IN SITU GYMNOSPERM POLLEN FROM THE MIDDLE JURASSIC OF YORKSHIRE

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SUMMARY

In this paper the morphology of pollen grains yielded by male Gymnosperm fructifications from the Jurassic flora of Yorkshire is studied and discussed.

Several new male fructifications were found and described: *Hastystrobus* gen. nov. was erected for male cones yielding the *Eucommiidites* type of pollen grains. This genus is monotypic and the type species *Hastystrobus muirii* yielded pollen grains that agree with *Eucommiidites troedssonii*. *Hastystrobus muirii* very probably has Cycadalean affinities, because the whole abaxial surface of the microsporophylls is covered with sporangia.

For the first time the male fructification of *Ginkgo huttoni* (Heer) Sternberg is described. It resembles in general the male fructification of the recent *Ginkgo biloba* L., and the pollen grains agree with those of *Ginkgo biloba*.

Male cones associated with *Brachyphyllum crucis* Kendall have been found and described. They yielded pollen grains that after short maceration were identifiable as *Circulina*, while after prolonged maceration they could be assigned to *Classopollis multistriatus* Burger. *Brachyphyllum crucis* is provisionally assigned to the *Hirmerella*-group on the basis of its male cone and pollen grains. The cones were compared with other male cones containing *Classopollis* pollen, which were also attributed to the *Hirmerella*-group. It is suggested that all members of the *Hirmerella*-group have an epidermis with a special type of stoma.

Masculostrobus harrisii sp. nov. is described. This male cone resembles closely the male cone of *Elatides williamsoni* (Brgt) Sew., but its pollen grains are of the *Inaperturopollenites*-type, instead of the *Perinopollenites*-type.

The new species *Pityanthus scalbiensis* yielding bisaccate pollen grains of a rather primitive type is described; there is almost no saccus infrastructure present.

The *Czekanowskia*-group (including *Leptostrobus* and *Solenites*) in all probability does not belong to the Ginkgoales but to the Conifers.

An interesting find was that the pollen grains of the Araucariaceous *Brachyphyllum mamillare* Brgt are of two types: In type 1 the nexine and sexine are attached to each other, while in type 2 the nexine is loose from the sexine and is somewhat shrunk. In the latter type also pollen grains were found that are somewhat trilobate. A similar dimorphism of pollen grains was also found in the recent *Araucaria araucana* (Molina) K. Koch.

The pollen grains from the various male fructifications were compared with those from other male fructifications related to them. If the cones were assigned to recent taxa, the pollen grains were compared with recent pollen grains from those taxa (Cycadales, Ginkgoales and Coniferospermae).

The pollen grains were also compared with dispersed pollen grains, mainly from the Jurassic.

1. INTRODUCTION

The Yorkshire Jurassic flora is a classical Jurassic flora. The investigations on this flora have already begun in 1822, and many palaeobotanists have made contributions to our knowledge of this flora. SEWARD (1900) and HARRIS (1961)

wrote historical surveys of the investigations; I do not want to repeat them here. I wish only to name some of the most eminent investigators who devoted much of their life to the study of this flora: A. C. Seward, H. Hamshaw Thomas and T. M. Harris.

The best known parts of the plants are the shoots and the leaves, on which the majority of the research has been done. Cuticle analysis has added much to our knowledge of the leaves. Male and female fructifications are also quite well known, especially in their general morphology. But, on material such as wood, seeds and pollen grains much less research has been done.

Recently, I have examined the morphology of the pollen grains yielded by male gymnosperm fructifications from the Jurassic flora of Yorkshire. Recent pollen morphology proves that also taxonomic data can be obtained from it, and this was one of the reasons for choosing this subject.

Most descriptions of male gymnosperm fructifications only give slight information on the pollen grains. COUPER (1958) was the first to give clear morphological descriptions. But nowadays many more male fructifications are known than when he published his paper. Also POTONIÉ (1962, 1967) gave pollen-morphological descriptions of some Yorkshire male fructifications, but he took the descriptions mainly from the literature, and dit not reach any new conclusions himself.

The aims of the present study are to examine:

1. Morphology of pollen grains yielded by male gymnosperm fructifications from the Jurassic of Yorkshire (in situ pollen grains), and if possible draw taxonomic conclusions from the pollen morphology.
2. In connection with this direct comparison with other male fossil fructifications.
3. Also comparison with recent pollen grains from the same or similar taxa (if possible).
4. Comparison with dispersed pollen grains from the same horizons as the *in situ* material. This was also done by COUPER (1958) and, to a lesser degree, by POTONIÉ (1962, 1967).

The aim of this is to find out the affinities of dispersed pollen grains. Because dispersed pollen is much more commonly found than macrofossils, it might be possible through this method to extend our knowledge of the distribution of Jurassic plants on the basis of the distribution of their pollen grains.

2. GEOLOGICAL BACKGROUND

The Middle Jurassic of Yorkshire includes both marine and continental deposits. For the continental deposits the term "Deltaic Series" is normally used, although the official term still is "Estuarine Series". But this latter name is very unfortunate, because the character of the rocks really is deltaic, as was already recognized by SIMPSON (1868). Later the term Estuarine Series came into use

Table 1. Stratigraphical subdivision of the Yorkshire Middle Jurassic.

Upper Deltaic (Scalby) Series Scarborough Limestone Series (marine)	Bathonian	
Upper Middle Deltaic (Gristhorpe) Series Millepore Oolite Series (marine) Lower Middle Deltaic (Sycarham) Series Ellerbeck Bed Series (marine) Lower Deltaic (Haiburn) Series	Bajocian	Middle Jurassic
Dogger (marine)	Aalenian	
Lias	Toarcian	Lower Jurassic

(FOX-STRANGWAYS 1892), but the work by KENDALL and WROOT (1924), BLACK (1928, 1929 and 1934) and WILSON, HEMINGWAY and BLACK (1934) made it clear that we are dealing with deltaic sediments.

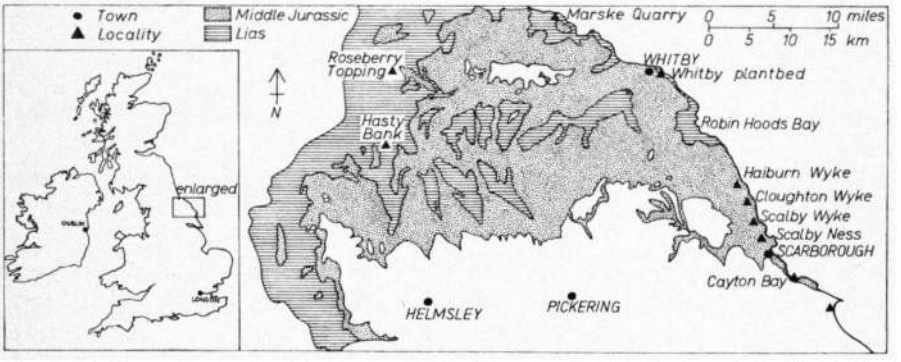
Table I gives the stratigraphical classification of the Middle Jurassic rocks of Yorkshire in general, as proposed by HEMINGWAY (1949) and adopted by HARRIS (1952). The terms between brackets are those proposed by SYLVESTER-BRADLEY (1949).

The word "Series" is in the literature on the Jurassic rocks of Yorkshire used in more than one sense: They are partly formations and partly facies. Although the use of "Series" in this way is not completely correct, the present author uses it, because it is in general use in the literature on the Yorkshire Jurassic.

The three marine formations between the Deltaic Series are all built of several marine horizons, hence the term "Series" instead of "Beds" came into use.

The Ellerbeck Bed consists of ironstones and shales, the Millepore Oolite and the Scarborough Limestone of limestones and shales, and all bear faunas of Molluscs and Brachiopods.

The plant beds that made the Middle Jurassic rocks of Yorkshire so famous, are found in the marine "Dogger" and in the four non-marine horizons of the Deltaic Series.



Text-fig. 1. Map showing the distribution of the Lias and the Middle Jurassic in Yorkshire, and the most important localities.

In Yorkshire the term "Dogger" is used to describe the marine beds between the Lias and the Lower Deltaic (see HEMINGWAY 1949). These beds vary in facies from limestones and coarse calcareous sandstones with marine invertebrate fossils on the coast at Whitby, through chamositic oolites (ironstone) to fine silts and shales which overlie the Lias unconformably at Hasty Bank (see locality map, text-fig. 1). The latter are rich in plant remains and form the well-known plant beds of Hasty Bank and Roseberry Topping; Roseberry Topping formerly believed by THOMAS (1915) to be Liassic in age and continental in origin. Their marine natur was postulated by HARRIS (1964), who sought to explain the erratic distribution of *Pachypteris papillosa*, by suggesting that this plant lived in a salt marsh environment at sea level, and that salt water had, at least, some effect on the whole assemblage. This supposition was strenghened by the discovery of marine microfossils (*Tasmanites* and Dinoflagellates) in every locality where the *Pachypteris* assemblage is found (M.D. Muir-pers. comm.).

Famous localities of the Lower Deltaic are the plant beds of Whitby, Marske Quarry, and Haiburn Wyke (see locality map). They are of two types: In situ plant beds (grey clays) with for instance *Williamsonia* and *Zamites*, and drifted plant beds (channel sands with washed-in fossils, e.g. *Brachyphyllum*) (see also BLACK 1928).

The Lower Middle Deltaic (Sycarham) consists of dark grey clays disturbed by many minor tectonic movements. Their strong carbonization is thought to be a result of these movements. This is the reason why only plant fragments are found. More complete material is found in ironstones, found as loose blocks at these localities. These blocks, however, belong probably to the marine Ellerbeck Bed and not to the Sycarham Series.

The Upper Middle Deltaic (Gristhorpe) consists of grey clays. The famous plant beds of this Series – Gristhorpe bed (Cayton Bay) and Cloughton Wyke – are in situ plant beds and very rich in extremely well preserved plant remains. Most of the reproductive organs we know are from these plant beds.

The plant beds of the Upper Deltaic (Scalby Ness, Scalby Wyke) are definitely drifted plant beds (see BLACK 1929) and consist of channel sands – from siltstone to coarse sandstone.

(For geological comments on all the four Deltaic Series, see WILSON 1958).

Plant beds: According to HARRIS (1952) there are five different types of plant beds in the Yorkshire Jurassic:

1. Truly autochtonous beds (i.e. beds with plants preserved in the position of growth). For example *Equisetum columnare* roots and stems in the Lower Deltaic.
2. Lagoon and sluggish river channel beds (fine mud). The richest is the Gristhorpe bed: Mainly large delicate leaves (suggesting that the plants grew near at hand) mixed with some water-worn material.
3. River channel beds (fine sand). The richest is the Whitby plant bed. They have a somewhat higher proportion of waterworn plants than group 2, but

there also occur well preserved leaves and reproductive organs (type 2 and 3 intergrade).
4. Drifted plant beds (sand), like Black's drifted plant bed at Scalby Wyke (BLACK 1929). Here all but the smallest plants are severely waterworn (type 3 and 4 intergrade).
5. Redeposited plant beds. Such beds have not been described, but are probably common. They consist mainly of though cuticles.

Plant distribution: One of the remarkable things of the Deltaic Series is, that it is impossible to make a fine zonation in each of the four Series. Another peculiarity is that each local plant bed may have its own special flora. Often a rare species (with one or a few known localities) is locally very abundant. This uneven occurrence is probably quite normal in floras from deltas.

Apart from the rare species of which both range and frequency are necessarily ill known, the flora can be divided according to its range and frequency into the following groups (HARRIS 1952):
1. A few species range all four Deltaic Series without any striking change in abundance, for example *Brachyphyllum mamillare*.
2. A few species range the Lower three Series, but are absent from the Upper Deltaic (*Equisetum columnare*).
3. Some species seem to be confined to the Lower Deltaic or the Dogger, and are absent from the other Series.
   For example: *Pachypteris papillosa* is only found in the Dogger and is very common there, but nowhere else.
4. A large group of species occur commonly in the Lower Deltaic, are rare or absent in the next two divisions, but are common again in the Upper Deltaic (*Pachypteris lanceolata, Ptilophyllum pectinoides*).
5. A considerable group of species are more or less abundant in the two middle divisions, but rare or absent above or below.

I would like to add another group to those five:
6. Some species are only known from the Upper Deltaic and are common there (some members of the Ginkgoales).

This may be due partly to the nature of these plant beds (drifted plant beds); the plants they contain may have grown inland and this may be the reason that they are absent from the other Series, where the plant beds are more in situ.

The groups 1, 2, 3, and 6 call for little comment as such groups are to be expected in a gradually changing flora. It is, however, remarkable that there is no group beginning in the Middle Deltaic and passing on into the Upper Deltaic.

The groups 4 and 5 need some comment. The explanation normally given for fluctuations like this, is that they reflect a fluctuation in climate occurring during a period shorter than the period of existing of the species. But there is no evidence at all for such climatic fluctuations in the Yorkshire Jurassic flora. The differences are more easily explained by invoking ecological changes caused by

the advance and retreat of the sea over the Delta area.

In any case, the fluctuations within the Yorkshire Jurassic flora are not very reliable (possibly apart from the small group of species confined to the Dogger and the Lower Deltaic), and it will be preferable to take the flora as a whole for purposes of correlation.

3. MATERIAL AND METHODS

Material: The material studied consisted partly of pollenslides from Yorkshire Jurassic cones, deposited in the British Museum of Natural History, Department of Palaeontology, labelled V. followed by a number. The other part of the material consisted of slides made by the author from Yorkshire material, either collected by herself, or by other members of the Division of Palaeobotany and Pollenmorphology, Botanical Museum and Herbarium, State University, Utrecht. These slides are labelled Yor- followed by a number. The slides with dispersed pollen grains were all from the collection of Dr. M. D. MUIR, made for her thesis (1964). They are all from Yorkshire Jurassic material.

Preparation of the material: The slides were made following two different methods.

1. If it was possible to obtain one or two pollen sacs from a cone or microsporophyll, these were macerated in a mixture of $KClO_3$ and concentrated HNO_3 (commercial grade). The time of maceration is depending on the state of fossilization. After this, they were washed in H_2O and transferred to a dilute solution of NH_4OH, until the brown colour vanished. The pollen sacs were then opened and the pollen grains mounted in glycerin jelly and sealed with paraffin (method after Punt 1962).
2. If it was impossible to obtain complete pollen sacs from a cone, the following method was used:

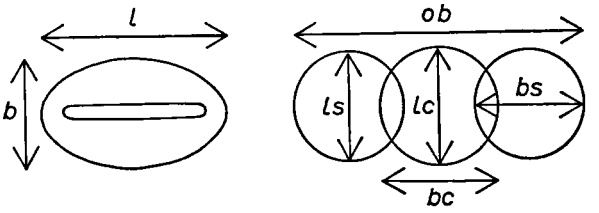
Part of the cone was prepared free from the specimen and transferred to a centrifuge tube. $KClO_3$ and HNO_3 concentrated (commercial grade) were added, and it was heated until boiling. The tube was then placed in a ultrasone (Phillips PH2101/00 21kHz) and vibrated for 1 minute. Because of this treatment, the cone fragment fell into little pieces, the pollen grains were freed and immediately macerated. The material was then centrifuged and decanted, and dilute NH_4OH was added. After 5 minutes the material was again centrifuged and decanted, washed with water, recentrifuged and decanted, and 50 % glycerin-water mixture was added. The material was again centrifuged and after decantation the tubes were placed upside, down for drying. After 20 minutes slides were made, usually six, by mounting the material in glycerin jelly and sealing with paraffin (method after Punt 1962).

Examination of the slides: The slides from the British Museum and the slides with the dispersed pollen grains were first examined and photographed using a Zeiss photomicroscope 0054 (property of Imperial College, London). Lateron I

borrowed the slides, and I examined them just as my own slides, using a Leitz Ortholux microscope, and made the photographs with the Leitz Orthomat camera in combination with the microscope. Some material has also been examined with the help of an electron scanning microscope (Cambridge "Stereoscan" mark II a), in the possession of Imperial College, London.

Nomenclature: The majority of the male fructifications from the Jurassic of Yorkshire are classified in special organ genera, for instance *Caytonanthus* for male Caytonialean fructifications. The specific names used by HARRIS (1961, 1964, 1969) are, according to the present author, in agreement with the International Code of Botanical Nomenclature, and are thus followed by her. Some male cones (especially of Conifers) are simply named by the name of the species to which they belong, with the addition male cone, for instance *Elatides williamsoni* (Brgt) Sew. male cone. In these cases, the cones have either been found attached to the shoots, or have been definitely attributed to the plants mainly on the basis of agreement of cuticle structure, or on the basis of very close association. As to the nomenclature of the dispersed pollen grains, POTONIÉ (1956, 1958, 1960) was mainly followed. Some advices were given by Mrs. Dr. M. D. Muir.

Pollenmorphological terminology: ERDTMAN'S terminology (1952, 1965) was used, especially with regard to the different layers of the exine. Although this terminology is mainly in use for recent (spores and) pollen grains, the present author found that it is quite adequate for fossil pollen grains as well. As to the terms used to indicate length, breadth etc. of colpate and saccate pollen grains COUPER (1958) was followed (see text-fig. 2).



Text-fig. 2. Showing the dimensions measured on monocolpate and saccate pollen grains.
l = length = longest axis; b = breadth; lc = length of corpus; bc = breadth of corpus; ls = length of saccus; bs = breadth of saccus; ob = overall breadth.

4. TAXONOMIC PART

CAYTONIALES

Caytonanthus Harris

Caytonanthus arberi (Thomas) Harris

Pl. 1, figs.: 1, 2, 4.

1925 *Antholithus arberi* – Thomas. p. 237, pl.14 fig. 33, probably also figs. 34, 35, 38, 40, 42 (general description; pollen – grains p. 330).
1931 *Antholithus arberi* – Thomas. p. 651 (discussion).
1937 "*Caytonanthus sp.A*" – Harris p. 44 text-figs. 4A, 6 (isolated Yorkshire – pollen grains).
1941 *Caytonanthus arberi* – Harris. p. 51, pl. 2 figs. 2–4, text-figs. 1, 2, 4, 5, 7, – 8 (general description; pollen grains text-figs. 4, – 5, 7, 8).
1946 "Coprolite of *Caytonia* pollen" – Harris. p. 373, text-fig. 6 (pollen grains).
1951 *Caytonanthus arberi* – Harris. p. 31, text-fig. 2(restoration and discus- – sion; pollen grains text-fig. 2E, F, G, H).
1956 Coprolite – Harris. p. 10, pl. 4 (pollen grains).
1958 *Caytonanthus arberi* – Couper. p. 119, pl. 26 figs. 1–6 (pollen grains).
1962 *Caytonanthus arberi* – Potonié. p. 151, pl. 16 figs. 434–437 (pollen – grains).
1962 *Caytonanthus arberi* – Townrow. p. 19, pl. 2A, D, text-figs. 3d, e, 8b – (pollen grains).
1964 *Caytonanthus arberi* – Harris. p. 15, pl. 1. figs. 11, 12, 16–19, pl. 2 figs. – 2, 3, text-figs. 7A, B, D, E, 8C-F, I (general description; pollen grains text-figs. 8C-F, I).

Harris 1964 also gives some references that may refer either to this species or to *Caytonanthus oncodes*. Some of these have been included in this list as according to the present author's conviction, they refer to *Caytonanthus arberi* and not *Caytonanthus oncodes*.

Age: Middle Deltaic Gristhorpe Series (Middle Jurassic), Yorkshire.

Locality: Gristhorpe bed (Cayton Bay).

Description: The following description is based on re-examination of slides V. 25903f and V. 29469, deposited in the British Museum of Natural History, Department of Palaeontology.

Pollen grains disaccate; sacci slightly offset distally in equatorial view, obscurely reticulate; muri about 1 μ wide, lumina 1–2 μ wide; nexine very thin (less than 0,5 μ); sexine with short columellae and spherical capita; corpus of grains longer than broad, with a pitted tectum; boundary between sacci and corpus not clearly marked, slightly sineous or straight in proximal view; colpus (sulcus) present on the distal surface. Size range in proximal view:

length of corpus: 14 μ (extremes 12–18 μ)
breadth of corpus: 9 μ (extremes 6–12 μ)
length of saccus: 14 μ (extremes 12–18 μ)
breadth of saccus: 10 μ (extremes 8–13 μ)
overall breadth: 25 μ (extremes 22–28 μ)
ratio length to breadth of corpus: 1,74 (1,20–2,83).

Discussion: All published descriptions of the pollen grains of *Caytonanthus arberi* agree in general, but differ in some small details. THOMAS 1925 gives as overall breadth 22–28 μ, COUPER (1958) 25 μ (21-29 μ), TOWNROW (1962) 26 μ, the present author 25 μ (22–28 μ), while HARRIS (1941, 1946, 1964) gives 22 μ (18–28 μ). So they all agree more or less, except Harris, who gives a somewhat smaller size.

As to the structure of the sacci, most authors agree that they have an indistinct fine reticulum. THOMAS (1925) states: "very fine granular appearance probably due to the presence of minute projections on the wall". Did he notice the columellae with their capita? Harris says: "surface of wings pitted, but pitting not very conspicuous". He probably means an indistinct reticulum. COUPER (1958): "bladders sculptured with rather obscure, fine, reticulate thickenings", and TOWNROW (1962): "ornament always faint, corpus smooth or nearly so (on sacci brochi ca. 1,5 μ in diameter, muri about 1 μ wide)".

Most authors describe the colpus (sulcus or leptoma), but neither Thomas nor Couper mention it.

Caytonanthus oncodes Harris

Pl. 1, figs. 3, 5.

1941 *Caytonanthus oncodes* – Harris. p. 52, pl. 2 figs. 5–11, text-figs. 3, 6 (general description; pollen grains text-figs. 3, 6).
1958 *Caytonanthus oncodes* – Couper. p. 199 (pollen grains).
1962 *Caytonanthus oncodes* – Potonié. p. 152, pl. 16 figs. 439, 440 (pollen grains).
1962 *Caytonanthus oncodes* – Townrow. p. 22, pl. 2G, text-figs. 3B, F, G, K, 8A (pollen grains).
1964 *Caytonanthus oncodes* – Harris. p. 17, text-figs. 7C, F, G, 8G, H (general description; pollen grains text-figs. 8G,H).

Age: Middle Deltaic Gristhorpe Series (Middle Jurassic), Yorkshire.

Locality: Gristhorpe bed (Cayton Bay).

Description: The following description is based on re-examination of slides V. 18595b and f, deposited in the British Museum of Natural History, Department of Palaeontology and on material collected by the present author and deposited in the Division of Palaeobotany and Pollenmorphology, Botanical Museum and Herbarium, State University, Utrecht, under no.: Yor-46, Yor-47 and Yor-48.

Pollen grains disaccate; sacci slightly offset distally in equatorial view, reticulate; muri about as wide as lumina, 1 μ wide; nexine very thin (less than 0,5 μ); sexine with rather short columellae and spherical capita; corpus of grains longer than broad, with a pitted tectum; boundary between sacci and corpus not clearly marked, slightly sineous in proximal view; ?no colpus (sulcus) visible on the distal surface. Size range in proximal view;

length of corpus: 18 μ (extremes 14–22 μ)
breadth of corpus: 11 μ (extremes 9–13 μ)
length of saccus: 17 μ (extremes 14–21 μ)
breadth of saccus: 12 μ (extremes 9–14 μ)
overall breadth: 31 μ (extremes 25–36 μ)
ratio length to breadth of corpus: 1,69 (extremes 1,27–2,44)

Discussion: The various published descriptions of the pollen grains of *Caytonanthus oncodes* agree in almost all features.
The only real difference between the present author's description and Harris' and Townrow's is, that I did not see a colpus (sulcus or leptoma). Harris only mentions a colpus in his generic diagnosis, not in his specific one. His figures do not show a colpus (in contrary with those of *Caytonanthus arberi*) except one, showing an immature tetrad. Couper does not mention this feature, so it is not clear if he saw a colpus or not. Couper states that the shape, sculpture and attachment of the sacci is the same as in *Caytonanthus arberi*, while Harris, Townrow and the present author find small differences. Potonié only repeats Harris' description.

