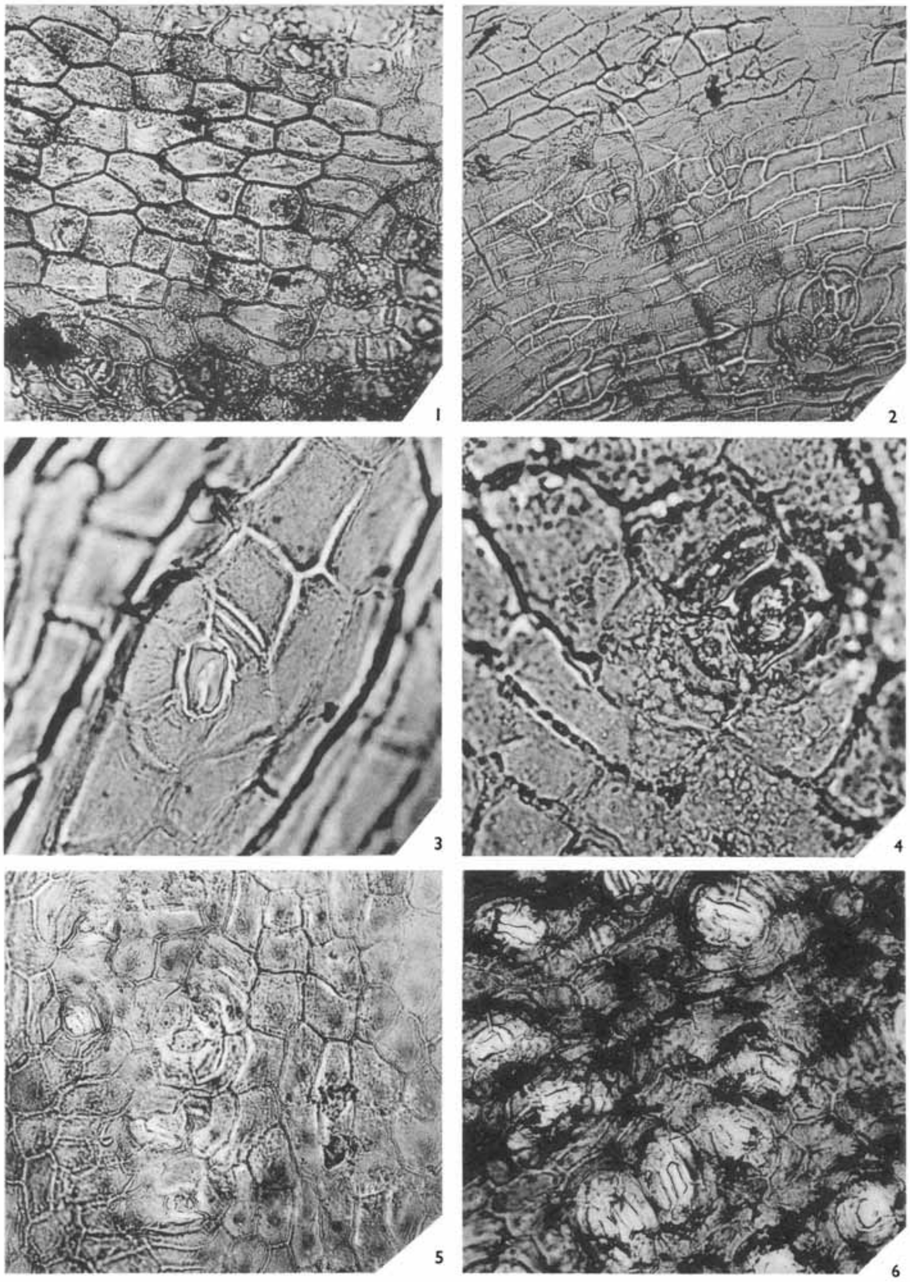
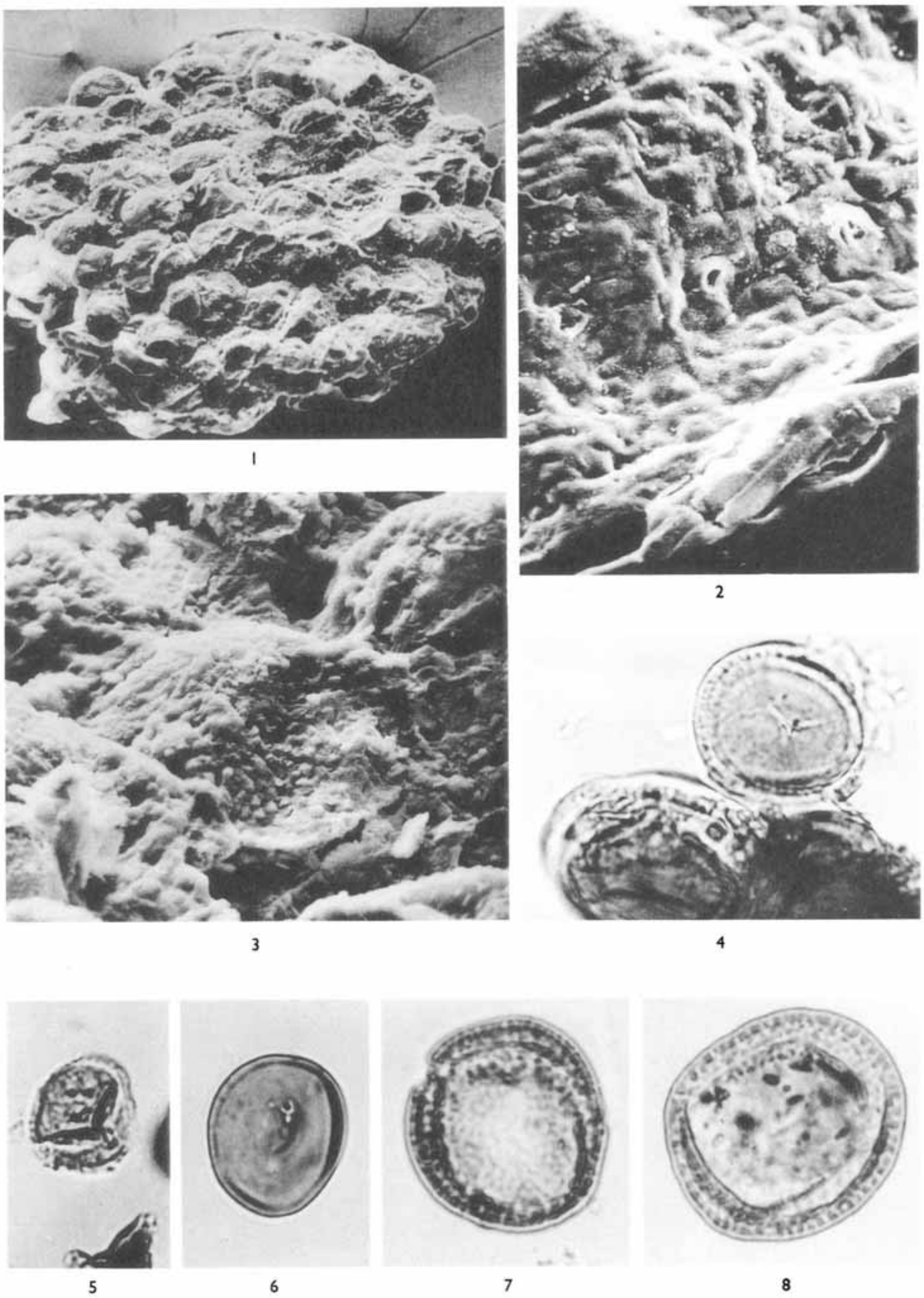
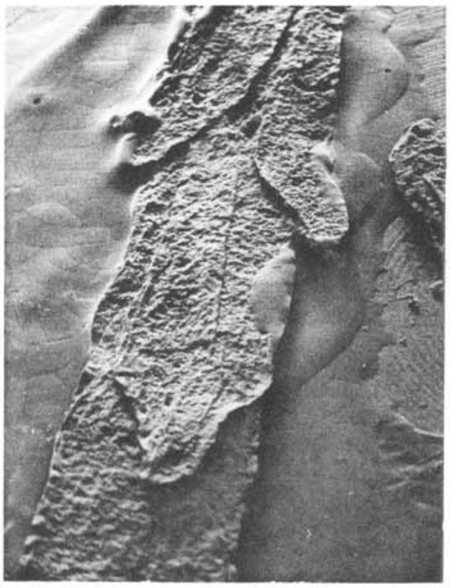