Caytonanthus sp. A Harris

1964 Caytonanthus sp.A – Harris. p. 17, text-fig. 8A, B (general description and pollen grains).

Age: Lower Deltaic Series (Middle Jurassic), Yorkshire.

Localities: Roseberry Topping and Boulby Alum Quarry.

Description: The following description is only based on HARRIS 1964, while the author was unable to examine the slides of this species. Terms between ( ) are according to Harris.

Pollen grains of the *Caytonanthus type*, intermediate between *Caytonanthus arberi* and *Caytonanthus oncodes*. Sacci (wings) are obscurely pitted and the overall breadth (mean length from wing to wing) is 25,5 μ (σ2,5 μ), and the length of the saccus (width of the wing) (measured at its middle) is 14,5 μ.

General discussion

In 1925 THOMAS described *Antholithus arberi*, a male Caytonialean fructification. In 1937 HARRIS established the genus *Caytonanthus* for male Caytonialean fructifications, while "*Antholithus* was merely an artificial group name for fossil 'flowers' ". He transferred *Antholithus arberi* to *Caytonanthus arberi* and described *Caytonanthus kochi*; later he also described *Caytonanthus oncodes* (1941) and *Caytonanthus sp. A* (1964).

From the beginning onwards, there has been little doubt that *Caytonanthus* belongs to the Caytoniales. THOMAS (1925) found already *Caytonanthus* pollen grains in the "stigmas" of *Caytonia* "fruits". In 1931 he summarized the different reasons for assuming that *Caytonanthus* and *Caytonia* belong to the same plants:

1. Association. *Antholithus arberi* occurs in the same bed of shale in Cayton Bay in close proximity to *Gristhorpia* (= *Caytonia nathorsti*) and *Caytonia*. Anthers and seeds referable to similar forms were found together in Scoresby Sound, East Greenland, by Dr. HARRIS (1926).
2. Morphology. Male and female sporophylls are both pinnate in general form, and show dichotomy at their apices. Lateral branches terminate in groups either of anthers, or of seeds enclosed in an "ovary" (cupule).
3. Structure. Epidermal cells (cuticles) of both sides of the microsporophylls are almost identical with the corresponding cells in *Gristhorpia*.
4. Pollination. Winged pollen grains characteristic of *Antholithus arberi* occur on the stigmatic surface of *Gristhorpia*.

He also gives the arguments that both the male and female fructifications belong to plants which bore leaves known as *Sagenopteris*.

HARRIS (1940) records that he has found in 38 preparations *Caytonanthus* pollen grains (and no other pollen grains) in the micropyle of *Caytonia nathorsti* and *Caytonia sewardi* seeds. In the case of *Caytonia sewardi* in seeds from intact "fruits" and also in isolated seeds, in the case of *Caytonia nathorsti* only in isolated seeds.

Since the attribution of *Caytonanthus* to the *Caytoniales* has been sufficiently proved, it has even been possible to attribute the different *Caytonanthus* species to species of *Sagenopteris* and *Caytonia*. HARRIS 1941 gives the following attributions:

Caytonanthus arberi to *Caytonia nathorsti* (Thomas) Harris and *Sagenopteris phillipsi* (Brgt) Presl.

Caytonanthus oncodes to *Caytonia sewardi* Thomas and *Sagenopteris colpodes* Harris.

All from the Middle Deltaic Gristhorpe Series, Yorkshire;
and *Caytonanthus kochi* to *Caytonia thomasi* Harris and *Sagenopteris nilssoniana* Halle, from the Lias of Scoresby Sound, East Greenland. HARRIS (1964) suggests that *Caytonanthus* sp. A. belongs to the same species as *Caytonia kendalli* Harris and the larger form of *Sagenopteris colpodes* (Lower Deltaic Series, Yorkshire).

There has been a long discussion about the systematic position of the Caytoniales, which until now is not completely finished; but nowadays almost everybody agrees as to the main points. In this paper the systematic position will only briefly be discussed.

THOMAS (1925) thought that the Caytoniales were very early and primitive Angiosperms, but far remote from the recent Angiosperms, and probably originated from Pteridosperms.

In 1931 he defends this view against Kräusel's idea that the Caytoniales might be Gymnosperms (KRÄUSEL 1926 in Engler). HARRIS 1940 proves that the pollination of the Caytoniales was gymnospermous and not angiospermous as Thomas believed.

In 1937 HARRIS already presumed that the Caytoniales did not have a phylogenetic relationship with the Angiosperms. He then discussed the difference between *Caytonanthus* and any type of Angiosperms stamen or flower: "The 'anther' appears to be a radially symmetrical synangium of the *Asterotheca* type, while in almost all flowering plants it is a bilaterally symmetrical organ with a connective (occasionally strongly developed) and two lateral thecae.

There is no similarity between the way the anthers of *Caytonanthus* and the flowering plant are borne on their filaments, but, on the other hand, if they were borne on the lower side they had a considerable resemblance to the type of fructification seen in certain ferns and Pteridosperms".

HARRIS (1951) gives a detailed account of the relationships of the Caytoniales. He states that the Caytoniales resemble mostly the Pteridosperms, "especially in relation to the general form of leaf, microsporophyll and megasporophyll. The group of Pteridosperms most favoured is Thomas' Corystospermaceae, which agree in their pollen as well as in the size of their parts. Formerly there seemed to be several points of agreement with the Angiosperms, now there are only two-the structure of the stoma and the distribution of the cuticles in the seeds, in both of which they agree better with the Angiosperms than with any known Gymnosperm (including the Pteridosperms). This, however, would be more impressive if these aspects of the Pteridosperms had been more studied".

When we compare the pollen grains of *Caytonanthus arberi*, *Caytonanthus oncodes* and *Caytonanthus sp. A.*, we see that they are quite similar in general, but that they differ in some minor aspects.

The main difference is their overall breadth: In *Caytonanthus arberi* it is 25 μ (22–28 μ), in *Caytonanthus oncodes* 31 μ (25–36 μ) and in *Caytonanthus sp. A.* 25,5 μ (σ2,5 μ). Although there are of course some intermediates, it will be

rather easy to separate pollen grains of *Caytonanthus oncodes* from those of *Caytonanthus arberi* and *Caytonanthus sp. A.* on the basis of their size.

Secondly the sacci of *Caytonanthus oncodes* have a clearer reticulum than in *Caytonanthus arberi*, and much more than in *Caytonanthus sp. A.*; and the sacci bulge more in *Caytonanthus oncodes* than in *Caytonanthus arberi*. All these differences have also been seen by various other authors (e.g. HARRIS 1941, 1964, TOWNROW 1962 and COUPER 1958 – the last mentioned author only saw the differences in size). According to TOWNROW 1962 the corpus of the pollen grains of *Caytonanthus oncodes* is nearly as broad as long, while that of *Caytonanthus arberi* is much longer than broad. This has not been observed by the other authors, including the present author.

The present author thinks that *Caytonanthus arberi* and *Caytonanthus oncodes* may also differ in their germination area: While *Caytonanthus arberi* normally has a quite clear colpus (sulcus or leptoma), it was not observed in *Caytonanthus oncodes* (I cannot say anything about *Caytonanthus sp. A.* for I did not examine the material.) The only species of *Caytonanthus* known from outside Yorkshire is *Caytonanthus kochi* HARRIS 1937 from the Lias of East Greenland. Those pollen grains differ from all the Yorkshire species in having a rather thick wall (exine), a very clear boundary between the corpus and the sacci, a smooth corpus and almost smooth sacci (they show some indistinct thickenings and pits very faintly). The pollen grains of *Caytonanthus kochi* have about the same size as those of *Caytonanthus oncodes*, thus being larger than those of *Caytonanthus arberi* or *Caytonanthus sp. A.*

Comparison Caytonanthus pollen grains

	Caytonanthus arberi	Caytonanthus oncodes	Caytonanthus sp. A.	Caytonanthus kochi
overall breadth	25 μ	31 μ	25,5 μ	30 μ
reticulum on sacci	medium clear	clear	indistinct	indistinct
boundary between corpus and sacci	indistinct	indistinct	indistinct	distinct
exine	thin	thin	thin	thick
colpus	present	? not present	?	?

Comparison with some other pollen-bearing organs

There are some pollen-bearing organs of unknown affinities that show some similarity to *Caytonanthus*, and have often been placed in the Caytoniales: *Pramelreuthia* and *Harrisiothecium*.

Pramelreuthia haberfelneri Krasser was first described as a male fructification without knowing anything of its internal structure, nor of its pollen grains. Later it was thought to be a female fructification like *Caytonia*.

KRÄUSEL's paper (1949) solved this problem. He proved that *Pramelreuthia* was a male fructification, while he got masses of pollen grains out of it. The pollen grains are disaccate, and have an overall breadth of 180–230 μ, according

to him. He thinks that on grounds of the habit and the pollen grains, *Pramelreuthia* must be placed in the Caytoniales. TOWNROW (1962) describes the pollen grains of *Pramelreuthia* in detail: Grain disaccate, monolept. The total width is ca. 160 μ, the corpus is smooth and the sacci are covered with an indistinct ornament (reticulum; muri ca. 3 μ wide, lumina ca. 7 μ wide).

POTONIÉ (1967) states that the total width of the pollen grain is normally less than 160 μ (75–100 μ).

HARRIS (1951) does not agree with Kräusel regarding the taxonomic position of *Pramelreuthia*; he thinks that *Pramelreuthia* is nearer *Harrisiothecium* than *Caytonanthus*.

TOWNROW (1962) thinks *Pramelreuthia* does not show any close resemblance to other microsporophylls. It resembles *Caytonanthus* and *Harrisiothecium* in having disaccate, monolept (= monocolpate) pollen grains, but they differ considerably in size of the pollen grains and in shape and insertion of the sacci.

I agree with him that there does not appear to be any close connection between *Pramelreuthia* and the Caytoniales.

KLAUS (1966) has re-examined the pollen grains of *Pramelreuthia haberfelneri*, and he comes to the conclusion that they are the same as his dispersed pollen species *Lueckisporites junior* (their overall breadth is according to him ca. 80 μ, the length ca. 58 μ). He states that these pollen grains are quite unlike those of the Caytoniales. Their affinities lie probably within the Pteridosperms.

Harrisiothecium marsiloides (Harris) Lundblad has disaccate pollen grains with a total breadth of about 40 μ (HARRIS 1932, TOWNROW 1962, POTONIÉ 1967). The corpus is about 1,5 times longer than broad and the sacci are inserted in the same way as in *Caytonanthus*, *Pteruchus* and *Pteroma*. Both corpus and saccus are covered with a distinct reticulum, somewhat finer on the corpus than on the sacci. HARRIS (1932) compares the pollen with those of *Caytonanthus* and *Pteruchus*.

The systematical position of *Harrisiothecium* is uncertain. Normally it is provisionally placed in the Pteridosperms, but the organ branches in three planes, unlike most Pteridosperm fructifications and also unlike *Caytonanthus*. The pollen grains, however, do show a great deal of resemblance to those of *Caytonanthus* (and to a less extent also to *Pteruchus* and *Pteroma*).

TOWNROW (1965) suggests that the difference between disaccate pollen grains with a distinct germinalum furrow (colpus) and those merely with a thin area (leptoma) between the saccus roots might not only be of generic value (TOWNROW 1962), but even useful at family level.

For among the "Mesozoic Pteridosperms" with disaccate pollen all Corystospermaceae (including *Pteroma* and *Pteruchus*) studied are colpate, while genera of other groups (*Caytonanthus*, *Harrisiothecium* and *Pramelreuthia*) are all leptomatous.

I do not quite agree with him. In the Conifers there occur pollen grains with a leptoma and also pollen grains with a colpus (as Townrow himself also remarks), and it may also be a matter of preservation if there is a colpus or a leptoma.

Moreover in my opinion the pollen grains of *Caytonanthus arberi* have a real colpus.

Comparison with dispersed pollen grains

Pollen grains like those of the Caytoniales have been recorded from all over the world, from the Middle Permian to the Upper Cretaceous (STAPLIN, POCOCK & JANSONIUS 1967). They are very uniform.

COUPER (1958) described pollen grains from the British Jurassic and Lower Cretaceous under the name of *Caytonipollenites pallidus* (Reissinger) Couper (Pl. I, fig. 6). There is little doubt that this species covers all the Yorkshire Caytonialean pollen grains, but it is not necessary that all specimens of *Caytonipollenites pallidus* have Caytonialean affinities.

In the same year NILSSON transferred this species to the genus *Vitreisporites* Leschik: *Vitreisporites pallidus* (Reissinger) Nilsson, while according to this views both genera are identical and *Vitreisporites* has priority. He also makes a new species – *Vitreisporites bjuvensis* – that differs from *Vitreisporites pallidus* in its size (overall breadth 27–36 μ, *pallidus* ca. 28 μ), a much more elongated corpus and in a coarser reticulum on the sacci. This species does not cover *Caytonanthus* pollen grains known until now.

DE JERSEY (1964) emendated *Vitreisporites* to include also pollen grains with little or no ornamentation on the sacci which otherwise have all the essential diagnostic features of the genus (to some extent like *Caytonanthus kochi*). He makes a new species for these pollen grains: *Vitreisporites microsaccus.*

POTONIÉ and KREMP (1956) stated that the Caytonialean pollen grains should be recorded as *Alisporites* Daugherty.

POTONIÉ (1962) stated that *Caytonanthus arberi and Caytonanthus kochi* should be placed in *Vitreisporites* as dispersed pollen grains, while *Caytonanthus oncodes* is more like *Alisporites* than *Vitreisporites.* But the general view of most authors is that dispersed *Caytonanthus* pollen grains should be placed in *Vitreisporites.* DE JERSEY (1964) even goes so far as to say that *Vitreisporites* belongs to the Caytoniaceae. Although it is highly probable that most *Vitreisporites* pollen grains should have belonged to Caytonialean plants, it is not necessary that they all have Caytonialean affinities (see also COUPER 1958).

LYGINOPTERIDALES

PTEROMA Harris

Until now, only one male pteridosperm-like fructification is known in the Jurassic flora of Yorkshire:

Pteroma thomasi Harris

Pl. II, figs. 1, 3, 4, 6.

1964 *Pteroma thomasi* – Harris. p. 170, pl. 7. figs. 1,3, 5, 7, 10, 11, text-figs. 66, 67 (general description; pollen grains text-fig. 67).

Age: Lower Deltaic Series (Middle Jurassic), Yorkshire.

Locality: Hasty Bank.

Description: The following description is based on re-examination of slide V. 45677, deposited in the British Museum of Natural History, Department of Palaeontology, and on material collected by the author and deposited in the Division of Palaeobotany and Pollenmorphology, Botanical Museum and Herbarium, State University, Utrecht under no. Yor-2, Yor-29a, Yor-38, Yor-39, Yor-40, Yor-41, Yor-42, and Yor-43.

Pollen grains disaccate; sacci slightly offset distally (only visible in suitable orientated specimens), obscurely reticulate; muri wider than lumina; lumina irregular, 1–2 μ wide; nexine thin, sexine consisting of columellae-layer and capita-layer; columellae long; capita small, spherical;
corpus of grains longer than broad, with pitted tectum; boundary between sacci and corpus obscurely marked, only slightly sineous in proximal view;
colpus (sulcus) present on the distal surface, about as long as the corpus, narrow. Size range in proximal view:

length of corpus: 49 μ (extremes 42–57 μ)
breadth of corpus: 34 μ (extremes 28–43 μ)
length of saccus: 46 μ (extremes 37–53 μ)
breadth of saccus: 29 μ (extremes 24–40 μ)
overall breadth: 76 μ (extremes 65–100 μ)
ratio length to breadth of corpus: 1,47 (extremes 1,17–1,89)

Discussion: The ornamentation of the sacci is rather difficult to see because most of the specimens are poorly preserved; it is certainly not a clear reticulum. The sulcus is only visible in a few specimens (plate II, fig. 1). The attachment of the sacci is very indistinct, giving rise to inaccurate measurements, and is in proximal view only slightly sineous.

General discussion and comparison with other Pteridosperm fructifications
Pteroma was established by HARRIS (1964) as an organ genus for male Pteridosperm fructifications resembling *Pteruchus* (Southern hemisphere-Middle Triassic) and to a lesser extent *Harrisiothecium* (LUNDBLAD 1961, Rhaetic of Greenland). *Pteroma thomasi* resembles most *Pteruchus simmondsi* (TOWNROW 1962) in appearance, but the pollen sacs in *Pteruchus simmondsi* point freely outwards, while they point slightly inwards in *Pteroma.*

Pteruchus africanus (TOWNROW 1962, including *Pteruchus papillatus* THOMAS 1933) has numerous pollen sacs borne along diverging veins and *Pteruchus dubius* (TOWNROW 1962) has very numerous pollen sacs crowded beneath an

elongated head, while those of *Pteroma* could be described as in two rows or as an elongated ring of radiating pollen sacs. *Pteruchus petasatus* has, like *Pteruchus dubius.* an elongated head, but with only about 20 pollen sacs in two or three rows (TOWNROW 1965).

In *Harrisiothecium* the branching of the organ is on all sides, while in *Pteruchus* and probably also in *Pteroma* it is pinnate (in one plane).

As to the pollen grains: *Pteroma thomasi* pollen grains are very much alike those of *Pteruchus*; they resemble especially *Pteruchus dubius* closely, but the lumina in the reticulum of the sacci of *Pteroma* are definitely smaller than in *Pteruchus dubius.* Also *Pteruchus dubius* has a distinct reticulum, while *Pteroma* pollen is obscurely reticulate.

Pteruchus simmondsi, also with pollen of similar size, has a much coarser reticulum, while *Pteruchus africanus* with smaller pollen grains also has a prominent reticulum (see TOWNROW 1962a, b, POTONIÉ 1962 and THOMAS 1933). *Pteroma thomasi* pollen grains differ from those of *Pteruchus petasatus* in being much smaller (overall breadth of *Pteruchus petasatus* 110 μ) and in having less-distinct saccus roots and a much less-distinct ornament. *Harrisiothecium* has much smaller pollen grains (overall breadth ca. 40 μ), with a distinct reticulum.

So these pollen grains are more closely comparable to those of the Caytoniasel, than to those of *Pteroma* and *Pteruchus* (see also the chapter about the Caytoniales).

Comparison with dispersed pollen grains

Of the dispersed pollen grains *Alisporites thomasi* Nilsson 1958 (= *Pteruchipollenites thomasi* Couper 1958) (Pl. II fig. 6) resembles *Pteroma thomasi* most, but there are some differences between them (see also HARRIS 1964):

The first point is that the measurements are not exactly the same, for example the overall breadth in *Alisporites thomasi* is 60 μ (extremes 45–78 μ), while it is 76 μ (extremes 65–100 μ) in *Pteroma*, and the ratio length to breadth of the corpus is 1,28 (extremes 0,95–2,1) in *Alisporites thomasi* and 1,47 (extremes 1,17–1,89) in *Pteroma.*

The sacci show a coarser reticulum in *Alisporites thomasi*; the line of attachment of the sacci is clearer than in *Pteroma* and the corpus is almost smooth, while it has a pitted tectum in *Pteroma.*

Alisporites thomasi was first described from the Brora Coal, N. E. Scotland (Middle Jurassic), but was later recorded from more places, for example Tubbergen borehole, Netherlands,Upper Jurassic (BURGER 1966) and Scania, Sweden, Lias (NILSSON 1958). It ranges at least from the Lower Lias to almost the top of the Cretaceous (STAPLIN, POCOCK and JANSONIUS 1967). It has also been recorded from the Jurassic of Yorkshire by Dr. M. D. Muir (see HARRIS 1964). Those pollen grains have all the characters of *Alisporites thomasi*, and in addition most of the grains have the sacci pointing strongly distally. In *Pteroma* the sacci point almost transversely or very slightly distally.

So I think that, although they are rather similar, *Alisporites thomasi* pollen

grains must have originated from fructifications different from *Pteroma thomasi.* But its affinities probably lie within the Pteridosperms, because this type of pollen grain has only been found in situ in the Pteridosperms. Dr. M. D. Muir (1964) described in her thesis on dispersed spores and pollen grains from Hasty Bank (Yorkshire), 1964, a new species of *Alisporites* which she provisionally calls *Alisporites sp. B.* (Pl. II, fig. 2). This *Alisporites sp. B.* differs in no respect from pollen of *Pteroma thomasi,* and therefore I think they must be identical; i.e.: *Alisporites sp. B.* must have originated from *Pteroma thomasi.* Moreover *Pteroma thomasi* (megafossil) has until now only been recorded from Hasty Bank. Dr. M. D. Muir recorded this *Alisporites sp. B.* next to Hasty Bank, also from various other Yorkshire localities, very often together with *Pachypteris papillosa* (Thomas et Bose) Harris, i.e. the leaf to which *Pteroma thomasi* belongs.

For details see HARRIS (1964).

The other *Alisporites* species described until now differ in many more respects from *Pteroma thomasi* than *Alisporites thomasi.*

CYCADALES

ANDROSTROBUS Schimper

Androstrobus manis Harris

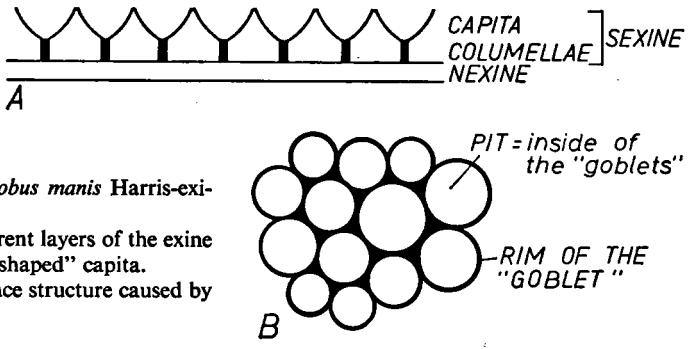
Pl. III, fig. 1, 4; pl. IV, fig, 1; text-fig. 3

1941 *Androstrobus manis* – Harris. p. 76, pl. 5, fig. 6–9; text-figs. 1, 3C, D, E, (general description; pollen grains text-fig. 1 A–D).
1958 *Androstrobus manis* – Couper. p. 122, pl. 26 figs. 15, 16 (pollen grains).
1960 *Androstrobus manis* – Thomas et Harris. p. 141, pl. 1 fig. 1 (pollen in micropyle of Beania).
1962 *Androstrobus manis* – Potonié. p. 154, pl. 16 fig. 447 (pollen).
1964 *Androstrobus manis* – Harris. p. 157, pl. 6. fig. 1–4, 12; text-fig. 63 A-D, J–L (general description; pollen grains text-fig. 63 A, B).
1967 *Androstrobus manis* – Potonié. p. 120, pl. 13 fig. 253 (pollen).

Age: Middle Deltaic Gristhorpe Series (Middle Jurassic), Yorkshire.

Locality: Gristhorpe bed (Cayton Bay).

Description: The following description is based both on re-examination of slides V. 25900a (type) and V. 25899d, deposited in the British Museum of Natural History, Department of Palaeontology, and on material collected by the author and deposited in the Division of Palaeobotany and Pollenmorphology, Botanical Museum and Herbarium, State University, Utrecht under no. Yor-18, Yor-18a, Yor-33, and Yor-34.



Text-fig. 3. *Androstrobus manis* Harris-exine structure.
A. showing the different layers of the exine with the "goblet-shaped" capita.
B. showing the surface structure caused by the "goblets".

Pollen grains monocolpate; outline elliptical to almost circular; longest axis 35 μ (extremes 30–41 μ); colpus extending over about 7/8th of length of the pollen grain, slitlike, often accompanied by folds on either side; wall consisting of two layers (nexine and sexine), 1–1,5 μ thick; nexine 0,5 μ, smooth; sexine with two components: columellae-layer and capita-layer; columellae rather distinct, rodlets, bearing goblet-shaped capita; capita laterally fused; surface pitted; pits shallow cavities, 0,5 μ in section.

Discussion: The structure of the surface can be explained by the shape of the columellae and their capita: The pits are the insides of the "goblets" (the goblet-shaped capita), while the walls around the pits are formed by the rims of the "goblets" (see text-fig. 3 and pl. III fig. 1).

Harris, Couper and Potonié all agree in their general description of the pollen grains, but they have slightly different opinions about the wall structure. Potonié simply states that it is smooth; Harris says: "Wall almost perfectly smooth, but appearing faintly and very finely mottled" (he seemed to have got the impressions of the "goblets") and Couper says that the exine is finely scabrate under oil immersion and smooth under high power. I definitely do not agree with him.

Androstrobus wonnacotti Harris

Pl. III, figs. 2, 3, 5.

1941 *Androstrobus wonnacotti* – Harris. p. 79, pl. 5 figs. 11, 15, text-fig. 2 (general description; pollen grains text-fig. 2D–F).
1958 *Androstrobus wonnacotti* – Couper. p. 122, pl. 26 figs. 17, 18 (pollen grains).
1960 *Androstrobus wonnacotti* – Thomas et Harris. p. 144, pl. 2 figs. 8–14 (further specimens and pollen).
1961 *Androstrobus wonnacotti* – Harris. p. 321, text-fig. 2 (restoration).
1962 *Androstrobus wonnacotti* – Potonié. p. 155, pl. 16 fig. 449, 450 (pollen grains).

1964 *Androstrobus wonnacotti* – Harris. p. 159, pl. 5 fig. 8, text-fig. 63 E–I (general description: pollen grains text-fig. 63 E–G).

Age: Lower Deltaic and Middle Deltaic Gristhorpe Series (Middle Jurassic), Yorkshire.

Localities: Hasty Bank, Whitby *N. tenuinervis* bed, Cloughton *Solenites* Bed, Gristhorpe Bed (Cayton Bay).

Description: The following description is based on re-examination of slides V. 25850c and d, deposited in the British Museum of Natural History, Department of Palaeontology.

Pollen grains monocolpate; outline slightly elliptical to circular; longest axis 29 μ (extremes 24–33 μ); colpus extending over about 7/8th of the length of the pollen grain, slitlike or broad; wall (consisting of nexine and sexine) 1,5–2 μ thick; nexine smooth, 0,5–1 μ thick; sexine with columellae- and capita-layer: columellae rodlike, rather distinct; capita goblet-shaped, fused laterally, rather indistinct; surface pitted; pits shallow cavities 0,5–1 μ in section.

Discussion: Probably the structure of the surface of the pollen grains of *Androstrobus wonnacotti* can be explained in the same way as in *Androstrobus manis*, but in *Androstrobus wonnacotti* the "goblets" are rather indistinct; only some specimers show them clearly (pl. III, fig. 5).

Harris, Couper and Potonié all agree that *Androstrobus wonnacotti* pollen grains are the same as those of *Androstrobus manis*, but of smaller size.

Androstrobus prisma Thomas et Harris

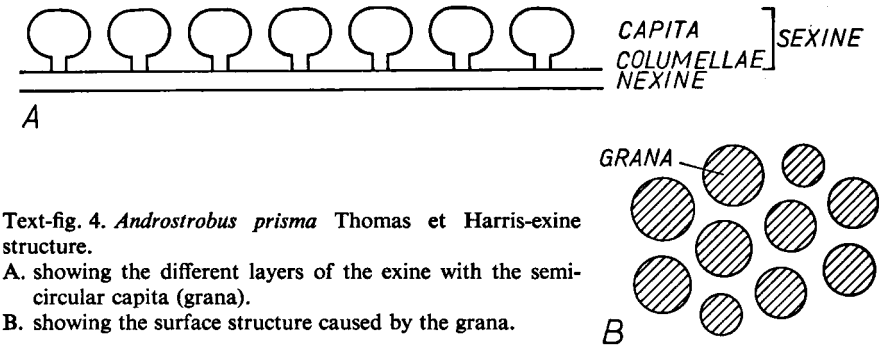
Pl. IV, figs. 6, 7; pl. V, figs. 1, 2; text-fig. 4.

1960 *Androstrobus prisma* – Thomas et Harris p. 148, pl. 3 figs. 18–21, pl. 4 figs. 23, 24, 26, 27; text-fig. 2 (general description; pollen grains pl. 4 fig. 24, text-fig. 2a, b).
1962 *Androstrobus prisma* – Potonié. p. 155, pl. 16 fig. 448 (pollen).
1964 *Androstrobus prisma* – Harris. p. 160, pl. 1 fig. 21, pl. 6 figs. 5, 8 (general description).

Age: Lower Deltaic (Middle Jurassic), Yorkshire.

Localities: Hasty Bank, Roseberry Topping, Marske Quarry.

Description: The following description is based on re-examination of slide 42386, deposited in the British Museum of Natural History, Department of Palaeontology, and on slides made of material collected by the author and depo-



Text-fig. 4. *Androstrobus prisma* Thomas et Harris-exine structure.
A. showing the different layers of the exine with the semi-circular capita (grana).
B. showing the surface structure caused by the grana.

sited in the Division of Palaeobotany and Pollenmorphology, Botanical Museum and Herbarium, State University, Utrecht under no. Yor-17, Yor-35, Yor-36, Yor-37, Yor-44, Yor-45, and Yor-68.

Pollen grains inaperturate; outline elliptical to circular; longest axis 32 μ (extremes 26–36 μ); wall 1 μ thick; nexine indistinct, very thin; sexine with columellae- and capita-layer: columellae-layer thin (less than 0,5 μ); capita about 1 μ, semispherical, rounded (grana); grana in surface view circular, about 1 μ in section.

Discussion: The pollen grains are often folded, giving the impression that there is a colpus present; some pollen grains were not folded, and they did not show a colpus, only sometimes a thin area. I have never been able to find a real colpus.

HARRIS (1964) does not describe a colpus either, but he does not use this as a difference with the other *Androstrobus* pollen grains, while he uses the difference in form (*Androstrobus prisma* pollen grains are more round).

Androstrobus prisma differs markedly from the other *Androstrobus* pollen grains by having grana instead of "gobletshaped" capita (text-fig. 4). The grana give the impression of a so called negative reticulum. The pits of the other *Androstrobus* pollen grains also give the impression of a reticulum, but under high power or with the aid of phase-contrast microscopy the difference is easy to see (pl. IV, figs. 6, 7).

The only real disagreement between Thomas et Harris' (and Harris') description and mine is in the measurements: They state that the longest axis of the pollen grain is 35 μ, while I find 32 μ. I re-examined their slides and again came to 32 μ.

Androstrobus szei Harris

pl. IV, figs. 4

1964 *Androstrobus szei* – Harris p. 162, pl. 6 figs. 9, 11, 13, text-fig. 64, A–C (general description; pollen grains text-fig. 64 B, C).

Age: Middle Deltaic Gristhorpe Series (Middle Jurassic), Yorkshire.

Locality: Gristhorpe Bed (Cayton Bay).

Description: The following description is based on re-examination of slide V. 45487 (type), deposited in the British Museum of Natural History, Department of Palaeontology.

Pollen grains monocolpate; outline elliptical to almost circular; longest axis 29 μ (extremes 24–32 μ); colpus extending over about 7/8 th of the length of the pollen grain, slitlike; wall 1–1,5 μ thick; nexine smooth, less than 0,5 μ thick; sexine with columellae- and capita-layer; columellae rodlets bearing goblet-shaped capita; capita fused laterally; surface pitted; pits shallow cavities, 0,5 μ in section.

Discussion: The surface structure can be explained in the same way as in *Androstrobus manis* (but is somewhat less clear than in that case) and in *Androstrobus wonnacotti*. Quite a few pollen grains show the goblet-shaped capita.
Harris' description agrees with mine, except that he did not see the wall structure.

Androstrobus major van Konijnenburg

pl. IV, figs. 5

1969 *Androstrobus major* – van Konijnenburg-van Cittert. p. 267, pl. 1, 2, text-figs. 1, 2, (general description; pollen grains pl. 1, 2 fig. B).

Age: Lower Deltaic (Middle Jurassic), Yorkshire.

Locality: Hasty Bank.

Description: The following description is based on slides from the type-specimen, deposited in the Division of Palaeobotany and Pollenmorphology, Botanical Museum and Herbarium, State University, Utrecht, under no. Yor-27.

Pollen grains monocolpate; outline elliptical to circular; longest axis 33 μ (extremes 29–38 μ); colpus extending over about 7/8th of the length of the pollen grains, slitlike; wall 1–1,5 μ thick; nexine smooth, thin (less than 0,5 μ); sexine with columellae- and capita-layer; columellae-layer almost invisible, supporting the capita-layer; surface pitted; pits shallow cavities, 1 μ in section.

Discussion: Probably the structure of the surface can be explained in the same way as in *Androstrobus manis, Androstrobus wonnacotti* and *Androstrobus szei,*

but in *Androstrobus major* there is nothing to be seen of goblet-shaped capita.

The only reason for assuming that they may be present is that the surface structure is exactly the same as in *Androstrobus manis*, *Androstrobus wonnacotti* and *Androstrobus szei.*

Androstrobus sp. A Harris

pl. IV, figs. 2, 3.

1964 *Androstrobus* sp. A – Harris. p. 163, pl. 6 fig. 2 (general description).

Age: Lower Deltaic (Middle Jurassic), Yorkshire.

Localities: Hasty Bank, Little Roseberry.

Description: The following description is based on re-examination of slide V. 51943, deposited in the British Museum of Natural History, Department of Palaeontology.

Pollen grains monocolpate; outline elliptical to almost circular; longest axis 30 μ (extremes 26–36 μ); colpus extending over about 7/8th of the length of the pollen grain; slitlike; wall 1–1,5 μ thick; nexine smooth, indistinct, thinner than 0,5 μ; sexine with columellae- and capita-layer: columellae rather distinct, rodlets, bearing goblet-shaped capita (rather indistinct,), capita fused laterally; surface pitted; pits shallow cavities, 0,5 μ in section.

Discussion: The surface structure can be explained in the same way as in *Androstrobus manis* (but is less clear), *Androstrobus wonnacotti* and *Androstrobus szei.* Only in some specimens the "goblets" are clearly visible. Harris' description agrees with mine, except that he did not examine the wall structure.

General discussion

The genus *Androstrobus* was established by SCHIMPER in 1872 for fossil male cones, attributed to the Cycadales. Schimpers' concept that *Androstrobus* was a fossil Cycad cone was further supported by HARRIS 1941 on the following grounds:

"The form of the microsporophyll is like that of the Cycads in general; it is particular similar to that of *Encephalartos* except that it is probably a good deal thinner in substance.

In no group but the Cycads is the whole under surface covered with sessile sporangia, and it appears that, as in the Cycads alone, the sporangia are grouped in small sori with their apertures facing one another. An important point of agreement with the Cycads is provided by the very thick wall of the sporangia: in this they agree also with some other groups (Pteridosperms, Bennettitales),

but differ from the Conifers, in which the sporangial wall is thin and in fossil specimens reduced to a delicate and translucent membrane.

The thickness of the wall is largely provided by the heavily thickened epidermal cells, which appear to agree in their strongly pitted walls with those of the living Cycads. Another point of agreement with the Cycads is provided by the inner cuticle of the sporangium, which it was found possible to demonstrate also in recent *Encephalartos* cone; I am unaware of its existence in Conifers, but it is seen also in certain Pteridosperms.

The cuticle of the microsporophyll provides stomata in which the subsidiary cells are arranged in a ring, having a different origin from the guard cells. This type is found in many plants, including nearly all gymnosperms except the Bennettitales. The thickenings of the surface of the guard cells themselves is also of the general gymnosperm type, but the scattering of the stomata and the rather irregular grouping of the subsidiary cells round the sunken stomata is a good deal more characteristic of the Cycads (and perhaps the Pteridosperms) than of the Ginkgoales or Conifers. The microspores agree with the type which is found throughout the Cycads, but also in many members of other Gymnosperm families, being that WODEHOUSE (1935) considers the primitive or generalised condition for this family.

Very perfect and fairly complete agreement has thus been established between *Androstrobus* and the Cycad male cone, but difference between it and the reproductive organs of all other families. It is thus clear that *Androstrobus* is to be classified as a Cycadean male cone".

I want to alter slightly the diagnosis of *Androstrobus*, in order to separate this genus from *Hastystrobus*, which has tricolpate pollen grains but is in most other respects like *Androstrobus* (see also the chapter on *Hastystrobus muirii*).

Diagnosis: Male cone, bearing numerous sporangia on lower (abaxial) sides

Comparison of Androstrobus pollen grains

	colpus	outline	length	thickness of wall	capita	surface
A. manis	present	elliptical-circular	25 μ	1–1,5 μ	goblets	pitted
A. wonnacotti	present	elliptical-circular	29 μ	1,5–2 μ	goblets	pitted
A. prisma	absent	almost circular	32 μ	1 μ	grana	granulate
A. szei	present	elliptical-circular	29 μ	1–1,5 μ	goblets	pitted
A. major	present	elliptical-circular	33 μ	1–1,5 μ	?goblets	pitted
A. sp. A.	present	elliptical-circular	30 μ	1–1,5 μ	goblets	pitted

of microsporophylls; cuticle unknown or, if known, with straight-walled cells and haplocheilic stomata; pollen grains unknown or, if known, circular to elliptical in outline, inaperturate or monocolpate.

It has been possible to attribute some of the *Androstrobus* species to Cycad leaf species, sometimes together with female cones and cone-scales, thus giving a fairly complete idea of a fossil Cycad plant.

These attributions have been made on the grounds of association and agreement of the cuticles. Up till now the following attributions have been made: *Androstrobus manis* to *Nilssonia compta* (Philips) Bronn (and also *Beania gracilis* Carruthers-female cone-, and *Deltolepis crepidota* Harris-scale leaf- to *Nilssonia compta*), all from the Middle Deltaic Gristhorpe Series, see HARRIS 1941, 1942.

Androstrobus wonnacotti to *Nilssonia tenuinervis* Seward (and also *Beania mamayi* Thomas et Harris –female cone –, and *Deltolepis calyptra* Harris – scale leaf –), from the Lower and Middle Deltaic Series, see THOMAS et HARRIS (1960) and HARRIS (1964).

Androstrobus prisma to *Pseudoctenis lanei* Thomas, from the Lower Deltaic Series, see THOMAS et HARRIS (1960) (in this case no female cone or scale leaf could be attributed.)

Androstrobus szei, *Androstrobus major*, and *Androstrobus sp. A.* have not been attributed to any leaf species so far.

From the preceding descriptions of the pollen grains we learn that almost all the *Androstrobus* species have the same type of pollen grains, except *Androstrobus prisma*, which pollen is granulate with a thin wall; the remaining species have pollen grains with thicker walls and a pitted surface. Now *Androstrobus prisma* is attributed to *Pseudoctenis lanei*, a plant with Cycad affinities, but not belonging to the family of the Nilssoniaceae, to which all the species of *Nilssonia* belong (including *Nilssonia compta* with *Androstrobus manis* and *Nilssonia tenuinervis* with *Androstrobus wonnacotti*).

THOMAS & HARRIS (1960) pointed out when they described and discussed *Androstrobus prisma*, that there are some differences with the other *Androstrobus* species; but they did not consider them of generic importance. Also the type of pollen grains of *Androstrobus prisma* seems to be different from the type of pollen grains of the other *Androstrobus* species currently known. So *Androstrobus prisma* might belong to another group of Cycadalean plants different from the other *Androstrobus* species. It might be possible to distinguish between the pollen grains of the Nilssoniaceae and of the group to which *Pseudoctenis* belongs (which also includes the genera *Ctenis* and *Paracycas*, and possibly also *Ctenozamites* – see HARRIS 1964). If this supposition is right, *Androstrobus major*, *Androstrobus szei* and *Androstrobus sp. A.* would belong to the Nilssoniaceae because of the characters of their pollen grains.

The species of *Nilssonia* known from Yorkshire, and to whom until now no male cones have been attributed, are the following:

Nilssonia thomasi	– Lower Deltaic Series	– rare
Nilssonia syllis	– Lower Deltaic Series	– rare
Nilssonia kendalli	– Lower Deltaic Series	– common
Nilssonia tenuicaulis	– Middle Deltaic Series	– rare
Nilssonia revoluta	– Upper Deltaic Series	–rare
Nilssonia sp. A.	– Lower Deltaic Series	– rare; there is a possibility that this is an abnormal form of *Nilssonia tenuinervis* (see HARris 1964).
Nilssonia sp. B.	– Lower and Middle Deltaic Series	– only known from cuticle fragments.

Androstrobus szei is known from the Middle Deltaic Series and might on the grounds of association be attributed to *Nilssonia tenuicaulis* or *Nilssonia sp. B.*, while *Androstrobus major* and *Androstrobus sp. A* are both from the Lower Deltaic Series and might for the same reason be attributed to *Nilssonia thomasi*, *Nilssonia syllis*, *Nilssonia kendalli*, *Nilssonia sp. A* or *Nilssonia sp. B.* But all this is sheer speculation, and nothing can be said definitely until we find grounds to attribute these *Androstrobus* species to leaf species, and until we find more male Cycad cones (especially if they can be attributed to the group of *Pseudoctenis-Ctenis*).

As for *Androstrobus* species from regions other than Yorkshire, for only four of them there is reason to believe that they resemble Cycad male cones (see VAN KONIJNENBURG-VAN CITTERT 1969) and there was no material available to the present author of any of those four. The pollen grains seem to resemble the general Cycadean type of pollen grain: elliptical to almost circular in outline, and monocolpate. Detailed photographs of the pollen grains have never been given.

Comparison of the pollen grains to those of the recent Cycads

In order to be able to compare the *Androstrobus* pollen grains with grains of recent Cycads, the following genera and species have been studied: *Cycas circinatis* L., *Stangeria paradoxa* T. Moore, *Zamia loddigesii* Miq., *Dioon edule* Lindl., and *Encephalartos barteri* Carruthers (of the other genera and species no material was available).

The following descriptions were made:

Cyas circinatis L. (pl. V, figs. 3, 4): based on slide 421, Division of Palaeobotany and Pollenmorphology, Botanical Museum and Herbarium, State University, Utrecht.

Pollen grains monocolpate; outline in polar view ellipsoid, in equatorial view trapezoid; longest axis ca. 30 μ; colpus extending over about 7/8th of the length of the pollen grain, rounded at the ends; exine thickest proximally 2 μ, distally 1 μ; nexine especially proximally thick in comparison with sexine; nexine smooth; sexine consisting of columellae- and capita-layer; columellae rodlike, indistinct; capita laterally fused, forming an irregular fine reticulum (semitectate); muri wider than section of lumina; meshes of reticulum up to 0,5 μ.

Stangeria paradoxa T. Moore (pl. V, figs. 5, 6, 7): based on slide 1880, Division of Palaeobotany and Pollenmorphology, Botanical Museum and Herbarium, State University, Utrecht.

Pollen grains monocolpate; outline in polar view ellipsoid, in equatorial view rounded rectangular; longest axis ca. 37 μ; colpus extending over 7/8th of the length of the pollen grain, not deeply sunken, rounded at the ends; exine laterally thickest up to 2,5 μ, proximally and distally 1,5 μ; nexine especially laterally thick in comparison with sexine, nexine smooth; sexine consisting of columellae- and capita-layer: columellae rodlike, indistinct; capita laterally fused forming a tectum.

Zamia loddigesii Miq. (pl. VI, figs. 3, 5): based on slide 423, Division of Palaeobotany and Pollenmorphology, Utrecht.

Pollen grains monocolpate; outline in polar view ellipsoid, in equatorial view rounded rectangular; longest axis ca. 28 μ; colpus extending over about 7/8th of the length of the pollen grain, rounded at the ends; exine laterally thickest, up to 1,5 μ, proximally and distally 1 μ; nexine especially laterally thick in comparison with sexine, nexine smooth; sexine consisting of columellae- and capita-layer: columellae rodlike, indistinct; capita laterally fused, forming a tectum.

Encephalartos barteri Carruthers (pl. VI, fig. 1): based on slide 2297, Division of Palaeobotany and Pollenmorphology, Utrecht.

Pollen grains monocolpate; outline in polar view ellipsoid, in equatorial view rounded rectangular; longest axis ca. 28 μ; colpus extending over 7/8th of the length of the pollen grain, rounded at the ends; exine laterally thickest, up to 2 μ, proximally and distally 1,5 μ; nexine especially laterally thick in comparison with sexine, nexine smooth; sexine consisting of columellae- and capita-layer: columellae rodlike, indistinct; capita laterally fused, forming a tectum.

Dioon edule Lindl. (pl. VI, figs, 2, 4, 6, 7): based on slide 2296, Division of Palaeobotany and Pollenmorphology, Utrecht.

Pollen grains monocolpate; outline in polar view ellipsoid, in equatorial view rounded rectangular; longest axis ca. 31 μ; colpus extending over 7/8th of the length of the pollen grain, rounded at the ends; exine thickest proximally, up to 3μ, laterally and distally 2 μ; nexine thin in comparison with sexine, nexine smooth; sexine consisting of columellae- and capita-layer: columellae rodlike, very long, distinct; capita spherical, small, laterally fused, forming a tectum.

Discussion: The pollen grains of *Dioon edule* give the impression that there is a tectum perforatum present. Mrs. Dr. M. D. Muir took Stereoscan pictures of those pollen grains, and they showed that there is a very thin but unperforated tectum present, in which the capita bulge – so giving the impression that there are small pits between them (pl. VI, fig. 6).

WODEHOUSE (1935) was the first to describe the pollen grains of some Cycads

(*Cycas*, *Zamia*, *Ceratozamia*, *Dioon* and *Microcycas*). He described *Cycas* as finely scabrate, *Zamia* as smooth or scabrate and *Dioon* as reticulate-pitted.

ERDTMAN (1943 and 1965) also described some Cycad pollen grains, and his descriptions agree very well with mine, except that he did not mention the difference in thickness of the various parts of the wall.

As far as I have studied the different pollen grains of the recent Cycads (I was unable to study material of *Ceratozamia*, *Microcycas* and *Macrozamia*), I can divide them into three different types:

1. *Cycas*-type: outline in equatorial view trapezoid, exine proximally thickest and a fine reticulum; nexine thick in comparison with sexine.
2. *Zamia*-type (including *Zamia*, *Stangeria* and *Encephalartos*): outline in equatorial view rounded rectangular, exine laterally thickest and a tectum; nexine thick in comparison with sexine.
3. *Dioon*-type: outline in equatorial view rounded rectangular, exine proximally thickest, and a tectum; nexine thin in comparison with sexine.

It would go beyond the purpose of this paper to discuss these different types of pollen grains in connection with their taxonomic position.

Comparing the *Androstrobus* pollen grains with those of the recent Cycads, one may say that the general impression is the same; elliptical (or ellipsoid in polar view) to circular pollen grains (longest axis between 20 and 40 μ), with a slitlike or sometimes broad colpus extending over about 7/8th of the length of the pollen grain.

But there are differences as well, especially in the structure of the exine; the goblet-shaped capita that occur in *Androstrobus manis*, *Androstrobus wonnacotti*, *Androstrobus szei*, *Androstrobus sp. A* and probably also in *Androstrobus major*, do not occur in recent Cycads. *Androstrobus prisma* is definitely granulate, and again this is not observed in recent Cycads. So it seems that in the course of time the structure of the exine of the Cycadales must have changed.

COUPER (1958) also compared the pollen grains of *Androstrobus manis* and *Androstrobus wonnacotti* with those of recent Cycads, but he was only able to examine pollen grains of *Zamia*, which he thought closely comparable with those of the *Androstrobus* species.

Couper's species *Clavatipollenites hughesii* (dispersed pollen from the Wealden and Aptian of Great Britain) is more or less similar to the pollen of *Dioon edule*; although the pollen grains are much smaller than those of *Dioon*, they have about the same exine structure. Couper suggested that they might be of angiosperm origin. He stated: "Whatever the true affinity of *Clavatipollenites hughesii* is, the writer considers it fair to claim from his knowledge of spore and pollen grain morphology, that it almost certainly does not belong to the Pteridophyta or Pteridosperms and is unlike any known fossil or recent pollen grain of the Gymnospermae".

KEMP (1968) emendated this species and described a new one: *Clavatipollenites rotundus*. She stated about the affinity: "In spite of the angiospermous character of some of the features of *Clavatipollenites* it still remains possible that the

grains were produced by a member of some extinct gymnospermous group. The over-all shape of the grains resembles that of both living and fossil cycadophyte pollen. The form of the sulcus, particularly where it is rounded at its extremities, is closer to that of living cycad pollens than to most angiosperms pollen".