MUIR and VAN KONIJNENBURG VAN CITTERT, Mesozoic conifer cuticles



MUIR and VAN KONIJNENBURG VAN CITTERT, Mesozoic conifer pollen



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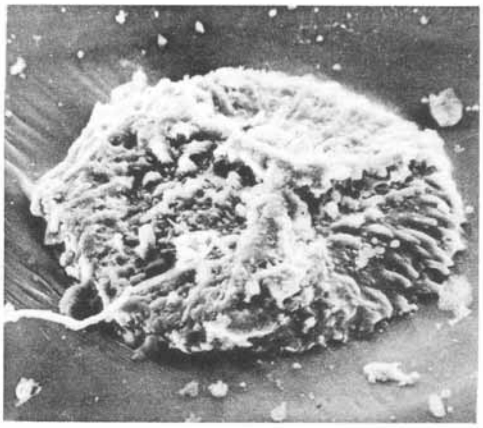

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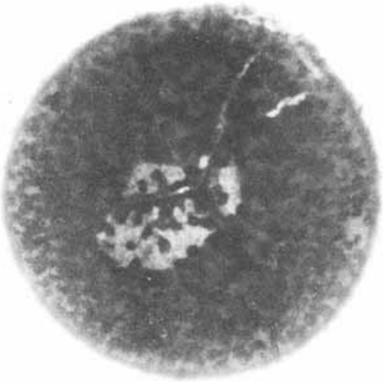

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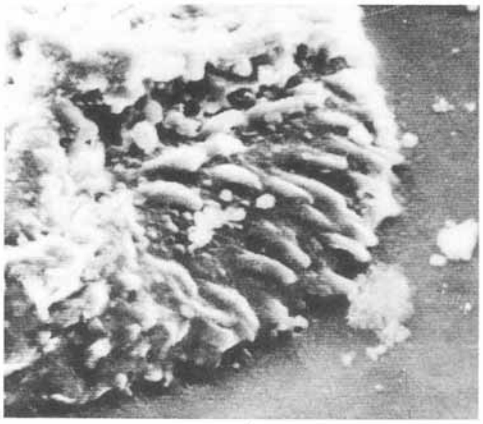

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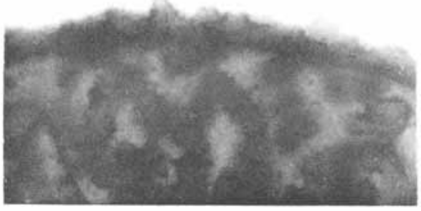

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