It now appears that also because of its exine ornamentation *Clavatipollenites* may have Cycadalean affinities, although of course the Angiosperms have to be considered as well.

Comparison with dispersed pollen grains

COUPER (1958) described three species of *Monosulcites* Cookson ex Couper from the Jurassic of England: *Monosulcites minimus* Cookson, *Monosulcites carpentieri* Delcourt et Sprumont and *Monosulcites subgranulosus* Couper. He states that "many specimens of *Monosulcites minimus* (pl. VII, fig. 1) from the Upper Deltaic specimens are an extremely good match with those of *Ginkgo huttoni*, which is abundant in this series". But he thinks that the dispersed pollen grains of the Cycads and some Bennettitales also fall in this species. *Monosulcites minimus* is elliptical in outline, with sometimes rather pointed ends in polar view; the latter of this features is typical for Ginkgoalean pollen grains and not for Cycadalean pollen grains, which are elliptical to circular and have rounded ends.

Many of Couper's *Monosulcites minimus* grains, however, appear to be folded up circular pollen grains (*Exesipollenites* or *Spheripollenites*) and the species is not so common as he thinks (Mrs. Dr. M. D. Muir, personal communication). So I think that it might be possible to divide *Monosulcites minimus* into three species (or sub-species), one presumably Ginkgoalean with elliptical outline and pointed ends, one presumably Cycadalean or Bennettitalean (see *Williamsoniella*) with elliptical to circular outline, rounded ends, and a pitted surface, and one presumably Cycadalean with an almost circular outline and a granulate surface (the *Androstrobus prisma*-type).

As far as I can see, it must be possible to distinguish between those types of dispersed pollen grains, although there will always be transitions and badly preserved specimens, in which case it will be very difficult to decide to which species they might belong.

Monosulcites carpentieri and *Monosulcites subgranulosus* are well-defined species; they have a much larger size than *Monosulcites minimus*, averages resp. 58 and 60 μ, and also than both Cycadalean and Ginkgoalean type pollen grains. They match more the common Bennettitalean type of pollen grain. But we will come to this when describing and discussing the Bennettitalean pollen grains.

BURGER (1966) recorded *Monosulcites minimus* and *Monosulcites subgranulosus* from the Upper Jurassic of the Netherlands. NILSSON (1958) stated that *Monosulcites minimus* and *Monosulcites carpentieri* do not belong to the genus *Chasmatosporites*, which he established for what he thought to be monolete spores, and to which he also assigned *Monosulcites magnolioides* Erdtman. Some of Nilsson's *Chasmatosporites* – pl. VII, fig. 2 – grains look rather like *Androstrobus prisma* pollen grains, especially specimens of *Chasmatosporites minor* and *Chasmatosporites elegans*.

The whole genus *Chasmatosporites* seems to me to be composed of both spores (monolete) and pollen grains (monocolpate and grains like *Androstrobus prisma*) and is thus rather a problematic genus.

POCOCK and JANSONIUS (1969) redescribed and emended the genus *Chasmatosporites*. They recognized (as well as other authors) its gymnospermous affinities, and it is now considered a genus of monosulcate pollen grains.

Many more authors described somilar pollen grains as *Monosulcites* or under various other names. This type of pollen grain is quite common from the Triassic onwards.

HASTYSTROBUS gen. nov.

Diagnosis: Microsporophylls borne spirally around the slender axis of the strobilus, which is at least 2 cm. long; distally exposed region of microsporophylls rhomboidal, 2–2,5 mm. broad, 1,5 mm. high; microsporophylls near apex slightly imbricate; under surface (abaxial side) of microsporophylls probably completely covered with sporangia; pollen grains as a rule tricolpate; one colpus more developed than the other two; colpi not symmetrically spaced on the pollen grain, the distance between the two shorter ones normally less than the distance between a short and the long one (*Eucommiidites*-type of pollen grain).

Type-species: *Hastystrobus muirii* spec. nov.
The generic name is from Hasty Bank, the type locality, and the type-species is named after Mrs. Dr. M. D. Muir.

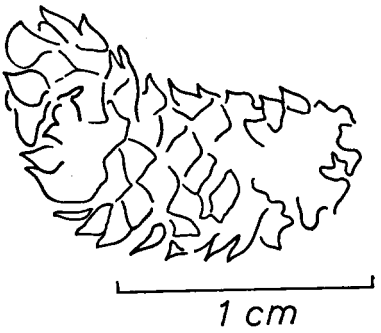
Discussion: This genus is erected for male fructifications which yield *Eucommiidites*-type of pollen grains. The genus very likely has cycadalean affinities (see the discussion of *Hastystrobus muirii*), but until this can be proved, it seems to be better to separate it from *Androstrobus*, the genus in which male Cycad fructifications are normally placed.

The new genus *Hastystrobus* only differs from *Androstrobus* by its tricolpate (*Eucommiidites*-type) pollen grains (*Androstrobus* has inaperturate or monocolpate pollen grains). I do not want to include *Hastystrobus* in *Androstrobus*, how much in common they may have, because I believe that even when more should be known about this genus, it still should be separated from *Androstrobus*. It might even be preferable to classify it in a different taxon above the rank of genus. In Conifers too, there are different genera in use for fossil male cones which are characterized by different types of pollen grains (*Masculostrobus* for cones with non-saccate pollen grains, and *Pityanthus* for cones with saccate pollen).

Hastystrobus muirii spec. nov.

Pl. IX, figs. 2, 4; text-fig. 5.

Diagnosis: Cone at least 2 cm. long, 7 mm. wide, cylindrically shaped, apex



Text-fig. 5. *Hastystrobus muirii* sp. nov. - holotype. Note the somewhat outpointing microsporophylls.

rounded, base unknown; cone axis slender; microsporophylls spirally arranged; distally exposed region rhomboidal, 2–2,5 mm. broad, 1–1,5 mm. high; near the apex, microsporophylls slightly imbricate; cuticle of microsporophyll unknown; under surface (abaxial side) probably completely covered with sporangia; pollen grains as a rule tricolpate, with one colpus better developed than the other two; outline elliptical, longest axis 33 μ (extremes 29–36 μ); pollen grains asymmetrical about their long axis, the surface carrying the main colpus (or the colpi) more flattened; the middle (main) colpus extending almost the whole length of the pollen grain, with obtuse ends; the other two, on either side of the main one, much shorter and slitlike; exine 1–2 μ thick, consisting of nexine and sexine; nexine 0,5–1 μ thick, smooth; sexine 0,5– 1,5 μ thick, smooth or slightly scabrate.

Age: Lower Deltaic (Dogger) (Middle Jurassic), Yorkshire.

Locality: Hasty Bank.

Description of the material: Besides the holotype (no. 1496, Division of Palaeobotany and Pollenmorphology, Botanical Museum and Herbarium, State University, Utrecht) there is only one other specimen, somewhat smaller and not showing either base or apex. Both specimens are from Hasty Bank. Looking through Prof. Harris' collection, I found one specimen which was like *Hastystrobus muirii*, but I was unable to study it in detail. This specimen was also from Hasty Bank.

Unfortunately, it has proved impossible to make cuticle preparations of the microsporophylls, although the specimens seemed well preserved. Apparently the cuticle is very thin, for it broke into tiny fragments, which gave no information at all. Luckily, however, the sporangia contained pollen grains.

The slides with the grains are deposited in the Division of Palaeobotany and Pollenmorphology, Botanical Museum and Herbarium, State University, Utrecht, under no. Yor-70 and Yor-71.

Discussion: This is the first time that a male cone yielding *Eucommiidites* pollen grains has been found and described, and, consequently, the first time that

Eucommiidites pollen grains have been found in situ. When we compare the pollen grains of *Hastystrobus muirii* with those of the various *Eucommiidites* species known until now, we see that they compare closely with *Eucommiidites troedssonii* Erdtman (Pl. IX, fig. 1). They differ from *Eucommiidites minor* Groot and Penny, and *Eucommiidites delcourtii* Hughes in size, outline of the pollen grain, and exine ornamentation. The affinities of *Eucommiidites* have long been subject to discussion. ERDTMAN (1948) first described *Eucommiidites troedssonii*; he believed it to have angiosperm affinities, and compared it with recent *Eucommia* pollen grains. KUYL, MULLER and WATERBOLK (1955) were the first to doubt this assignment. They stated: "One of the colpi is longer than the other two, and is provided with rounded-off ends. The distance between the short furrows may be smaller than between a long and a short furrow. Finely, the grains are not ellipsoidal, but flattened. Accordingly, radial symmetry which, in our opinion, is a most important feature of dicotyledonous pollen, is absent. The grains can perhaps best be considered as monocolpate with two additional furrows on the proximal side". According to them, the relationship might be sought with the Chlamydospermae.

COUPER (1956, 1958) made very detailed studies of *Eucommiidites troedssonii*. He came to the same conclusions as Kuyl, Muller and Waterbolk about the main, broad colpus and the two smaller ones, and about the asymmetry of the grains. He, too, says that the main colpus is very similar to the single colpus of monocolpate gymnospermous pollen grains (like those of the Cycads). The two other colpi are generally less well developed and in some cases represented only by a slit in the exine, according to him. I agree with this, and I noted among the pollen grains from *Hastystrobus muirii* some grains that, so far as I could see, only have the main colpus and not the two additional ones. I also noted one specimen which showed only one of the two additional colpi (and the main one). Couper also observed that the orientation at the *Eucommiidites* grains is like that of monocolpate gymnospermous pollen grains, and differs markedly from that of tricolpate angiosperm pollen. Thus, he concluded, *Eucommiidites troedssonii* is probably a monocolpate pollen grain of possible gymnospermous affinity. (N.B. He also compared *Eucommiidites* with recent *Eucommia*, and found that the pollen grains of the latter are not tricolpate, but tricolporate, thus differing markedly from *Eucommiidites*. The present author also made this comparison and came to the same conclusion).

DELCOURT & SPRUMONT (1956) described a new variety of *Eucommiidites* from the Wealden: *Eucommiidites troedssonii var. baldurnensis* (which according to HUGHES 1961 is very likely the same as *Eucommiidites minor*), but they added nothing to our knowledge of this genus.

GROOT & PENNY (1960) described a new species: the much smaller Cretaceous *Eucommiidites minor*.

HUGHES (1961) emended the genus *Eucommiidites*, saying that the two smaller colpi are not separate colpi, but a ring-furrow near the margin. The ring may be incomplete at the ends in the long axis (this view is neither shared by the present author – at least not for *Eucommiidites troedssonii* –, nor by some other authors).

In addition to this he described a new species, *Eucommiidites delcourtii*, which he found in the micropyle and pollenchamber of the seed *Spermatites pettensis* Hughes (both Lower Cretaceous), thus showing unequivocably that the origin of at least *Eucommiidites delcourtii* must be gymnospermous. He thinks that the affinity of *Eucommiidites* is likely to be with the Chlamydospermae.

BRENNER (1967) also found *Eucommiidites* in the micropyle and pollenchamber of seeds, but both the grains and the seed belonged to different species, resp. *Eucommiidites minor* and *Spermatites patuxensis* Brenner (both Lower Cretaceous).

REYMANOWNA (1968) reported that she found *Eucommiidites troedssonii* grains in the micropyle and pollenchamber of *Allicospermum retemirum* Harris from the Upper Liassic-Aalenian of Poland, but according to the present author the grains (the same as described by OSZAST 1957) are more like *Eucommiidites minor* than *Eucommiidites troedssonii*, except that they have the same size range as *Eucommiidites troedssonii*. They might belong to a new species. Reymanowna thinks that the structure of *Allicospermum* is like that of seeds of the Ginkgoales, Cycadales, certain Pteridosperms and certain Coniferales. The structure of *Eucommiidites* excludes the affinity with this last group. The presence of a membrane and the absence of a thickly cutinized nucellus excludes affinities with the Bennettitales and the Caytoniales (and also with the Angiosperms).

Also, *Allicospermum retemirum* differs considerably from the Chlamydospermae in having a thick megaspore membrane. Therefore, she concludes, the seed is possible related to the Ginkgoales, Cycadales or certain Pteridosperms, or to an altogether new group of plants.

The discovery of the here described male cone *Hastystrobus muirii* yielding *Eucommiidites troedssonii*-type of pollen grains, adds much to our knowledge of the affinities of this species of *Eucommiidites*. For, in this cone, the whole abaxial surface of the microsporophylls is very probably covered with sporangia, a feature which is only known from the Cycadales. Thus the affinity of *Eucommiidites* (at least of *E. troedssonii*) will very probably be found to lie with the Cycadales, or with a new group of plants yet unknown to us.

BENNETTITALES

WILLIAMSONIELLA Thomas

Williamsoniella coronata Thomas

Pl. VII, figs. 3, 4.

1915 *Williamsoniella coronata* – Thomas. p. 113, pl. 12, 13, 14, text-figs. 1–6 (general description; pollen grains pl. 13 fig. 11, 13, 14,)

1917 *Williamsoniella coronata* – Seward. p. 467, text-figs. 569–573 (general description).
1944 *Williamsoniella coronata* – Harris. p. 313, text-fig. 3 (general description and revision; pollen grains text-fig. 3A, B, F,)
1958 *Williamsoniella coronata* – Couper. p. 127, pl. 26 fig. 22 (pollen grains)
1962 *Williamsoniella coronata* – Potonié. p. 157, pl. 17 fig. 459 (pollen grains)
1969 *Williamsoniella coronata* – Harris. p. 142, pl. 4 figs. 3, 4, 7–9, 12, 13, text-figs. 61, 62 (general description; pollen grains text-fig. 61D).

Age: Middle Deltaic Gristhorpe Series (Middle Jurassic), Yorkshire.

Locality: Mainly Gristhorpe Bed (Cayton Bay).

Description: The following description is based on re-examination of slides V. 23947 and V. 25937 deposited in the British Museum, Natural History, Department of Palaeontology, and on material collected by the author and deposited in the Division of Palaeobotany and Pollenmorphology, Botanical Museum and Herbarium, State University, Utrecht, under no. Yor-22 and Yor-49.

Pollen grains monocolpate; outline elliptical to almost circular; longest axis 27 μ (extremes 22–33 μ); colpus extending almost the whole length of the pollen grain; wall (exine) very thin, about 0,5–1 μ thick; no different layers visible; surface scabrate.

Discussion: Most previous authors do not give very elaborate descriptions of the pollen grains of *Williamsoniella coronata.*

THOMAS (1915) states that the pollen grains "appear circular or elliptical and were probably flattened spheres; their walls were thin and they were about 0,02 mm. in diameter".

HARRIS (1944) does not fully describe the pollen grains either; he only says: "Ripe oval pollen grains showing a longitudinal furrow lie scattered in pollen sacs and over the sporophylls, and others are found among the hairs of the bracts. Immature pollen, often in tetrads, occurs in the sporangia of many isolated sporophylls, and abnormal pollen was noted". I agree with him that many isolated microsporophylls contain unripe pollen.

COUPER's description (1958) is similar to the present author's but according to Couper, the wall of the pollen grain is somewhat thicker (1 μ) and smooth to finely scabrate, while I find it to be normally about 0,5 μ thick, and invariably scabrate.

POTONIÉ (1962) only repeats Coupers' description and in 1969 HARRIS briefly states: "Pollen grains are 30 μ × 20 μ and have fairly thin, smooth walls".

Williamsoniella papillosa Cridland

Pl. VII, fig. 5

1957 *Williamsoniella papillosa* – Cridland. p. 383, text-fig. 1–3 (general description; pollen grains text-fig. 2A).
1969 *Williamsoniella papillosa* – Harris. p. 146, text-figs. 63, 64 (general description; pollen grains text-fig. 64C).

Age: Lower Deltaic and Middle Deltaic Gristhorpe Series (Middle Jurassic), Yorkshire.

Localities: Whitby Plant Bed and Gristhorpe Bed (Cayton Bay)

Description: The following description is based on re-examination of slide V. 34254 deposited in the British Museum, Natural History, Department of Palaeontology.

Pollen grains monocolpate(?); outline somewhat elliptical to circular; longest axis 26 μ (extremes 23–30 μ; only 11 specimens measured); colpus, if present, extending almost the whole length of the pollen grain, rather indistinct; wall (exine) 0,5–1 μ thick; nexine smooth, very thin; sexine with columellae- and capita-layer; columellae very short, indistinct; capita spherical, laterally fused, forming a reticulum; lumina of reticulum wider than muri; muri about 0,5 μ wide, lumina 1 μ.

Discussion: Only eleven specimens were available for measuring and description, and they were corroded to a high degree. The pollen grains were adhering to the inner lining of the pollen capsule (i.e. the synangium formed by the connate pollen sacs), no full pollen sacs were found. Cridland described the pollen as: "oval, about 27 μ long and with a single longitudinal furrow. The wall is very delicate and smooth".

HARRIS (1969) says: "The grains are oval, with thin smooth walls and typically 27 μ long". He does not mention a colpus, but his figures (which are the same as Cridland's) show a colpus. Both authors state that the pollen grains are smooth, but the present author disagrees. Although the grains are rather corroded, they definitely show a reticulum.

General discussion

Williamsoniella is a genus established in 1915 by THOMAS for hermaphrodite Bennettitalean flowers, with a rather special structure: An elongated floral axis, at its base bearing involucral bracts, then microsporophylls, then seeds and interseminal scales, and at the apex it projects as a corona. Thomas described two more species of *Williamsoniella* from Yorkshire, viz. *Williamsoniella roseberriensis* Thomas and *Williamsoniella lignieri* (Nathorst) Thomas, but HARRIS

(1969) supposes that both are different states of preservation of *Williamsoniella coronata*. Several species of *Williamsoniella* have been described by BRICK (1963), which agree in general aspect with *Williamsoniella coronata* and *Williamsoniella papillosa*, but do not show the essential characters (see also HARRIS 1969).
Both *Williamsoniella coronata* and *Williamsoniella papillosa* have been attributed to leaf species: *Williamsoniella coronata* to *Nilssoniopteris vittata* (Brgt) Florin (see THOMAS 1915, HARRIS 1944 and 1969), on grounds of association and because involucral bracts of *Williamsoniella coronata* were found bearing a diminutive *Nilssonopteris vittata* lamina. There is thus a transition between the bracts and the leaves. Also stems have been found that show scars, the size of which agrees very well with that of the (associated) flowers and leaves.

Williamsoniella papillosa is attributed to *Nilssoniopteris major* Harris (see CRIDLAND 1957, and HARRIS 1969) on grounds of association.

When we compare the pollen grains of *Williamsoniella coronata* with those of *Williamsoniella papillosa*, we see that they are of the same type (HARRIS 1969 says that the pollen grains look the same): monocolpate grains with an elliptical to circular outline and a very thin wall. But the exine ornamentation is somewhat different: While the grains of *Williamsoniella coronata* are scabrate, those of *Williamsoniella papillosa* show a reticulum.

Comparison with dispersed pollen grains will be given for all the Bennettitales together at the end of this chapter.

WELTRICHIA C. F. W. Braun

Weltrichia setosa (Nathorst) Harris

1909 *Williamsonia gigas* – Nathorst, in part. pl. 7 fig. 1 (no pollen grains)
1911 *Williamsonia setosa* – Nathorst. p. 17, pl. 4 figs. 1–11 (general description; pollen grains, pl. 4, fig. 11).
1917 *Williamsonia setosa* – Krasser. pl. 2, fig. 3 (short description)
1917 *Williamsonia setosa* – Seward. p. 443 (discussion)
1953 *Williamsonia setosa* – Harris. p. 47, text-figs. 5D–G, 6A–H (general description; pollen grains text-fig. 6C).
1958 *Williamsonia setosa* – Couper. p. 126 (pollen grains)
1969 *Weltrichia setosa* – Harris. p. 159, pl. 7, fig. 3, text-figs. 67, 68 (general description; pollen grains text-fig. 68B).

Age: Lower Deltaic Series (Middle Jurassic), Yorkshire.

Locality: Whitby Plant Bed.

Description: The following description is based on the literature, while the author was unable to examine the slides made by Harris and deposited in the Oxford Museum.

Pollen grains elliptical in outline; longest axis 37 μ, width 20 μ; exine thin and finely granular.

Discussion: NATHORST (1911) says about the pollen: "Ihre Länge ist etwa dieselbe wie bei *W. whitbiensis* und beträgt 40–44 μ". Krasser only states regarding the pollen grains that they resemble those of *Williamsonia whitbiensis* (= *Weltrichia whitbiensis* (Nathorst) Harris). HARRIS' description (1953, 1969) is given above; Couper also gives this description, but he adds "pollen grains presumably monosulcate", although neither Harris' description, nor his illustration indicate this feature. The pollen grains seem to be inaperturate; an uncommon feature in the Bennettitales, whose pollen is usually monocolpate. It may be that close examination will show a colpus.

Weltrichia sol Harris

Pl. VIII, figs. 1, 2, 3.

1900 *Williamsonia gigas* – Seward. p. 188, pl. 8 fig. 1 (regarded as top of *Williamsonia gigas* gynoecium)

1915 *Williamsonia gigas* – Thomas. p. 105, pl. 6 figs. 1, 2; text-figs. 1, 2 (general description; no pollen grains described or figured)

1917 *Williamsonia gigas* – Seward. p. 435, text-figs. 549–550 (general description).

1969 *Weltrichia sol* – Harris. p. 163, pl. 5 figs. 1–6, pl. 7 fig. 6, text-fig. 69 (general description; pollen grains pl. 5 figs. 3, 4, text-fig. 69A, B).

Age: Lower Deltaic Series (Middle Jurassic), Yorkshire.

Localities: Whitby Plant Bed and Haiburn Wyke.

Description: The following description is based on re-examination of slides V. 53486 and V. 53458c (type-specimen), deposited in the British Museum, Natural History, Department of Palaeontology, and on material collected by the author and deposited in the Division of Palaeobotany and Pollenmorphology, Botanical Museum and Herbarium, State University, Utrecht under no. Yor-55.

Pollen grains monocolpate; outline elliptical to elongate-elliptical with acute ends; often split into two halves; longest axis 46 μ (extremes 41–54 μ); colpus extending almost the whole length of the pollen grain; wall (exine) 1–1,5 μ thick; no different layers visible; surface finely granulate; granula about 1 μ in diameter.

Discussion: The first description of the pollen grains of *Weltrichia sol* is by

HARRIS (1969), and his description agrees very well with mine, except that he says that the wall is smooth (while both his photographs and his drawings show surface structure). But the surface structure may be partly due to corrosion, since the grains are rather corroded (making it impossible to determine any differentiation in the exine). Harris describes this male flower under the new name *Weltrichia sol*, as he is not absolutely certain that the *Williamsonia gigas* male flower described by THOMAS (1915) was rightly determined.

Weltrichia spectabilis (Nathorst) Harris

1909 *Williamsonia spectabilis* – Nathorst. p. 6, pl. 1 figs. 1–3, 4a (?), 5, 6, pl. 2 figs. 1–10 (general description; pollen grains pl. 2 figs. 2–10).
1911 *Williamsonia spectabilis* – Nathorst. p. 5, pl. 1 figs. 1–11, pl. 3 fig. 1, text-fig. 1 (general description; pollen grains pl. 3, fig. 1).
1913 *Williamsonia spectabilis* – Thomas. p. 230, pl. 24 figs. 1a, b, 2, text-fig. 2 (general description).
1917 *Williamsonia spectabilis* – Seward. p. 436, text-figs. 551, 552 (general description)
1958 *Williamsonia spectabilis* – Couper. p. 126 (pollen grains)
1962 *Williamsonia spectabilis* – Potonié. p. 157, pl. 16 figs. 457, 458 (pollen grains)
1967 *Williamsonia spectabilis* – Potonié. p. 122, pl. 13 figs. 259–267 (pollen grains)
1969 *Weltrichia spectabilis* – Harris. p. 166, pl. 7 fig. 8 (general description)

Age: Lower Deltaic Series (Middle Jurassic), Yorkshire.

Localities: Whitby Plant Bed and Marske Quarry.

Description: The following description is based on the literature.

Pollen grains monocolpate; outline elliptical to elongate-elliptical; longest axis about 60 μ; colpus extending almost the whole length of the pollen grain; wall (exine) thin, smooth (or finely reticulate according to Potonié).

Discussion: The first description of the pollen grains was made by NATHORST (1909): "Sie sind meistens zusammen geschrumpft, spulenförmig, gerade oder etwas gekrümmt, mit einer Längsrinne, den Pollenkörner ähnlich, die Solms zuerst bei *Cycadeoidea etrusca* beobachtete. Andere sind eiförmig, diese treten aber auf Grund ihrer Durchsichtigkeit weniger als die vorigen in den Gewebenpartieen oder Geweberesiduen hervor. Die Länge der Pollenkörner beträgt in Mittel etwa 58–65 μ".

Most authors give this description or a part of it (COUPER 1958, POTONIÉ

1962). POTONIÉ (1967) has re-examined Nathorst's slides and came to the following description: "Spore oval bis spindelförmig, an einem Ende oft stärker verjüngt. Monocolpat, Colpus fast von Achsenlänge. Bei den spindelförmigen Exemplaren Colpus geschlossen, tief eingeschlagen; bei den mehr ovalen Stücken zum Teil breit geöffnet; die Colpusarea ist oft auch dann noch beiderseits an ihrem Rand ± schmal eingefaltet; der gröszere Teil ihrer Fläche liegt entblöszt. Exine fein reticulat. Extrema lineamenta fein gewellt".

The present author thinks it likely that the exine will show some ornamentation (and not be completely smooth), as the other Bennettitalean pollen grains.

HARRIS (1969) gives a short description.

Weltrichia pecten (Leckenby) Harris

1864 *Palaeozamia pecten* – Leckenby. p. 77, pl. 9 fig. 4a right (name and figure)
1870 *Williamsonia pecten* – Carruthers. p. 694 (name, no real description)
1880 *Williamsonia leckenbyi* – Nathorst, in part. p. 39, pl. 8 fig. 5 left
1891 *Williamsonia leckenbyi* – Saporta. p. 161, pl. 248 fig. 1
1900 *Williamsonia pecten* – Seward (in part?). p. 190 (general description)
1909 *Williamsonia pecten* – Nathorst, in part. p. 8, pl. 2 fig. 11, pl. 3 figs. 1, 2 (general description)
1911 *Williamsonia pecten* – Nathorst, p. 19, pl. 5 figs. 1–8, pl. 6 figs. 1–3 (general description)
1969 *Weltrichia pecten* – Harris. p. 168, pl. 6 fig. 6

Age: Middle Deltaic Gristhorpe Series (Middle Jurassic), Yorkshire.

Locality: Mainly Cloughton Wyke *Solenites* Bed.

Description: The following description is based on the literature.

Pollen grains monocolpate; outline elliptical to elongate-elliptical; longest axis 45 μ (extremes 37–53 μ); colpus extending almost the whole length of the pollen grain; wall (exine) probably smooth, thickness not given.

Discussion: Various authors described pollen grains of *Weltrichia pecten* (NATHORST 1909, COUPER 1958, POTONIÉ 1962), but according to HARRIS (1969) those grains are all from the very similar *Weltrichia whitbiensis*. HARRIS (1969) does not give a real description of the grains (all his pollen sacs had shed their pollen, but numerous grains of a single type remained sticking to the granular membrane lining the sporangia), but he only compares them to the very similar grains of *Weltrichia whitbiensis*. From this comparison I have deduced the description given above.

Weltrichia whitbiensis (Nathorst) Harris

1828 "Head of a plant"	– Young and Bird. p. 191, pl. 1 fig. 2 (this specimen has often been described and figured as *Williamsonia gigas*)
1870 *Williamsonia pecten*	– Carruthers. p. 694 (in part)
1870 "Carpellary disc"	– Williamson. pl. 52 fig. 1
1900 *Williamsonia pecten*	– Seward, in part. p. 190, pl. 2, fig. 7 (general description)
1909 *Williamsonia pecten*	– Nathorst, in part. p. 8, pl. 1 fig. 4b, pl. 2 figs. 12–15 (general description; pollen grains pl. 2 figs. 12–15)
1909 *Williamsonia bituberculata*	– Nathorst. p. 10, text-fig. 1 (Williamson's carpellary disc)
1909 *Williamsonia gigas* funnel-shaped appendage	– Nathorst. p. 12 text-fig. 2
1911 *Williamsonia whitbiensis*	– Nathorst. p. 9, pl. 2 figs. 1–15, pl. 3 figs. 2–9, text-figs. 1–3 (including *Williamsonia bituberculata*; general description)
1911 *Williamsonia* sp.	– Nathorst. p. 16, pl. 3 fig. 10
1911 Williamson's carpellary disc	– Nathorst. p. 14, pl. 3 figs. 8, 9
1912 *Williamsonia whitbiensis*	– Krasser. p. 961, pl. 11 figs. 13, 14 (general description)
1913 *Williamsonia whitbiensis*	– Thomas. p. 233 (short description)
1917 *Williamsonia whitbiensis*	– Krasser. p. 5, pl. 3 figs. 4–6 (general discussion)
1917 *Williamsonia sewardi*	– Krasser. p. 7, pl. 3 figs. 1–3 (discussion)
1917 *Williamsonia whitbiensis*	– Seward. p. 440, text-figs. 555, 556 (general description)
1958 *Williamsonia pecten*	– Couper. p. 127 (pollen grains)
1962 *Williamsonia pecten*	– Potonié. p. 157, pl. 16 fig. 456a–c (pollen grains)
1969 *Weltrichia whitbiensis*	– Harris. p. 170, pl. 7 figs. 5, 7, 9, 10 (general description)

Age: Dogger and Lower Deltaic Series (Middle Jurassic), Yorkshire.

Localities: Hasty Bank and Whitby Plant Bed

Description: The following description is based on the literature.

Pollen grains monocolpate; outline elliptical to elongate-elliptical; longest axis ca. 46 μ (extremes 35–53 μ); colpus extending almost the whole length of the pollen grain; wall (exine) smooth and a little thinner than that of *Weltrichia pecten.*

Discussion: NATHORST (1909) was the first to describe the pollen grains: "Diese sind denjenigen von *Williamsonia spectabilis* ähnlich, sind aber etwas kleiner und messen meistens nur 36–44, bisweilen jedoch 50 μ." This description has been repeated by some subsequent authors (COUPER 1958, POTONIÉ 1962). HARRIS (1969) does not give a description, but merely a comparison with the grains of *Weltrichia pecten*, which are very similar (see also *Weltrichia pecten*).

General discussion

HARRIS (1969) restores the genus *Weltrichia* (BRAUN 1849) for male Bennettitalean flowers consisting of a massive cup dividing above into numerous equal lobes or rays (normally described as "male *Williamsonia*"). While *Weltrichia* has priority over *Williamsonia* (used for male or female flowers) he uses *Weltrichia* for the male flowers and keeps *Williamsonia* for the female ones only.

All the species of *Weltrichia* from Yorkshire have been (more or less provisionally) attributed to leaf species (to which also in some cases female flowers, stems and scale-leaves have been attributed-thus giving a fairly complete idea of the plant). The attributions have been made on grounds of association, cuticle structure and sometimes of transitions between scale-leaves and normal leaves.

The following attributions have been made:

Weltrichia setosa very provisionally to *Otozamites beani* (L. et H.) Brgt. (on base of association and the hairy surface of both).

Weltrichia sol to *Zamites gigas* (L. et H.) Morris (together with the female *Williamsonia gigas*)-on base of association and cuticle structure.

Weltrichia spectabilis to *Otozamites gramineus* (Phillips) Phillips (together with the scale-leaf *Cycadolepis spheniscus* Harris) – on base of association.

Weltrichia pecten to *Ptilophyllum pecten* (Phillips) Morris (together with the female *Williamsonia leckenbyi* Nathorst, the scale-leaf *Cycadolepis nitens* Harris and the stem *Bucklandia pustulosa* Harris – the latter is shared with *Ptilophyllum pectinoides* (Phillips) Morris) – on base of association.

Weltrichia whitbiensis to *Ptilophyllum pectinoides* (Phillips) Morris (together with the female *Williamsonia hildae* Harris, the scale-leaf *Cycadolepis hypene* Harris and the stem *Bucklandia pustulosa* Harris – the latter is shared with *Ptilophyllum pecten* (Phil.) Morris – on base of association.

When we compare the pollen grains of those five species of *Weltrichia* with each other, we see that they are all of the same type (except perhaps *Weltrichia setosa*): monocolpate pollen grains with an elliptical to elongate-elliptical outline. All grains seem to split easily. Their main differences are their size (between 37 and 60 μ) and the exine structure. However, except for *Weltrichia sol*, the exine structure is imperfectly known, so no definite conclusions can be drawn. The pollen grains of *Weltrichia spectabilis* are the largest of all (60 μ), those of *Weltrichia setosa* the smallest (37 μ), while those of the three remaining species are all about 45 μ. Except for this I could not find any real differences.

In addition to the five species of *Weltrichia* from Yorkshire, HARRIS (1969) recognises 5 species that were already classified in *Weltrichia*: *W. mirabilis* Braun – the type species *W. ovalis* Braun and *W. campanulata* Braun, which both may be conspecific with *W. mirabilis*, *W. fabrei* Saporta and *W. oolithica* Saporta.

Four species previously described in *Williamsonia* were transferred to *Weltrichia*: *W. blandfordi* (Feistmantel) Harris, *W. mexicana* (Wiel.) Harris, *W. santalensis* (Sitholey and Bose) Harris and *W. alfredi* (Krasser) Harris. The pollen grains of those species (at least if known) agree with the general type of Bennettitalean pollen grains: monocolpate, outline elliptical to elongate-elliptical, longest axis between 40 and 60 μ.

WILLIAMSONIA Carruthers

Williamsonia himas Harris

1953 *Williamsonia himas* – Harris. p. 43, text-figs. 4, 5A–C (general description; pollen grains text-fig. 4C, D)
1958 *Williamsonia himas* – Couper. p. 126 (pollen grains)
1962 *Williamsonia himas* – Potonié. p. 156, pl. 16 figs. 453, 454 (pollen grains)
1969 *Williamsonia himas* – Harris. p. 139. text-fig. 60 (general description; pollen grains text-fig. 60C, D)

Age: Lower Deltaic Series (Middle Jurassic), Yorkshire.

Locality: Unknown

Description: The following description is based on the literature.

Pollen grains monocolpate; outline elliptical to elongate-elliptical; longest axis ca. 50 μ; colpus extending almost the whole length of the pollen grain; wall (exine) fairly thick, scabrate.

Discussion: Numerous pollen grains were found sticking on the ovules of the female flower *Williamsonia himas*, and on this ground they were attributed to this specis (HARRIS 1953). They are of the usual Bennettitalean type. Harris described the pollen grains: "Associated pollen grains oval, averaging 50 μ × 30 μ, monosulcate, often split longitudinally, wall fairly thick, almost smooth". All the other authors made their descriptions on base of this one, and Harris' figures.

Williamsonia himes has not been attributed to any Bennettitalean leaf species, but it occurs on the same block as *Otozamites beani* (L. et H.) Brgt – to which *Weltrichia setosa* is provisionally assigned.

In 1942 HARRIS described the Bennettitalean microsporophyll *Wonnacottia*

crispa, but in his volume on the Bennettitales (1969) he says about this species: "The specimen Harris described as *Wonnacottia crispa* consists of a leaf 12 cm long in which every segment of the lamina is more or less strongly curled and bears, on the abaxial side, numerous round pouches formerly regarded as pollen sacs but now regarded as galls". And somewhat further in his account: "Most of the galls macerated yielded no pollen but one (unfortunately) was found to give about a hundred grains, and on this fact I concluded that they were sporangia. The grains are monocolpate as usual in the Bennettitales. Subsequently I found a few specimens which look like ordinary *A. nilssoni* leaves but bear just a few galls". So this species is now reinterpreted.

General discussion

The Order of the Bennettitales is distinguished from all other groups mainly by their stomata, which show a pair of subsidiary cells opposite the two guard cells, the whole group of cells looking as though formed by the division of a single cell (syndetocheilic arrangement). In almost all other Gymnosperms the subsidiary cells are differently arranged, not being sister cells of the guard cells, but having an independent origin (haplocheilic). FLORIN (1933) in particular has discussed this character. As to the taxonomic position of the Bennettitales, they are normally placed in the Cycadospermae, together with the Cycadales. However, THOMAS (1950) states that these two groups are not so closely related as the similarity of their vegetative structure would suggest. There are great differences in the form of their reproductive organs. HARRIS (1969) goes even further: "Although the Bennettitales were originally classed as Cycads, and later linked with Cycads, it seems that any phylogenetic connection between them must be remote. One can indeed imagine many alternative possible links between those two classes, but until there is good reason for preferring a particular link, it is best to consider them unconnected. This is true also of other classes; the Bennettitales are or seem remarkably isolated. Thus the term "Cycadophyte" which was intended as a major phyletic group means no more than "Gymnosperm with a pinnate leaf".

When we compare the pollen grains of the Bennettitales of Yorkshire with each other, we see that they fall into two groups: The first group includes both species of *Williamsoniella*; the second group includes probably all species of *Weltrichia* and the pollen associated with *Williamsonia himas*. While all the pollen is monocolpate, the first group is characterized by their elliptical to circular outline, their thin wall and their size (25–30 μ). The pollen grains of the second group have an elongate-elliptical outline, somewhat thicker walls and their size is mostly considerably larger (ca. 40 μ for *Weltrichia setosa*, ca. 45 μ for *Weltrichia sol*, *Weltrichia pecten* and *Weltrichia whitbiensis*, ca. 50 μ for *Williamsonia himas* and ca. 60 μ for *Weltrichia spectabilis*).

Pollen grains from Bennettitalean fructifications from other regions than Yorkshire, all fall within the latter group.

Pollen from this Class seems, therefore, to be fairly uniform.

Comparison of the Bennettitalean pollen grains

	colpus	outline	size	exine	surface
Williamsoniella coronata	present	elliptical -circular	27 μ	thin	scabrate
Williamsoniella papillosa	present	elliptical -circular	26 μ	thin	reticulate
Weltrichia setosa	?absent	elliptical	37 μ	thin?	granulate
Weltrichia sol	present	elongate-elliptical	46 μ	medium thick	granulate
Weltrichia spectabilis	present	elongate-elliptical	60 μ	medium thick	?smooth
Weltrichia pecten	present	elongate-elliptical	45 μ	medium thick?	?smooth
Weltrichia whitbiensis	present	elongate-elliptical	46 μ	medium thick?	smooth
Williamsonia himas	present	elongate-elliptical	50 μ	medium thick	scabrate

Comparison with dispersed pollen grains

COUPER (1958) described from the Jurassic of England three species of *Monosulcites* (= *Cycadopites* Wodehouse):

Monosulcites minimus, *Monosulcites carpentieri* and *Monosulcites subgranulosus (see also the chapters about the Cycadales and Ginkgoales)*. *Monosulcites minimus* includes pollen with cycadalean, ginkgoalean and bennettitalean affinities (the pollen grains of the first group of the Bennettitales fall in this species) while *Monosulcites carpentieri* (pl. VIII, fig. 5) and *Monosulcites subgranulosus* (pl. VIII, fig. 4) include mostly bennettitalean grains (being much larger in size 45–80 μ). The pollen of both the *Williamsoniella* species are similar to one type of *Monosulcites minimus* grains, but can be distinguished from the other types within this species (e.g. pollen of the Nilssoniaceae, of the *Androstrobus prisma*-group and of the Ginkgoales) mainly by their wall structure and the form of the colpus.

According to Couper, *Monosulcites carpentieri* grains compare closely with those of *Williamsonia himas* and *Weltrichia spectabilis*. I would also like to include *Weltrichia pecten* and *Weltrichia whitbiensis* in this species, differing from *Williamsonia himas* and *Weltrichia spectabilis* only in size, especially as nothing is known of their wall structure.

Because we know a little more about the wall structure of *Weltrichia sol* (finely granulate), I think that these grains are more like *Monosulcites subgranulosus*, but the exine is somewhat thinner (although thicker than in *Monosulcites carpentieri*).

NILSON (1958) describes some species of *Monocolpopollenites* Leschik (he uses this genus for the same type of grains as *Monosulcites* or *Cycadopites*) with,

according to him, Bennettitalean affinities. According to STAPLIN *et al.* (1967) the dispersed pollen of the Bennettitales should be classified within the genus *Bennettiteaepollenites*, which ranges from the Middle Triassic through the Jurassic system. Since, however, all those genera are closely similar, it seems correct, for reasons of priority, to use the generic name *Cycadopites* Wodehouse.

GINKGOALES

GINKGO L.

Ginkgo huttoni (Sternberg) Heer, male fructification

Pl. IX, figs. 3, 5; Pl. X, fig. 2; text-fig. 6

1948 ?*Ginkgo huttoni* – Harris. p. 205; text-fig. 6A, B (pollen grains).
1958 ?*Ginkgo huttoni* – Couper. p. 123, pl. 26 fig. 21 (pollen grains).
1962 ?*Ginkgo huttoni* – Potonié. p. 160, pl. 17 fig. 473, a, b, 474 (pollen grains).

Age: Upper Deltaic Series (Middle Jurassic), Yorkshire.

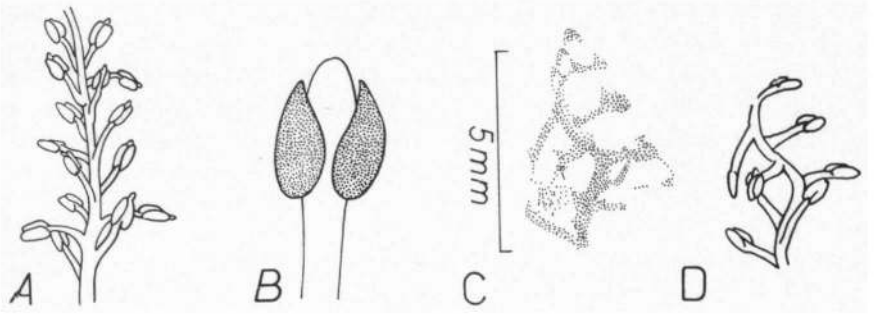
Locality: Scalby Ness, *Ginkgo huttoni* bed.

Diagnosis of male fructification:
Male fructification, about 10 mm long and 2 mm in diameter, consisting of a rather thin central axis and microsporophylls loosely placed around it; no special arrangement of the microsporophylls around axis discernable; form of microsporophylls rather indistinct, cuticle unknown; at each microsporophyll probably two pollen-sacs; pollen grains monocolpate; outline elongate-elliptical, with acute ends; longest axis 35 μ (extremes 29–42 μ); colpus (in the distal surface) extending about the whole length of the pollen grain, slitlike to broad; wall (exine) 1–1,5 μ thick; consisting of two layers: nexine and sexine; nexine smooth, 0,5 μ thick; sexine 0,5–1 μ thick, not completely smooth, but structure rather vague.

Description of the material: There is only one specimen of the male fructification, and it is rather badly preserved. Because of this it appeared to be impossible to make any cuticle preparation.

The specimen was found at Scalby Ness, the Ginkgo bed, and is deposited in the Division of Palaeobotany and Pollenmorphology, Botanical Museum and Herbarium, State University, Utrecht under no. 2967, and the slides with the pollen preparations under no. Yor-72.

Although the male fructification was not found attached to *Ginkgo huttoni* leaves/stem, it is attributed to it on the following grounds:



Text-fig. 6. *Ginkgo huttoni* (Heer) Sternberg-male cone.
A. Reconstruction of the male cone.
B. Reconstruction of microsporophyll.
C. Male cone-holotype
D. Reconstruction of the holotype.

1. Association. The specimen is from Scalby Ness, Ginkgo plant bed, where *Ginkgo huttoni* is by far the most common fossil.

On the block the male fructification is associated with *Ginkgo huttoni* and *Haiburnia blacki* Harris.

Haiburnia blacki is a Conifer, and the structure of the fructification and the shape of the pollen grains do not suggest a coniferous origin for the fructification.

Consequently *Ginkgo huttoni* remains the most reasonable parent plant.

2. Agreement in structure with the male fructification of the recent *Ginkgo biloba* L.

Although the microstrobilus of *Ginkgo biloba* is somewhat larger than the specimen here described, it agrees with it in almost all essential characters: The microstrobilus of *Ginkgo biloba* is built of a central axis with irregularly arranged microsporophylls around it just as observed in *Ginkgo huttoni*; although bad preservation might, in the case of the latter, have obscured any arrangement of the microsporophylls.

In *Ginkgo biloba* the microsporophylls bear 2 (sometimes 3 or 4 or even more) pollen-scas, in *Ginkgo huttoni* probably 2. Finely the pollen grains are both of the same type: monocolpate grains. For exact comparison, see under "Comparison with recent pollen grains". Cuticle preparations, could they have been made, might have been able to confirm this attribution.

Discussion of the description of the pollen grains

HARRIS (1948) described pollen grains that he found sticking to inner bud scales associated with *Ginkgo huttoni*. The slide with those grains is deposited in the British Museum (Natural History, Department of Palaeontology) under no. V. 27499a. This slide was also studied by COUPER (1958), but he states that "the pollen grains are still in the pollen-sac, making it difficult to obtain adequate

illustrations". HARRIS (1948 and personal communication) definitely says that the grains are not in pollen sacs but on bud scales, and he is not even sure that they are really pollen grains of *Ginkgo huttoni*:
"*Associated pollen*: The inner (triangular) bud scales have pollen grains sticking to them; one has a few grains, another nearly a hundred, some on both sides.

The pollen grains are of uniform size and show a well-developed longitudinal groove and a rather thin, smooth extine. This pollen is of an unspecialized Gymnosperm type, occuring in Ginkgo and many other genera, and there is no evidence, apart from its association, for refering it to this species.

In view of the fact that the pollen is sometimes met on leaf cuticles of the same species (e.g. *Cayttonanhus* pollen on *Sagenopteris*), it would be most interesting if this same association were met elsewhere in *G. huttoni*. If it were, it would provide evidence that *G. huttoni*, like *G. biloba*, shed its pollen shortly after its resting buds opened".

The present author also examined this slide. She quite agrees with Harris about it being bud scales, and she also thinks that the pollen grains very probably do belong to *Ginkgo huttoni*, for they agree in all aspects with those here described from the microstrobilus, and on grounds of association. Couper's description of the pollen grains agrees with the present in all main aspects; he only does not mention the acute ends of the grains, and he states that the exine is smooth to faintly scabrate, while the present author could not discern the exact exine ornamentation.

POTONIÉ (1962) only gives the description of Couper, and mentions Harris' work saying: "Die Sporen fig. 473 a, b (nach HARRIS 1948) brauchen nicht unbedingt zu Species *huttoni* gehören, entsprechen jedoch *Ginkgo* im Habitus".

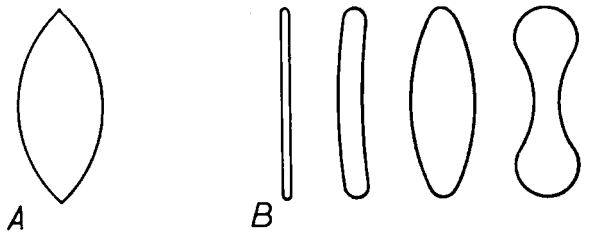
Antholithus wettsteinii Krasser, a fossil male fructification from the Triassic of Lunz, Austria, which is often considered a Ginkgophyte, has pollen grains of the same type as the Ginkgoales, but differs in other respects quite a lot from the Ginkgoales (KRÄUSEL 1943).

Comparison with recent pollen grains

In order to compare the pollen grains of *Ginkgo huttoni* with those of recent Ginkgoales, various slides of the only recent species, *Ginkgo biloba* L., were studied (Pl. X, figs. 4, 6).

Description: The slides are under no. 143, no. 236 and no. 424 in the Division of Palaeobotany and Pollenmorphology, Botanical Museum and Herbarium, State University, Utrecht.

Pollen grains monocolpate; outline in polar view ellipsoid, often with rather acute ends; in equatorial view rounded rectangular; longest axis about 40,5 μ (extremes 34–46 μ); colpus extending over nearly the whole length of the pollen grain, widest in the middle, acute at the ends; colpus membrane smooth; exine of equal thickness throughout the pollen grain, 1,5–2 μ thick; nexine 0,5 μ thick, smooth; sexine 1–1,5 μ thick, consisting of columellae- and capita-layer:



Text-fig. 7. Showing the different types of colpus found in the Ginkgoales (A) and Cycadales (B). Note that in the Ginkgoales the ends of the colpus are acute, while in the Cycadales they are obtuse, whatever the form of the colpus may be.

short, stout columellae bearing for the greater part laterally fused capita, thus forming a tectum perforatum.

COUPER (1958) also compares the pollen of *Ginkgo huttoni* with those of *Ginkgo biloba*, and his description is rather different from mine: "Grains monocolpate, sulcus running almost the whole length of the grain, broad, with rounded ends and a clear furrow floor; grains ellipsoidal with rather pointed ends in polar view; exine smooth and 0,75 to 1 μ thick". He gives as size range for the longest axis 33 μ (extremes 25–38 μ). There is a considerable difference in the size of the grains and in the thickness of the exine, with my description. I cannot put forward any explanation for this difference, except that his grains may have been unripe, or mine overmacerated.

POTONIÉ (1962) does not give any description of *Ginkgo biloba* grains, only some pictures; according to his magnification the grains are about 40 μ long; the colpus is broad and pointed at the ends. Potonié (1967) gives a short description which agrees well with mine.

WODEHOUSE (1935) gives 30 μ as longest axis for *Ginkgo biloba* and ERDTMAN 1956 gives 32 μ for the same parameter.

In any case, the pollen grains of *Ginkgo huttoni* are very much like those of the recent *Ginkgo biloba*. They are somewhat smaller and have a less clearer exine structure, but their general appearance, especially the elongated form of the grains and the long, acute colpus, is the same.

Comparison with dispersed pollen grains

COUPER (1958) described *Monosulcites minimus* from the Jurassic of England, and he stated "that many specimens of *M. minimus* from the Upper Deltaic of Yorkshire are almost certainly of Ginkgoalean origin. The Upper Deltaic specimens are an extremely good match with those of *Ginkgo huttoni* which is abundant in this series" (see also the chapter on the Cycadales). When found dispersed, all grains of *Ginkgo huttoni* will certainly fall within *Monosulcites minimus*, but Cycadalean and Bennettitalean grains also fall within this species (see the chapters on those groups). Most authors (COUPER 1958, POTONIÉ 1962, 1967, NILSON 1958, BURGER 1966, STAPLIN, POCOCK and JANSONIUS 1967) agree that it is impossible to separate the pollen grains of the Cycadales, Bennettitales and Ginkgoales, at least the fossil ones.

According to POTONIÉ (1967) it is possible to separate the recent grains of *Cycas* and *Ginkgo* by electron microscopy, and according to some other authors

also by normal-light microscopy. The present author is inclined to think that it is possible to distinguish at least the typical Ginkgoalean pollen grains from those of the Cycadospermae, by their elongated form with acute ends (the ratio length/breadth is much larger with the Ginkgoales than with the Cycads: resp. 1,6 and 1,2; see also COUPER 1958), by the form of the colpus (see text-fig. 7) and its acute ends, while Cycad pollen grains have rounded colpus ends, and also by the exine structure if that is clear. But of course there will often occur badly preserved grains etc. whose accurate determination will always be impossible.

DOUBTFUL GINKGOALES

Leptostrobus Heer

Leptostrobus cancer Harris

Pl. X, figs. 1, 3.

1951 *Leptostrobus cancer* – Harris. p. 483, text-figs. 1–4 (general description)
1962 *Leptostrobus cancer* – Potonié. p. 162, pl. 17 figs. 479, 480 (pollen grains)

Age: Middle Deltaic Gristhorpe Series (Middle Jurassic), Yorkshire.

Locality: Cloughton Wyke, *Solenites* bed.

HARRIS (1951) describes the female fructification *Leptostrobus cancer* from the Middle Deltaic Gristhorpe Series, Yorkshire. All *Leptostrobus* species (*Leptostrobus* is known from the Jurassic of Greenland, Yorkshire, Siberia, Russia and presumably also Japan) belong to a group of plants, mostly indicated as the *Czekanowskia*-group. To this group belongs the plant to which *Leptostrobus cancer* is attributed, namely *Solenites vimineus* (Philips) L. et H. (= *Solenites murrayana* L. et H. = *Czekanowskia murrayana* L. et H.).

Formerly this group of plants was regarded as belonging to the Ginkgoales (on base of their leaf structure and their cuticles), but the discovery of the female fructifications made this attribution rather doubtful. HARRIS (1951) discusses this subject at some length, saying amongst other things: "*Leptostrobus* (with *Czekanowskia*) has in fact the same sort of relation to the Ginkgoales as *Taxus* has to the Conifers. *Taxus* and its immediate allies agree perfectly with the Conifers in their vegetative organs, but the organization of the female organs is so different as to make any relationship too obscure to be profitable to follow at the present time."

Within the "capsules" (the seed bearing organs) of *Leptostrobus cancer* masses of pollen grains were seen, just beneath the place of the presumed micropyle. Also scattered pollen grains were seen. Unfortunately the pollen is not uniform at all, although one type seems to dominate. Harris says about the pollen grains:

"None of the present specimens is as richly provided with pollen grains as the Greenland ones (especially "*Microcheiris*") but all those that still possess the fibrous inner membrane show moderate numbers of grains scattered over it. The specimen shown in fig. 26 has, in addition, several compact masses of pollen situated just below the embryosacs, in positions which correspond with those of "*Microcheiris*", and there are similar pollen masses among the broken fragments from inside other specimens. It is very difficult to make out the form of the pollen grains in these masses as they overlap; the only thing certain is that there are many large grains, some about 50 μ wide, with rather thin, very finely punctate walls. I am not able to say whether wings and triradiate scars are absent, but I could see none. Around these pollen masses there are scattered pollen grains which can be observed better; some of these are large oval grains up to 80 × 50 μ with longitudinal groove, and others roundish grains about 35 μ wide, also with a longitudinal groove. I dit not recognize any winged pollen at all, but I saw a few thick-walled grains looking like fern spores. I feel certain that these pollen grains are of more than one species".

POTONIÉ (1962) gives the same description as Harris, but he simply takes the most common type of grains in *Leptostrobus cancer* as *the* pollen grains belonging to this fructification. The present author re-examined the slides made by Harris, deposited in the British Museum, Natural History, Department of Palaeontology under no. V. 28577, V. 28578 and V. 28580. I agree with Harris in almost all respects, but I think that one can say somewhat more about the grains. I came to the following description of the most common type of pollen grains (which, I think, may belong to the fructification): pollen grains probably monosaccate; circular in outline; ca. 55–60 μ wide; corpus only a little smaller than the saccus; saccus wall rather thin, scabrate.

When we compare those grains (as far as we can) with dispersed pollen grains, we see that they are rather like *Tsugaepollenites lucidus* (Pl. X, fig. 5). This pollen is not at all like the type of pollen grains that we know from the Ginkgoales (monosulcate grains with acute ends – see the chapter on Ginkgoales) but more like that of certain Conifers (e.g. see *Brachyphyllum mamillare*). So the only agreement between *Leptostrobus cancer* and the Ginkgoales is on this moment the cuticle, although in some Conifers cuticles occur that are rather like this one. Thus, the present author is inclined to think that *Leptostrobus cancer* (and with it probably the whole *Czekanowskia-group*) has more relationships to Conifers than to Ginkgoales.

Krasilov (1968) mentions *Ixostrobus*, a genus for microstrobili that are linked with the leaves of the *Czekanowskia* group, but he does not give any description of this genus, nor of its pollen grains. He also thinks that this group of plants differs markedly from the Ginkgoales.

CONIFEROSPERMAE

ARAUCARIACEAE

BRACHYPHYLLUM Brgt

Brachyphyllum mamillare Brgt, male cone

1949 *Brachyphyllum mamillare* – Kendall. p. 160, text-fig. 3A–E, 4 (general description; pollen grains text-fig. 3A)
1958 *Brachyphyllum mamillare* – Couper. p. 129, pl. 27, figs. 1, 2 (pollen grains).
1962 *Brachyphyllum mamillare* – Potonié. p. 174, pl. 19 figs. 516, 517 (pollen grains).

Age: Lower, Middle and Upper Deltaic (Middle Jurassic) Yorkshire.

Localities: *Brachyphyllum mamillare* male cones were found in a great many localities, but all the cones from which pollen grains were prepared by the present author are from the Whitby plant bed.

Description: The following description is based on re-examination of slide V. 27554 a, deposited in the British Museum of Natural History, Department of Palaeontology, and on material collected by the author and deposited in the Division of Palaeobotany and Pollenmorphology, Botanical Museum and Herbarium, State University, Utrecht under no. Yor- 21.

Pollen grains inaperturate; outline circular to roughly triangular, diameter 71 μ (extremes 56–84 μ); wall (exine) 1–2 μ thick (if undivided), consisting of two layers: nexine and sexine; nexine often separated from the sexine, forming an "inner body" inside the sexine; nexine smooth, 0,5–1 μ thick; diameter of inner body (if present) 58 μ (extremes 48–70 μ); sexine ca. 1 μ thick, finely granulate; granula about 1 μ in section; brim of sexine around the nexine (if the two layers are separate) 6,5 μ (extremes 4,5–10 μ).

Discussion: *Brachyphyllum mamillare* was attributed by KENDALL (1949) to the Araucariaceae mainly on the basis of the structure of the female cone-scales (including their cuticle) and seeds, which typically agree with those of recent *Araucaria*.

There is remarkably close agreement between the cuticle of the outside of the cone-scale in *Araucarites phillipsi* Carruthers (the female cone-scale of *Brachyphyllum mamillare*) and the recent *Araucaria araucana*. *Araucarites phillipsi* is of the broad type of cone-scales with membranous wings, as is also seen in the Section Colymbae. In no respect does *A. phillipsi* resemble the cone-scale of *Agathis* rather than *Araucaria*. It differs still more from the cone-scale of any other genus of the Conifers.

KENDALL (1949) was also the first to describe male cones of *Brachyphyllum mamillare*. Some cones were attached to the shoots, others were found separately but in close association with *Brachyphyllum mamillare*. With respect to the pollen grains she states: "Pollen grains are obtainable in small numbers at least from every cone macerated. They are small, round, and 60–80 μ in diameter. The wall has been thrown into a series of irregular folds on collapsing. Pits and granules are absent from the exine".

COUPER (1958) examined Kendall's slide and came to the following description: "Pollen grains originally more or less spherical, normally folded in the fossil state; exine very thin, about 0,75 μ, scabrate to sub-granular; no trace of any germinal aperture. Size range: 70 to 80 μ in equatorial diameter (only six specimens available for accurate measurement)."

POTONIÉ (1962) just repeats Kendall's and Couper's description.

The present author also examined Kendall's slide, which only contains six pollen grains and is rather deeply stained (pl. XI, fig. 1).

My own material consisted of several attached and separated cones. All of them yielded some pollen grains, and one yielded over 50 grains out of a few microsporophylls.

The pollen grains appeared to be of two types:

1. The "normal" type of araucariaceous pollen grains: pollen grains that are circular in outline, diameter ca. 71 μ exine 1–2 μ thick, with a nexine and sexine that are attached to each other, sexine finely granulate (pl. XI, figs. 2, 3).
2. In the second type of pollen grains, the nexine is loose from the sexine, and seem to have shrunk. The total diameter of these pollen grains is, just as in type 1,71 μ; the diameter of the nexine only ("inner body") 58 μ; the nexine (1 μ thick) is smooth, and the sexine (also 1 μ thick) is, just as in type 1, granulate. In some cases the nexine is only slightly shrunk, so that there is only a small brim of sexine around the "inner body" (4,5 μ), in other cases the nexine is to a high degree shrunk, giving rise to a brim of about 10 μ (Pl. XI, figs. 4, 5, 6). There are also pollen grains in which the nexine is loose from the sexine, but not or almost not shrunk. Normally the brim of sexine is unfolded, sometimes, it is somewhat wrinkled or scalloped. In most pollen grains the "inner body" is circular in outline, but in some grains it tends to be triangular (Pl. XI, fig. 6). Also in some grains the brim of sexine seemed to be almost trilobate instead of circular (Pl. XI, fig. 4).

I studied about a fifty pollen grains and found that 59 % were of type 1, or had a nexine that was loose from the sexine but not shrunk; 41 % of the pollen grains were definitely of type 2. Of those grains, one fifth was more or less trilobate instead of circular in outline.

Comparison with some other male cones

1. ARCHANGELSKY (1963) described male cones associated with the Lower Cretaceous *Brachyphyllum mirandai* Arch. They yielded pollen grains that "are circular, 50–55 μ wide, with an exine 3 μ thick. There are no wings. The surface is almost smooth but may be very faintly granular". The pollen grains have a

middle thinner area, probably corresponding to the sulcus, according to him. He also states: "One grain shows a separate round body, 30 μ wide, with a well-developed wall. This feature has not been seen in any of the other specimens, and its nature is unknown". This certainly recalls *Brachyphyllum mamillare*.

2. GAMERRO (1965a) described male cones from the Lower Cretaceous *Apterocladus lanceolatus* Arch. 1966, which yielded pollen grains that agree in some respects with those of *Brachyphyllum mamillare*. The pollen grains are somewhat smaller (equatorial diameter 45 μ); they have a circular thinner area (colpus?), and are normally round with a finely granulate exine. Sometimes there is a kind of inner body with a brim around it, with a tendency to become trilobate, and in some cases there seem to be three rudimentary sacci (see GAMERRO 1965a and Archangelsky 1966). This certainly looks like the pollen grains of *Brachyphyllum mamillare*, but since I did not study the material, I can say nothing for certain. *Apterocladus lanceolatus* was provisionally attributed to the Podocarpaceae by ARCHANGELSKY (1966), mainly on the basis of the leaf cuticle, but there are several points of disagreement between *Apterocladus* and the Podocarpaceae. The pollen grains resemble, according to him, the pollen grains of the Araucariaceae but there are some differences in the structure of the exine. They differ from those of the Podocarpaceae, in not having clearly saccate grains; but *Saxegothaea* of the Podocarpaceae does not have sacci either. However, its exine structure is rather different. Therefore, it seems that the pollen grains have some points of agreement with those of Araucariaceae, and it would be worth to re-examine the material.

N.B. Gamerro believes that the saccus (as he calls it) arises through a separation of the extine and intine around the colpus.

3. TOWNROW (1967) described a Jurassic male cone from Antarctica: *Masculostrobus warrenii*, which yielded pollen grains that also have some resemblance to *Brachyphyullm mamillare* grains. He described the grains: "Pollen of more or less rounded outline, diameter about 110 μ (78 to 153 μ, amb equilateral triangular, but with well rounded corners, of side about 88 μ (62 to 110 μ), and usually reaching outside edge of grain at three places. Grain with three sacci, rarely confluent. Sacci about 16 μ (3 to 24 μ) wide, not always of equal size. Sacci sometimes showing small radial foldings. Exine of amb 1,5 μ thick, at saccus edge (exoexine) 2 μ; sometimes very faintly showing more or less reticulate pattern, and sometimes faint triradiate mark, with arms running more or less straight and reaching almost to the equator".

Those pollen resemble to some degree the trilobate form of the *Brachyphyllum mamillare* pollen, but as the other types of the *Brachyphyllum mamillare* pollen have not been found in these cones, this is the only point of agreement between these two species. *Masculostrobus warrenii* is thought to belong to the Podocarpaceae, also on the basis of the structure of *Nothodacrium warrenii* Townrow, the species to which *Masculostrobus warrenii* is attributed.

Comparison with recent pollen grains

I studied the pollen grains of some recent species of the Araucariaceae and found

that the majority of those species had pollen grains of the normal araucariaceous type (large pollen grains, circular in outline, diameter ca. 70 μ, with a nexine and sexine that are attached to each other; only the exine ornamentation is variable, but not, however, very much). But *Araucaria araucana* (slide 2523 Division of Palaeobotany and Pollenmorphology, Botanical Museum and Herbarium, State University, Utrecht) showed the same two types of pollen grains as *Brachyphyllum mamillare* (Pl. XII, figs. 1–4). Here the majority of the grains had the nexine loose from the sexine, and to some degree shrunk. When the nexine was shrunk, especially if it was considerably shrunk, the brim of sexine was wrinkled and scalloped (Pl. XII, figs. 1, 2). Where the nexine was only slightly shrunk, the sexine is almost unfolded (Pl. XII, fig. 4). But in all cases the total diameter of the pollen grain (i.e. the diameter of the sexine) is about the same. The diameter of the nexine is of course quite variable. Here again, as in *Brachyphyllum mamillare*, the nexine is smooth and the sexine granulate. I measured 100 pollen grains of *Araucaria araucana* and found that 42 % were of the normal type, in 39 % the nexine was somewhat shrunk, and in 19 % the nexine was considerably shrunk. I also noticed a triradiate mark on some of the pollen grains (Pl. XII, fig. 1). So we see that the dimorphism of the pollen grains of *Brachyphyllum mamillare* also occurs in the recent *Araucaria araucana*. As a dimorphism like this one is not very common, we can say that either *Araucaria araucana* must have originated from *Brachyphyllum mamillare* or a related plant, or that in the Araucariaceae there is a trend in the pollen grains to separate the nexine from the sexine and produce pollen grains that appear to be monosaccate.

Comparison with dispersed pollen grains

When we compare the pollen grains of *Brachyphyllum mamillare* with dispersed pollen, we see that type 1 of *Brachyphyllum mamillare* grains resembles *Araucariacites australis* Cookson (Pl. XII, fig. 5).

Araucariacites australis was described by Cookson from the Tertiary of the Kerguelen, but the Jurassic and Lower Cretaceous grains are indistinguishable from this species, and are thus included in it (see COUPER 1958). According to Couper *Araucariacites australis* grains are comparable in all respects with those of *Brachyphyllum mamillare*. I would like to qualify this, that they may only be compared with *Brachyphyllum mamillare* grains type 1. *Araucariacites australis* is recorded from Jurassic times from all over the world. There are some other species of the genus but they are of minor importance.

When we come to *Brachyphyllum mamillare* type 2 pollen grains, we meet much more difficulties. They resemble pollen grains that fall within the genus *Applanopsis* Doering. This is a genus that has caused much confusion, especially in its nomenclature. A short review of the most important literature will be given here.

BALME (1957) described 3 species of the genus *Zonalapollenites*: *Zonalapollenites dampieri*, *Zonalapollenites trilobatus* and *Zonalapollenites segmentatus*. Because the diagnoses of these three species are quite important, they are repeated here.

1. *Zonalapollenites dampieri*: Amb circular. Pollen grain complex, consisting of a circular or rounded triangular central body surrounded equatorially by a narrow bladder. No germinal mechanism visible, although some specimens show vestigial triradiate markings. Exine of central body 1–2 μ thick, finely granulate or indeterminately marked. Bladder 8–15 μ wide, outline indented, very finely reticulate, characterized by radially directed folds giving it a frilled appearance. Total diameter 53–78 μ (63 μ average) central body 37–53 μ (average 45 μ) (Pl. XIII, fig. 1).
2. *Zonalapollenites trilobatus*: Amb rounded triangular. Pollen grains complex, consisting of a sub-triangular central body with three equatorially attached bladders, sometimes fusing to form a single trilobate bladder constricted at the apices of the central body.

No visible germinal mechanism, but a vestigial triradiate scar is sometimes present. Exine of central body 1–2 μ thick, rugose or with a wrinkled appearance. Bladders about 15 μ wide, finely granulate, marked by radial folds. Total diameter 65–91 μ (average 80 μ) (Pl. XII, fig. 6).

3. *Zonalapollenites segmentatus*: Amb circular, outline indented. Pollen grain complex, consisting of a circular central body surrounded distalo-equatorially by a narrow bladder. No germinal aperture or tetrad markings observed. Exine of central body 2–3 μ thick, dark in colour, rugose or finely granulate. Bladder 6–10 μ wide, crumpled by numerous radial folds giving it a frilled appearance, smooth or faintly granulate. Total diameter 44–60 μ (average 53 μ), central body 31–48 μ (average 39 μ).

The three species have much in common, and apparently might form together a good genus. The genus *Zonalapollenites* which was described in 1953 by THOMSON and PFLUG, is, however, synonymous with *Tsugaepollenites* Potonié 1948. DETTMAN (1963) for the first time changed *Zonalapollenites* into *Tsugaepollenites* because they are synonyms, and *Tsugaepollenites* has priority.

DÖRING (1961) transferred *Z. dampieri* to his new genus *Applanopsis*, and *Z. trilobatus* to his new genus *Triangulopsis*. The type species of these genera are resp. *Applanopsis lenticularis* and *Triangulopsis discoidalis*. He considered them to be plankton species, but the publication is effective.

Also in 1961, DEV transferred *Z. dampieri*, *Z. trilobatus*, and *Z. segmentatus* to his new genus *Callialasporites*. He stated that *Zonalapollenites* was a synonym of *Tsugaepollenites*. While these three species, however, do not fall within *Tsugaepollenites* because they do not have the type of velum characteristic for this genus, they had to be transferred to a new genus (in casu *Calliasporites*). Dev described, besides the already known species, a new species *C. monoalasporus*, with an unfolded "saccus" and a very clear boundary between "corpus" and "saccus". Unfortunately his paper appeared some months after Döring's, so consequently *Applanopsis* has priority over *Callialasporites*.

POCOCK (1962) transferred the same three species of *Zonalapollenites* to his new genus *Pflugipollenites* for the same reason as Dev whose paper he had not seen. He also described a new species *P. lucidus* (see the chapter on *Leptostrobus cancer*).

H. P. SINGH *et al.* (1964) described two new species from the Lower Cretaceous: *Callialasporites rimalis* (with a thick brim around a "body" with folds) and *C. triletes* (with a clear tetrad scar).

MUIR (1964) described in her thesis a new species *Tsugaepollenites sp. A* from Hasty Bank (Yorkshire). It resembles type 2 of *Brachyphyllum mamillare* pollen grains (Pl. XIII, fig. 2).

GOUBIN *et al.* (1965) discussed in detail the taxonomic position of *Z. dampieri* and *Z. trilobatus* and came to the conclusion that both should be placed within Döring's genus *Applanopsis*. They emended *Applanopsis* to include also *Triangulopsis*.

BURGER (1966) combined *Applanopsis dampieri* and *A. segmentatus* to one species (*A. dampieri*) because he found in the Dutch Upper Jurassic and Lower Cretaceous many transitions between them.

REISER & WILLIAMS (1969) said that there appears to be a gradation from *Tsugaepollenites segmentatus* through *T. dampieri* to *T. trilobatus*.

NORRIS (1969) emended *Callialasporites dampieri* to include pollen grains with a "saccus" that is slightly lobed, but not completely trilobate (like some of the grains of *Brachyphyllum mamillare*).

The present author is of the opinion that *Zonalapollenites dampieri*, *Z. trilobatus* and *Z. segmentatus* of Balme do not belong to *Tsugaepollenites*. They form, together with *Tsugaepollenites sp. A*, a good genus of which the correct generic name is, in accordance with the opinion of Goubin, Taugourdeau and Balme, *Applanopsis* Doering. In this genus the genus *Triangulopsis* Doering has to be included. The generic names *Callialasporites* Dev and *Pflugipollenites* Pocock are synonyms of *Applanopsis* Doering.

Different opinions are expressed by the following authors: JAIN (1968) discussed the genus *Triangulopsis* (with *T. trilobatus*) and stated that it should be separated from *Applanopsis* and *Tsugaepollenites*, because of its triangular body and thick "perinosaccus".

H. P. SINGH & PRAMOD KUMAR (1968) decided that most species of *Applanopsis* should be placed in *Tsugaepollenites*, but that *A. trilobatus* should be placed in *Triangulopsis*.

When we compare the pollen grains of type 2 of *Brachyphyllum mamillare* with *Applanopsis*, we see that the majority resembles most *Applanopsis dampieri*, but some pollen grains come quite near *Applanopsis trilobatus*, while a few are more like *Appl. segmentatus* or *Tsugaepollenites sp. A*. This is also in agreement with HOROWITZ (1968), who says that *Appl. dampieri* is more common in the Upper Jurassic of Israël than both *Appl. trilobatus* and *Appl. segmentatus*. This has also been recorded by various other authors.

We therefore,, conclude that from one cone (*Brachyphyllum mamillare*) pollen grains come that when found dispersed should fall not only into different species (*Appl. dampieri*, *Appl. trilobatus* and *App. segmentatus*), but even into different genera (*Araucariacites* and *Applanopsis*) (as stated above, I believe that *Tsug. sp. A* also belongs to *Applanopsis*).

In almost all sediments from which *Applanopsis* is recorded, also *Araucaria-*

cites is found, often in large quantities (see for instance BALME 1957, DETTMANN 1963, LEVET-CARETTE 1964, SINGH *et al* 1964, HOROWITZ 1968, NORRIS 1969). This again is in agreement with the fact, that all these grains are found together within one cone.

It should be pointed out that not all *Applanopsis* species might have belonged to the Araucariaceae, but that at least some grains of this genus did originate from an araucariaceous male cone. The pollen grains that were described by COUPER (1958) under the name *Tsugaepollenites mesozoicus*, and were transferred by NILSSON (1958) to *Cerebropollenites mesozoicus* are, in my opinion, unrelated to *Applanopsis* and the Araucariaceae.

When we compare the pollen grains of the male cones that showed some resemblance with *Brachyphyllum mamillare* with dispersed pollen, we see that the grains of *Brachyphyllum mirandai* agree with *Araucariacites australis*, except for the pollen grain with the "inner body".

The pollen grains of *Apterocladus lanceolatus* are partly like *Applanopsis dampieri* and partly like *Applanopsis trilobatus* (see GAMERRO (1965).

TOWNROW (1967) states that the pollen of *Masculostrobus warrenii* is closely similar to *Applanopsis trilobatus*.

So I believe that there must be some relationship between these three cones and *Brachyphyllum mamillare*.

Distribution of the fossil Araucariaceae

The fact that these two types of pollen grains have been found within one cone, has also consequences for the distribution of the fossil Araucariaceae. SEWARD & CONWAY (1934) published a detailed account on the fossil distribution of this family.

The first definite araucariaceous fossils are found in the Jurassic in Europa, India, and Antarctica. In North America they have only been found in the Lower Cretaceous, not before the Cretaceous, nor after, although there are many Tertiary floras known from America. In the Creaceous araucariaceous remains are also recorded from Europe, India, and Australia. During the Tertiary the Araucariaceae are known from Europe. Nowadays there are 15 species, 6 belonging to the Section Colymbea (which occur in New Guinea and South America) and 9 to the Section Eutacta (Australia, Kerguelen).

But, as the fossil pollen genus *Applanopsis* (and also *Araucariacites*) is known from all over the world during Jurassic and Cretaceous times, we may assume that the Araucariaceae might have been distributed over almost the whole world during those times, and not only over Europe, India and Australia. However, we have found no remains other than the pollen until now. It means, however, that the concept based on the distribution of the recent species, that the family spread from an Antarctic centre of origin, is not as obvious as sometimes thought.

TAXODIACEAE

ELATIDES Heer

Elatides williamsoni (Brgt) Seward, male cone

Pl. XIII, figs. 3, 4; Pl. XIV, fig. 2.

1875 *Walchia williamsonis*	– Phillips. p. 230, pl. VIII, figs. 1, 3, lign. 61 (shoot, male cone)
1900 *Pagiophyllum williamsoni*	– Seward. p. 291, pl. X, figs. 2, 3, text-fig. 52 (shoots, female and male cones)
1919 *Elatides williamsonis*	– Seward. p. 271, text-fig. 742 (discussion)
1943 *Elatides williamsoni*	– Harris. p. 325, pl. VIII,text-figs. 1–3 (general description; pollen grains text-fig. 2E)
1958 *Elatides williamsoni*	– Couper. p. 129, pl. 27 figs. 7, 8 (pollen grains)
1962 *Elatides williamsoni*	– Potonié. p. 172, pl. 19 fig. 506 (pollen grains)
1967 *Elatides williamsoni*	– Potonié. p. 160 (discussion pollen)

Age: Middle Deltaic Gristhorpe Series (Middle Jurassic), Yorkshire.

Locality: Mainly Gristhorpe bed (Cayton Bay).

Description: The following description is based on re-examination of slide V. 28481, British Museum of Natural History, Department of Palaeontology, and on material collected by the author and deposited in the Division of Palaeobotany and Pollenmorphology, Botanical Museum and Herbarium, State University, Utrecht, under no. Yor-19, Yor-20, Yor-56-67.

Pollen grains monoporate or inaperturate; outline almost circular, but often folded; diameter 52 μ (extremes 42–62 μ); porus, if present, with a weak annulus; exine consisting of two layers: nexine and sexine; nexine 0,5–1 μ thick, smooth; sexine ("perine") loosely fitting, normally wrinkled or torn, very thin (less than 0,5 μ), scabrate; size of pollen grains without sexine 39 μ (extremes 30–47 μ).

Discussion: PHILLIPS (1875) was the first to describe a male cone of *Elatides williamsoni* but he did not describe its pollen grains, neither did SEWARD (1900, 1919).

HARRIS (1943) described them as follows: "Most of the pollen studied, was obtained from half-sized immature cones, but in a few mature ones a single pollen sac had failed to open and yielded pollen. The grains are round, 30 μ in diameter, and show a longitudinal furrow. The extine is moderately thick, and smooth or very faintly dotted".

COUPER (1958) gave a detailed description which agrees with the one given here.

He only says that the grains are monoporate, but that the pore is not always clearly shown. The present author thinks that the grains are partly monoporate and partly inaperturate.

POTONIÉ (1962) just gives Couper's description.

The affinity of *Elatides williamsoni* was discussed in detail by HARRIS 1943. He concluded that *Elatides williamsoni* agreed on all major points with the Taxodiaceae (shoots, microsporophylls, pollen grains, female cone-scales and seeds): "It is concluded that *Elatides williamsoni* is certainly a member of the Taxodiaceae and is nearest to *Cunninghamia* in several respects but not ancestral to it".

Comparison with recent pollen grains

When we compare the pollen of *Elatides williamsoni* with those of the recent ELATIDES Heer

Taxodiaceae, we see that they are very close to the grains of *Cunninghamia lanceolata* (Pl. XIV, fig. 1) having also a loosely fitting sexine. They are also similar to grains of other genera of the Taxodiaceae, like *Sequioa* and *Cryptomeria.* This was also noted by HARRIS (1943) and COUPER (1958). POTONIÉ (1967) stated, that according to him, the pollen grains might better be classified with the Araucariaceae than with the Taxodiaceae (in 1962 he still included them in the Taxodiaceae).

Comparison with dispersed pollen grains

COUPER 1958 made a new genus *Perinopollenites*, with a single species, *Perinopollenites elatoides* (Pl. XIII, fig. 6) for dispersed pollen grains that are just like the pollen of *Elatides williamsoni.*

This species has later been recorded by various authors from all over the world during Jurassic times.

When the "inner bodies" of *Elatides williamsoni* are found dispersed, they are like pollen from the genus *Spheripollenites* Couper 1958 (Pl. XIII, fig. 5) (=*Exesipollenites* Balme 1957). Pollen grains that are thought to belong to this genus, may have had very different origins, for example the "inner bodies" of *Classopollis*-type pollen grains (see the section on *Brachyphyllum crucis*) or of *Elatides williamsoni.*

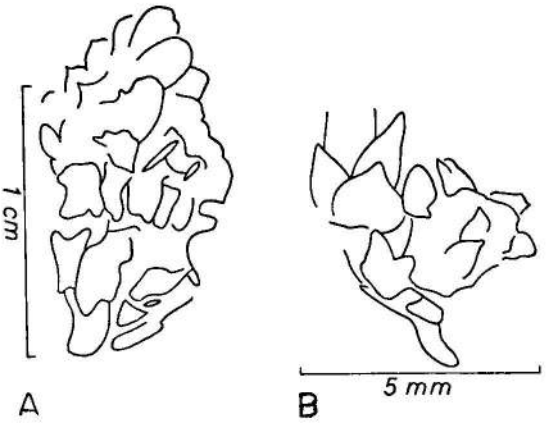
HIRMERELLA-GROUP

BRACHYPHYLLUM Brgt

Brachyphyllum crucis Kendall, male cone

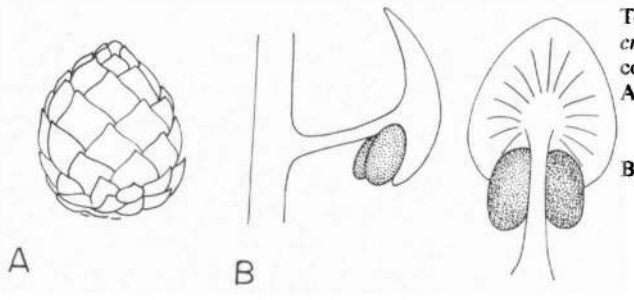
Pl. XIV, figs. 3–6, Pl. XV, figs. 1, 2, 4, PL . XVI fig. 1; text-fig. 8, 9.

Diagnosis: Male cone 7 mm. long, 3,3 mm. wide; microsporophylls borne spirally, consisting of a rather slender stalk and a sporophyllhead 0,5–0,7 mm. high,



Text-fig. 8. *Brachyphyllum crucis* Kendall, male cone.
A. Holotype
B. Male cone in very close association with a shoot of *Brachyphyllum crucis* (to the left).

0,5 mm. broad, rhomboidal in outline; outer cuticle of microsporophyllhead about 4 μ thick; normally some scattered stomata present, stomata sunken; guard-cells surrounded by a ring of subsidiary cells; stomatal pit oval to circular; papillae of subsidiary cells forming a thickened ring around the guard cells; periclinal walls of subsidiary cells marked with fine striations running radially from centre of stomatal apparatus; encircling cells indistinct; epidermal cells rectangular, 15–20 μ wide, 20–40 μ long with thick walls, arranged in longitudinal rows; margin of microsporophyllhead scarious; microsporophyll bearing two pollen sacs; pollen grains spherical with somewhat flattened poles; equatorial diameter 35 μ (extremes 30–40 μ); exine divided into two caps by an indistinct equatorial belt, 5 μ wide; exine of the caps 1–2 μ thick, baculate; striae of the equatorial belt not very distinct, usually 8 striae, sometimes up to 12; distal cap separated from the equatorial belt by a distinct thin region (rimula) 1–2 μ wide; distal pole with a circular thin area about 9 μ in diameter; proximal pole with a triangular thin area, extending over the largest part of the pollen grain (in polar view).



Text-fig. 9. *Brachyphyllum crucis* Kendall, male cone reconstructions.
A. Possible reconstruction of the male cone (see also Barnard 1968).
B. Reconstruction of the microsporophylls with the two pollen sacs.

Age: Lower Deltaic (Middle Jurassic), Yorkshire.

Locality: Hasty Bank

Description of the material: Besides the specimen on which the diagnosis is based (no. 2984 Division of Palaeobotany and Pollenmorphology, Botanical Museum and Herbarium, State University, Utrecht), there are three more cones (no. 3957 and 3958 two cones). All four cones are complete, without a stalk, and yielded masses of pollen grains of the *Classopollis*-type (Slides with the pollen grains under no. Yor-75, Yor-78, Yor-79 and Yor-80 in the same Division).

Discussion: The cones were found in very close association with (but were not attached to) shoots of *Brachyphyllum crucis*. On two of the specimens only *Brachyphyllum crucis* occured, on the other one this species was the most common fossil on the block. But the attribution was made not only on the basis of this association. The cuticle of the microsporophyllhead is extremely like the cuticle of the leaf of *Brachyphyllum crusis*. Both have scattered stomata (although the microsporophyllhead has of course many fewer stomata than the leaves). It is impossible to distinguish between the stomata of the cone and of the leaves, they appear to be exactly the same. In addition to this, both the leaf and the microsporophyllhead have a scarious margin (a feature that is not very common in cuticles).

The agreement in cuticle structure, therefore, is the main reason for this attribution.

Comparison with other cones containing Classopollis

Cones like this one yielding the *Classopollis*-type of pollen grains, are known from Germany, France, England, Iran and Argentina:
Hirmerella muensteri (Schenk) Jung, (= *Cheirolepis muensteri* Schenk), *Hirmerella airelensis* Muir et v. Konijnenburg, *Brachyphyllum scotti* Kendall, *Pagiophyllum connivens* Kendall, *Masculostrobus rishra* Barnard (attributed to *Brachyphyllum expansum* (Sternberg) Seward), and *Tomaxellia biforme* Archangelsky. The first two belong to the *Hirmerella*-group, on the basis of the structure of the female cones. Possibly *Pag. connivens* as well (Harris pers. comm.)

HOERHAMMER (1933) and later JUNG (1968) made elaborate studies of *Hirmerella muensteri*, and described the male cone as having peltate sporophylls with radially arranged pollen sacs (up to twelve).

Fragments of male cones of *Hirmerella airelensis* were described by MUIR & v. KONIJNENBURG (1970) as having microsporophylls bearing probably two pollen sacs. They attributed the material from Cape Twt described by HARRIS (1957) as *Cheirolepis muensteri* and also having only two pollen sacs on each microsporophyll, to this species.

Of the male cone associated with *Brachyphyllum scotti* (KENDALL 1949) we know little; only the pollen grains are well known, and they are considered below.

We also know very little about the male cone associated with *Pagiophyllum connivens* (KENDALL 1952).
The pollen grains are compared below.

Masculostrobus rishra (BARNARD 1968) has microsporohylls bearing a number

of pollen sacs (6–8), and resembles in this respect *Hirmerella muensteri.*

Tomaxellia biforme (ARCHANGELSKY et GAMERRO 1967) probably has a number of pollen sacs on each microsporophyll, but Archangelsky and Gamerro's account does not make this clear. They compare the cones with those of *Hirmerella.*

As only the female cone-scales of both the *Hirmerella* species are known, we can only attribute these species with certainty to the *Hirmerella*-group; but there is no reason why the other species would not belong to this group (and indeed it is highly probable that they will belong to it), only we have not the proof yet.

When we compare the male cones of these 7 species with each other, we see that they fall into two groups on base of the number of pollen sacs on each microsporophyll. There is a group with a number of pollen sacs (6–8 for *Masculostrobus rishra*, and up to 12 for *Hirmerella muensteri*), and a group with only 2 pollen sacs (*Hirmerella airelensis* and *Brachyphyllum crucis*). We do not know the number of pollen sacs of *Pagiophyllum connivens* and *Brachyphyllum scotti*; and *Tomaxellia biforme* will probably fall within the first group. The pollen grains will be considered later in this section.

There is another point of agreement between those 7 species, namely the type of stoma of the leaf-cuticle (and of the microsporophyll if known): In all species the subsidiary cells form a thickened ring around the stomatal pit. In some cases there are papillae on this ring: *P. connivens*, *Br. expansum* very strongly developed, *Br. crucis* and both the *Hirmerella* species somewhat less so. Only *Br. scotti* and *Tomaxellia biforme* do not seem to have papillae on top of this ring. Four of these species have striae on the periclinal walls of the subsidiary cells (*Br. crucis*, *Hir. muensteri*, *Hir. airelensis* and *Tomaxellia biforme*). So I believe that Conifers having cuticles with one or all of these characteristic features – and especially with the stomatal "ring", (like *P. peregrinum* (L. et H.) Schenk and *Pag. maculosum* Kendall) – may all belong to the *Hirmerella*-group.

Comparison with Classopollis and Circulina

A short account of the most important literature on *Classopollis* is given first.

REISSINGER (1950) described dispersed pollen grains like those found in the male cones of *Hirmerella muensteri* under the name *Pollenites torosus.* He also mentioned some other grains that were rather like *Pollenites torosus* but not identical according to hem, and he did not name them.

PFLUG (1953) described those grains (so far as I can judge from the illustrations they are the same) under the new name *Classopollis classoides.* He thought them to be tricolporate or sometimes tetracolporate and with a so called "rimula". He misinterpreted the grains completely,but the name is valid, and so long as it is not proved that *Pollenites torosus* is the same as *Classopollis classoides*, the specific epithet must be maintained and the latter species is the type species of the genus *Classopollis.*

COUPER (1955) gave a much better morphological description and compared the grains with those from the *Pagiophyllum connivens* cone. He thought them to be identical. In 1958 the same author emended the genus *Classopollis*, and he

took *Classopollis torosus* (Reis.) Couper as type species, because according to him it is conspecific with *Classopollis classoides* (Pl. XV, fig. 5).

POCOCK & JANSONIUS (1961) in their revision of *Classopollis* emend the genus again, and they take *Classopollis classoides* as type species, for the same reason as discussed above by the present author. They give an elaborate morphological description and interpretation, saying among others: "Exoexinal ornament appears to consist of small pits". They describe three new species: *Classopollis belloyensis*, *Classopollis minor* and *Classopollis pflugii*. *Classopollis belloyensis* was found in the Permian, and there are only a few rather badly preserved specimens. *Classopollis minor* is a rather small form of *Classopollis* with prominent striations. The Lower Cretaceous *Classopollis pflugii* has "the exoexine loosely enveloping the intexine, which forms a more or less spherical central body".

CHALONER & CLARKE (1962) describe the Permian spore *Vittatina hiltonensis*, and compare it with *Classopollis belloyensis*, which they think is rather like it. If *Classopollis belloyensis* is excluded from the genus *Classopollis*, the genus then ranges from the Rhaetic to the Cretaceous, and not as stated by Pocock and Jansonius from the Permian to the Cretaceous (there are no Triassic records older than Rhaetic).

In 1964 PETTITT & CHALONER investigated the problem of the morphological structure of *Classopollis* by electron microscope work. They did this work on the material from Cape Twt (HARRIS 1957) which was later assigned to *Classopollis harrisii* (MUIR & v. KONIJNENBURG 1970). They state: "The exine is tegillate (tectate) but in addition the ectonexinous layer bears a series of relatively large inwardly-directed rods. The sexine and ectonexine are of homogenous composition and beneath them a lamellated endonexine may also be present. The wall structure proves to be as distinctive as the general morphology of the pollen, and in its complexity is unmatched even among living Angiosperms". This is the direct opposite of what Pocock and Jansonius thought about the ornamentation.

DE JERSEY & PATEN (1964) emend the generic diagnosis given by Pocock & Jansonius to include grains with a smooth equatorial girdle (like their new species *Classopollis simplex*). This species could not be included in *Circulina* Maljavkina (see KLAUS 1960) because it had an equatorial girdle, and not in *Classopollis* because it did not have striations on this girdle. So they widened the diagnosis of *Classopollis* to include species like this.

BURGER (1965, 1966) describes four new species of *Classopollis*: *Classopollis alexi*, *Classopollis echinatus*, *Classopollis hammenii* and *Classopollis multistriatus*. He gives descriptions and illustrations of these species but does not compare them. According to the present author it is possible that *Classopollis echinatus* and *Classopollis hammenii* (both having echinae, those of *Classopollis hammenii* are somewhat smaller), are two forms of one species, and also that *Classopollis alexi* and *Classopollis multistriatus* are two forms of another species.

BOLTENHAGEN (1968) revises the genus *Classopollis* and related genera (like *Circulina* (Pl XV fig. 3), but adds nothing really new to our knowledge.

When we look at the *Brachyphyllum crucis* pollen grains to compare them with *Classopollis* and *Circulina*, we note a very peculiar feature: When we macerate *Brachyphyllum crucis* grains for a very short time, they are exactly like *Circulina*; but when we macerate them during a longer period, the exine ornamentation (with the striae) appears, and then the pollen grains are rather like *Classopollis multistriatus*, having 8–12 striae in their equatorial belt.

The pollen of *Brachyphyllum scotti* (Pl. XVI fig. 7) is also like *Circulina*, and here again exine ornamentation and striations appear, but only after maceration during a very long time. Thus, it appears that there is no fundamental difference between *Classopollis* and *Circulina*, but that *Circulina* grains are *Classopollis* grains with a thick, but removable layer on top of their exine ornamentation.

When we consider the pollen grains from the other male cones that are like *Brachyphyllum crucis*, we see that the pollen from *Hirmerella muensteri*, is just like *Classopollis classoides*. Dispersed pollen grains that agree with those from *Hirmerella airelensis* were described by MUIR & V. KONIJNENBURG (1970) as *Classopollis harrisii*, differing from the other *Classopollis* species by the absence of equatorial striations (as in *Classopollis simplex*) and of the distal pore, and from *Circulina* by the prominent exine structure.

Brachyphyllum scotti grains are as a rule like *Circulina*, but after long maceration they show some *Classopollis* features (see above), and are like *Classopollis classoides*.

The grains from *Pagiophyllum connivens* are ill known (see the paragraph on *Pagiophyllum connivens* male cone), but they are of the *Classopollis*-type.

Masculostrobus rishra pollen grains resemble according to Barnard *Classopollis torosus* sensu COUPER (1958), but according to the present author they agree better with *Classopollis multistriatus* and are thus rather like those of *Brachyphyllum crucis*.

Tomaxellia biforme grains agree with *Classopollis classoides*.

Finally, there is one more possible member of the Cheirolepidaceae. T. M. Harris informed me that *Pagiophyllum maculosum* Kend. has female cones that are rather like the female cones of *Hirmerella*, thus belonging very probably to the Hirmerella-group.

A great many *Classopollis* grains are sticking to the cone surface and on the seed nucellus.

The dispersed pollen genus *Spheripollenites* Couper may contain among other things, the "inner bodies" (i.e. the nexine) of *Classopollis* grains.

PAGIOPHYLLUM Heer

Pagiophyllum connivens Kendall, male cone

Pl. XVI figs. 2, 3

1952 *Pagiophyllum connivens* – Kendall, p. 586, text-fig. 2 (general description; pollen grains text-fig. 2C).

1958 *Pagiophyllum connivens* – Couper. p. 130, pl. 28 fig. 1 (pollen)
1962 *Pagiophyllum connivens* – Potonié. p. 175, pl. 19 figs. 520a, b, 521. (pollen grains.)

Age: Lower and Middle Deltaic (Middle Jurassic), Yorkshire.

Locality: Eston Moor Quarry.

Description: Five poorly preserved male cones were described by Kendall (1952) as male cones of *Pagiophyllum connivens*. This attribution was made on basis of association with *Pagiophyllum connivens* shoots, and the female cone scales *Araucarites estonensis*, and on basis of the agreement in cuticle structure. She describes the pollen grains: "The pollen grains are round, 20–30 μ in diameter, and often marked by a ridge about 6 μ wide, which may be merely a fold resulting from collapse. The extine is about 4 μ thick." She attributes the cones provisionally to the Araucariaceae.

COUPER (1958) examined Kendall's slides and came to the following description: "Pollen grains circular to oval in equatorial contour; exine scabrate and about 1 μ thick at polar regions, thickened in equatorial region. Size range: 28–37 μ in equatorial diameter". He compares the grains with the dispersed *Classopollis torosus* (Reis.) Couper and states: "Unfortunately, the pollen preparation is rather deeply stained and undermacerated and most of the pollen grains are still stuck together in the pollen sac and are not clearly displayed. For this reason, reference should be made to the detailed description of *Classopollis torosus* (Reissinger) Couper, which is based on many hundreds of specimens of dispersed grains from the "*Pagiophyllum connivens* bed" of T. M. Harris. They are closely comparable with those of *P. connivens* and almost certainly belong to this species". According to him Prof. T. M. Harris (pers. comm.) did not consider the affinity of *Pagiophyllum connivens* as by any means certain. *Pagiophyllum connivens* is now thought to belong probably to the Hirmerella-group (see paragraph on *Brachyphyllum crucis*).

POTONIÉ (1962) just gives Kendall's and Couper's descriptions.

The present author also examined Kendall's slides (V. 29561a, b, c and V. 29562 in the Department of Palaeontology, British Museum, Natural History), and she agrees with Couper about the state of preservation, the general impression and the size of the pollen grains. But, according to her, it is impossible to say with which species of *Classopollis* the pollen grains agree. The fact however, that *Classopollis classoides* (= *Classopollis torosus* sensu Couper) is dispersed very common in the *Pagiophyllum connivens* bed, makes it probable that those grains belong to *Pagiophyllum connivens*.

N.B. Prof. T. M. Harris (pers. comm.) informed me, that *Pagiophyllum connivens* is identical with *Pagiophyllum kurri* Kräusel, and because *Pagiophyllum kurri* is the older name, it has priority over *Pagiophyllum connivens*.

CONIFERAE INCERTAE SEDES

MASCULOSTROBUS Seward

Masculostrobus harrisii n. sp.

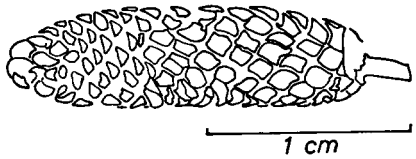
Pl. XVI, fig. 5; text-fig. 10.

Diagnosis: Male cone, 20 mm. long, 5 mm. wide, with a small stalk 1,5 mm. long, 0,5 mm. wide and longitudinally grooved; cone axis fairly robust; microsporophylls borne spirally, phyllotaxis probably 5/13, but not quite distinct; microsporophyll consisting of a stalk 1,5–2 mm. long, and a sporophyllhead 1,2 mm. high, 1 mm. wide, somewhat diamond shaped, with a thickened keel ending just below the apex; cuticle of microsporophyll unknown; number and structure of pollensacs indistinct, probably two; pollen grains inaperturate; outline almost circular to somewhat elliptical, often folded; diameter 64 μ (extremes 59–70 μ); exine 1–1,5 μ thick, no different layers visible; surface smooth.

Age: Middle Deltaic Gristhorpe Series (Middle Jurassic), Yorkshire.

Locality: Gristhorpe bed (Cayton Bay).

Type specimen: No. 1354, Division of Palaeobotany and Pollenmorphology, Botanical Museum and Herbarium, State University, Utrecht.
Pollen slides under no. Yor-69 in the same Division.
The species is named after Professor T. M. Harris.



Text-fig. 10. *Masculostrobus harrisii* sp. nov.–holotype.

Description of the material: There is only the type specimen. It was found at the Gristhorpe bed and is in good condition. However, the cuticle of the microsporophyll broke into tiny fragments, which gave no information at all.

Because there is only one specimen, I did not section it to study the number of pollensacs. So far as I could see, there are two pollensacs on each microsporophyll, but there might be more.

Discussion: This cone was discovered during a routine examination of male *Elatides williamsoni* cones. It was included in the genus *Masculostrobus* Seward because it yielded non-saccate pollen grains.

Maculostrobus was redefined by BARNARD (1968) so that it only includes male cones of those Conifers which do not produce winged pollen. The genus *Pityanthus* Nathorst is used for male coniferous cones with saccate pollen grains.

Masculostrobus harrisii is exactly like male *Elatides williamsoni* cones, but it yielded different pollen grains. Because the cuticle of *Masculostrobus harrisii* is unknown, the pollen grains are the only difference from *Elatides williamsoni.* Also the number of pollensacs might be different (three for *E. williamsoni* – see HARRIS 1943 –, and possibly two for *M. harrisii*), but this has not been proved. When we compare the pollen grains with those known from other Conifer cones, we see that they agree more or less with those of *Brachyphyllum mamillare* – type 1. But there are differences: The exine does not show different layers in *M. harrisii* while in *Br. mamillare* it has a clear differentiation in nexine and sexine. Also the sexine of *M. harrisii* is smooth, while it is granulate in *Br. mamillare.*

ARCHANGELSKY & GAMERRO (1967) described a male cone from the Lower Cretaceous of Argentina, attached to *Brachyphyllum irregulare* Archangelsky, which yielded pollen grains that dispersed are known as *Inaperturopollenites limbatus* Balme. Those grains agree quite well with those of *Masculostrobus harrisii,* only in the *Brachyphyllum irregulare* grains the exine is thicker on the equator (6 μ) and becomes much thinner towards the poles, while in *M. harrisii* I could not see any variation in exine thickness. There also seemed to be a thinner area on one of the poles of *Brachyphyllum irregulare* pollen grains, suggesting a colpus; nothing of this kind was found in *Masculostrobus harrisii.*

It is impossible to say anything about the plant to which *Masculostrobus harrisii* might have belonged. The only really common Conifer in the Gristhorpe bed is *Elatides williamsoni,* to which already a male cone is attributed. Besides, we do not know anything about the cuticle of *Masculostrobus harrisii* making it very difficult to conclude anything at all about its affinities.

Comparison with dispersed pollen grains

When we compare *Masculostrobus harrisii* pollen grains with dispersed pollen, we notice that they resemble the pollen grains of the genus *Inaperturopollenites* Thomson and Pflug, but it is difficult to say with which species they agree best.

They differ from *Inaperturopollenites limbatus* Balme in their somewhat smaller size, somewhat thinner and smooth exine. They do not show colour differentiation in the exine like *Inapertorupollenites limbatus.* They are distinguished from *Inaperturopollenites turbatus* Balme by their thicker and smooth exine, and the absence of a much thicker polar area about 40 μ in diameter.

PITYANTHUS Nathorst

Pityanthus scalbiensis n. sp.

Pl. XVI, figs. 4, 6; text-fig. 11

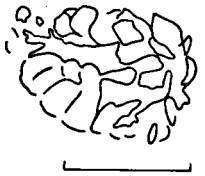
Diagnosis: Male cones at least 8 mm. long, 5 mm. wide; microsporophylls borne

spirally, distally exposed part rhomboidal, 1mm. wide, 1–1,2 mm. high; cuticle of microsporophyll unknown; number and structure of pollen sacs unknown; pollen grains disaccate or ?trisaccate, often folded; sacci offset distally in equatorial view, sometimes showing a faint reticulum; then muri 1 μ wide, lumina 2 μ in diameter; nexine very thin (less than 0,5 μ); sexine about 1 μ thick, with short columellae and spherical capita; corpus about as long as broad, with a pitted tectum, 0,5–1 μ thick; boundary between corpus and sacci clearly marked.
Size range (only 9 specimens for accurate measuring):
length of corpus 42 μ (extremes 34–48 μ)
breadth of corpus 43 μ (extremes 31–53 μ)
length of saccus 27 μ (extremes 22–31 μ)
breadth of saccus 21 μ (extremes 17–28 μ)
overall breadth 54 μ (extremes 42–67 μ)
ratio l/b of corpus 0,99 (extremes 0,90–1,12)

Age: Upper Deltaic (Middle Jurassic), Yorkshire.

Localities: Scalby Ness and Black's drifted plant bed at Scalby Wyke.

Description of the material: Besides the type specimen (no. 2966 Division of Palaeobotany and Pollenmorphology, Botanical Museum and Herbarium, State University, Utrecht), which is from Scalby Ness – the Ginkgo bed, there is only one other specimen (no. 2961) which is from Black's drifted plant bed. The pollen slides of both cones are deposited in the same Division under resp. no. Yor-74 and Yor-73. Both cones are rather corroded, thus giving not very much information. Many pollen grains were heavily folded, thus not being available for accurate measurements.



Text-fig. 11. *Pityanthus scalbiensis* sp. nov.-holotype.

Discussion: Although the cones are in bad condition, they were described because they yielded disaccate pollen grains, which until now have not been found in a Jurassic Conifer cone. Some pollen grains are definitely disaccate (Pl. XVI, fig. 6) while others appear to be trisaccate (Pl. XVI, fig. 4). The cones were included in the genus *Pityanthus* because they produced saccate pollen grains (see BARNARD 1968 and the section on *Masculostrobus*). We cannot say anything definite about the plant to which *Pityanthus scalbiensis* might have belonged, because there is too little information about the cones. The only point worth mentioning is that the type specimen *Pityanthus scalbiensis* was associated with *Ginkgo huttoni* (Heer) Sternb. and *Haiburnia blacki* Harris, and the other

specimen only with *Haiburnia blacki*. So there is a slight possibility that *Pityanthus scalbiensis* might have belonged to *Haiburnia blacki*.

When we compare *Pityanthus scalbiensis* with other male cones, we see that there is some resemblance with the Lower Cretaceous *Trisacocladus tigrensis* Arch. (see GAMERRO 1965b). But there the pollen grains are normally trisaccate, smaller than those of *P. scalbiensis* and have a clearer exine ornamentation. Gamerro considers *Trisacocladus tigrensis* a member of the Podocarpaceae, and this would also be a possible assignment for *P. scalbiensis* on basis of its pollen grains. But so long as we do not have more information about these cones, this attribution should be regarded as very tentative.

Comparison with dispersed pollen grains

DE JERSEY & PATEN (1964) described dispersed pollen grains that show a great deal of resemblance to the grains of *Pityanthus scalbiensis* as *Podosporites* sp. Those grains are trisaccate, but agree exactly with *P. scalbiensis* in overall size, size of the sacci and exine ornamentation. They compare their grains with *Microcachryidites antarcticus* Cookson and *Podosporites microsaccatus* (Couper) Dettm. *Microcachryidites antarcticus* differs from both *Pityanthus scalbiensis* and *Podosporites sp.* in being much smaller and having sometimes more than three sacci. *Podosporites microsaccatus* differs from the above mentioned species in its subtriangular corpus, and small rudimentary bladders with radial thickenings.

5. FINAL CONCLUSIONS

Formerly it was thought that we knew a great deal about the Yorkshire Jurassic flora. But the more we learn about this flora, the more we come to the conclusion that our knowledge is only fragmentary. We still find new plants or new data about already known plants, every time we study new material.

Also this study on the pollen grains from the male fructifications has revealed some new facts. The main conclusions that can be drawn from this study are given below.

Caytoniales: Although they were formerly thought to be almost identical, the present investigations show that the pollen grains of *Caytonanthus arberi* are different from those of *Caytonanthus oncodes* in several respects: in size (those of *C. arberi* are smaller than those of *C. oncodes*), in the presence of a sulcus (there is no sulcus in *C. oncodes*), and in the presence of a radiating structure on the sacci near the boundary with the corpus (this is absent in *C. oncodes*). *Caytonanthus sp. A* is intermediate between those two species but is too ill known to draw conclusions. Dispersed pollen grains of the Caytoniales fall within the species *Vitreisporites* (= *Caytonipollenites*) *pallidus*.

Lyginopteridales: There is only one male fructification known from Yorkshire (*Pteroma thomasi*), and no new facts were discovered about its pollen grains. Dispersed they resemble more *Alisporites sp. B* than *Alisporites thomasi* as was formerly thought.

Cycadales: Within the Cycadales two types of pollen grains could be distinguished:

1. *Nilssonia*-type: monocolpate pollen grains with a circular to elliptical outline, a moderately thick exine, divided into nexine and sexine; sexine with rodlike columellae and "goblet-shaped" capita, giving rise to a pitted surface. Most *Androstrobus* have this type of pollen grain.
2. *Androstrobus prisma*-type: pollen grains inaperturate with an almost circular outline; exine thin, divided into nexine and sexine; sexine with short, broad columellae and semispherical capita, giving rise to a granulate surface. Only *Androstrobus prisma* is so far known to have this type of pollen grains.

It was concluded that the *Androstrobus* species which have type 1 pollen grains, probably belong to species of *Nilssonia* (as is proved for *A. manis* and *A. wonnacotti*), while the *Androstrobus* species yielding type 2 pollen grains, might belong to the *Pseudoctenis-Ctenis* group (*A. prisma* belongs to *Pseudoctenis lanei*).

The pollen grains were also compared to recent Cycad pollen grains, and it was concluded that they agree in general respects but differ in detail especially in exine ornamentation.

In any case, fossil Cycad pollen has wall structure, and thus, it is possible that fossil monocolpate pollen is not necessarily of Angiospermous origin as was formerly thought (see for instance *Clavatipollenites*) but may also point to Cycadalean origin.

Dispersed fossil Cycad pollen grains fall within *Cycadopites* (= *Monosulcites*) *minimus*, although the present author is inclined to think that it should be possible to distinguish between the different types of Cycadalean pollen grains within this species.

The new genus *Hastystrobus* is described. This is a genus for fossil male cones which yield *Eucommiidites* type of pollen grains. It is the first time that a cone yielding *Eucommiidites* pollen had been described. Only the type-species is known: *Hastystrobus muirii* (yielding *Eucommiidites troedssonii*) which very likely has Cycadalean affinities, as probably the whole under (abaxial) surface of the microsporophylls is covered with sporangia, a feature that is known only from the Cycadales. The pollen grains are normally tricolpate, with a large main colpus and two smaller additional ones. Some pollen grains show only the main colpus, or the main colpus plus one additional one. Thus, it seems likely that *Eucommiidites troedssonii* must have evolved from monocolpate pollen grains, like those of the Cycads.

There are other *Eucommiidites* species known, and some of them are recorded from the micropyles and pollenchambers of seeds (*E. delcourtii* in *Spermatites pettensis*, *E. minor* in *Spermatites patuxensis* and *E. troedssonii* (although the present author believes that these pollen grains belong to a new species and not to *E. troedssonii*) in *Allicospermum retemirum*), proving that *Eucommiidites* has gymnospermous affinities, and is not of Angiosperm origin as was thought by Erdtman. Although *Hastystrobus muirii* and therefore the *E. troedssonii* associa-

ted with it is very likely of Cycadalean origin, it is possible that the other *Eucommiidites* species do not have Cycadalean affinities.

Bennettitales: Within the Bennettitales two types of pollen grains were recognized:

1. *Williamsoniella*-type, to which both *Williamsoniella* species belong: pollen grains monocolpate, outline elliptical to circular, length 25–30 μ, exine thin.
2. *Weltrichia*-type, to which all *Weltrichia* species (with the possible exception of *W. setosa*) and *Williamsonia himas* belong: pollen grains monocolpate, outline elliptical to elongate-elliptical, length 40–60 μ, medium thick exine.

Dispersed pollen grains of type 1 fall within *Cycadopites minimus* while those of type 2 agree with either *Cycadopites carpentieri* or *Cycadopites subgranulosus.*

Ginkgoales: For the first time the male cone of *Ginkgo huttoni* has been described. The pollen grains yielded by it are of the normal Ginkgoalean type. The pollen grains were compared with those of the recent *Ginkgo biloba* and they agree closely. Dispersed they resemble *Cycadopites minimus*, but the present author believes that the *C. minimus* pollen grains of Ginkgoalean origin can be distinguished from *C. minimus* grains of Cycadalean or Bennettitalean origin because of the more elongate outline and acute ends of the pollen grains.

Doubtful Ginkgoales: Within the female fructification *Leptostrobus cancer* pollen grains were found in compact masses near the micropyles of the seeds. Although it is not definitely proved that those pollen grains belong to it, it seems highly probable.

The slides are not very clear, so it was difficult to describe the grains, but they resemble the dispersed *Applanopsis lucidus*. Because *A. lucidus* has very probably (just as the other *Applanopsis* species) affinities with the Coniferae (see *Brachyphyllum mamillare*), it appears that *Leptostrobus cancer* may be of Coniferous origin and not Ginkgoalean as was formerly thought.

Coniferospermae:

Araucariaceae: The pollen grains of *Brachyphyllum mamillare* are of two types:

1. Pollen grains in which the nexine is connected with the sexine; diameter 71 μ and
2. Pollen grains in which the sexine is loose from the nexine, and the nexine is shrunk forming an "inner body"; diameter of sexine 71 μ, diameter of the "inner body" 58 μ. Some pollen grains tend to be somewhat trilobate.

59 % are of type 1, 41 % of type 2 (including 8 % trilobate).

The pollen grains were compared with those of the recent Araucariaceae. Most *Araucaria* species have pollen grains that are like type 1 of *Brachyphyllum mamillare* (normal *Araucaria* type) but *Araucaria araucana* showed the same dimorphism of pollen grains as *Brachyphyllum mamillare*. Here 42 % were of type 1, 39 % had a slightly shrunken nexine, and 19 % had a strongly shrunken

nexine. In some cases, the pollen grains showed a tetrad scar. No trilobate forms were found.

Dispersed *Brachyphyllum mamillare* pollen grains type 1 agree with *Araucariacites australis*, while *B. mamillare* type 2 grains resemble those of *Applanopsis dampieri*, *A. segmentatus* and *A. trilobatus* (and possibly also *Tsugaepollenites sp. A*).

Thus, pollen grains yielded by one cone, may dispersed be classified not only in different species but also in different genera. N.B. *Araucariacites* and *Applanopsis* are often recorded together. Because the three *Applanopsis* species and *Araucariacites* have been recorded from all over the world in Jurassic times, it seems very likely that the Araucariaceae were universally distributed in those days.

Taxodiaceae: The pollen grains of *Elatides williamsoni* were already well known, and nothing new was found. Dispersed they resemble closely *Perinopollenites elatoides.*

Hirmerella-group: For the first time male cones of *Brachyphyllum crucis* were described and they yielded pollen grains of the *Circulina* and *Classopollis* type. When the pollen grains were only slightly macerated, they resembled *Circulina* but after prolonged maceration exine ornamentation including the striae on the equatorial belt became apparent and the grains were comparable to *Classopollis multistriatus.* Because of its pollen grains *B. crucis* was provisionally assigned to the *Hirmerella*-group. It is suggested by the author that all Conifers that belong to the *Hirmerella*-group have a cuticle with a special type of stoma: the stomatal pit is surrounded by a thickened "ring" formed by the subsidiary cells. The ring may bear papillae. Also the periclinal walls of the subsidiary cells may have striae.

Coniferospermae incertae sedes:

Masculostrobus harrisii is described for the first time; its pollen grains are of the *Inaperturopollenites* type. The only difference between the male cone of *Elatides williamsoni* and *Masculostrobus harrisii* are the pollen grains. Otherwise they agree in almost all respects.

Pityanthus scalbiensis was also described for the first time; it yielded disaccate pollen grains, that are rather primitive because the sacci are almost without structure. As the cones were badly preserved not very much information could be gleaned from them.

I would like to finish this paper by making some suggestions for future work on male cones and their pollen grains:

1. Fresh examination of the present material may reveal more information.
2. Further collecting is absolutely necessary.
3. Examination with electron microscope and scanning electron microscope will yield much new information.
4. Chemical tests, for instance fluorescence microscopy and staining, are promising.
5. Study of the wooden axes of cones and comparison with other fossil wood may gain an insight into their taxonomic position and relationship.

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EXPLANATION OF THE PLATES

Pl. I. Caytoniales

Fig. 1. *Caytonanthus arberi* (Thomas) Harris, slide V.29469, mag. 1750×.
Fig. 2. *Caytonanthus arberi* (Thomas) Harris, slide V.29469, radiating structure on the sacci, mag. 1750×.
Fig. 3. *Caytonanthus oncodes* Harris, slide V.18585f mag. 1750×.
Fig. 4. *Caytonanthus arberi* (Thomas) Harris, slide V.29469, sulcus. mag. 1750×.
Fig. 5. *Caytonanthus oncodes* Harris, slide Yor–48, saccus, mag. 1350×.
Fig. 6. *Vitreisporites pallidus* (Couper) Nilsson, mag. 2000×.

Pl. II. Pteridospermae

Fig. 1. *Pteroma thomasi* Harris, slide Yor–2, sacci slightly offset distally, mag. 750×.
Fig. 2. *Alisporites sp.B* Muir, mag. 750×.
Fig. 3. *Pteroma thomasi* Harris, slide Yor–39, mag. 850×.
Fig. 4. *Pteroma thomasi* Harris, slide V.45681, mag. 750×.
Fig. 5. *Alisporites thomasi* (Couper) Nilsson, 900×.
Fig. 6. *Pteroma thomasi* Harris, slide Yor–2, mag. 800×.

Pl. III. Cycadales

Fig. 1. *Androstrobus manis* Harris, slide Yor–18, "goblet-shaped" capita near the arrow, mag. 2000×.
Fig. 2. *Androstrobus wonnacotti* Harris, slide V.25850c, broad sulcus, mag. 1500×.
Fig. 3. *Androstrobus wonnacotti* Harris, slide V.25850c, slitlike sulcus, mag. 1500×.
Fig. 4. *Androstrobus manis* Harris, slide Yor–18, surface, mag. 2000×.
Fig. 5. *Androstrobus wonnacotti* Harris, slide V.25850c, "goblet-shaped" capita, mag. 3000×.

Pl. IV. Cycadales

Fig. 1. *Androstrobus manis* Harris, slide Yor–18, mag. 1400×.
Fig. 2. *Androstrobus sp.A* Harris, slide V.51943, mag. 1700×.
Fig. 3. *Androstrobus sp.A* Harris, slide V.51943, mag. 1700×.
Fig. 4. *Androstrobus szei* Harris, slide V.45487, surface, and "goblets" near arrow, mag. 1600×.
Fig. 5. *Androstrobus major* van Konijnenburg-van C., slide Yor–27, mag. 1450×.
Fig. 6. *Androstrobus prisma* Thomas et Harris, slide Yor–36, surface, mag. 1500×.
Fig. 7. *Androstrobus prisma* Thomas et Harris, slide Yor–36, same pollen grains under phase contrast, showing the granula, mag. 1500×.

Pl. V. Cycadales

Fig. 1. *Androstrobus prisma* Thomas et Harris, slide V.42386, mag. 1500×.
Fig. 2. *Androstrobus prisma* Thomas et Harris, slide Yor–17, mag. 1700×.
Fig. 3. *Cycas circinnatus* L., slide 421, surface, mag. 1250×.
Fig. 4. *Cycas circinnatus* L., slide 421, equatorial view, mag. 1250×.
Fig. 5. *Stangeria paradoxa* T.M., slide 1880, surface, mag. 1350×.
Fig. 6. *Stangeria paradoxa* T.M., slide 1880, exine, mag. 1200×.
Fig. 7. *Stangeria paradoxa* T.M., slide 1880, equatorial view, mag. 1000×.

Pl. VI. Cycadales

Fig. 1. *Encephalartos barteri* L., slide 2297, surface, mag. 1500×.
Fig. 2. *Dioon edule* Lindl., slide 2296, exine, mag. 1550×.
Fig. 3. *Zamia loddigesii* Miq., slide 423, surface, exine, sulcus, mag. 1700×.
Fig. 4. *Dioon edule* Lindl., slide 2296, stereoscan picture, mag. 1550×.
Fig. 5. *Zamia loddigesii* Miq. slide 423, equatorial view, mag. 1400×.
Fig. 6. *Dioon edule* Lindl., slide 2296, stereoscan surface, mag. 5000×.
Fig. 7. *Dioon edule* Lindl., slide 2296, equatorial view, mag. 1000×.

Pl. VII. Cycadales and Bennettitales
Fig. 1. *Monosulcites* (= *Cycadopites*) *minimus* Cookson, mag. 2000×.
Fig. 2. *Chasmatosporites apertus* (Rogalska) Nilsson, mag. 1750×.
Fig. 3. *Williamsoniella coronata* Thomas, slide Yor–49, surface, mag. 1500×.
Fig. 4. *Williamsoniella coronata* Thomas, slide Yor–49, exine, mag. 1500×.
Fig. 5. *Williamsoniella papillosa* Cridland, slide V. 34254, mag. 1500×.

Pl. VIII. Bennettitales
Fig. 1. *Weltrichia sol* Harris, slide V.53486c, surface, mag. 1250×.
Fig. 2. *Weltrichia sol* Harris, slide Yor–55, exine, mag. 1250×.
Fig. 3. *Weltrichia sol* Harris, slide V. 53486, mag. 1000×.
Fig. 4. *Monosulcites* (= *Cycadopites*) *subgranulosus* Couper, mag. 1150×.
Fig. 5. *Monosulcites* (= *Cycadopites*) *carpentieri* Delc. et Spr., mag. 1150×.

Pl. IX. Cycadales and Ginkgoales
Fig. 1. *Eucommiidites troedssonii* Erdtman, mag. 1600×.
Fig. 2. *Hastystrobus muirii* sp. nov., slide Yor–71, three colpi, mag. 1400×.
Fig. 3. *Ginkgo huttoni* (Heer) Sternberg, slide V.27499a, mag. 1500×.
Fig. 4. *Hastystrobus muirii* sp. nov., slide Yor–71, surface, mag. 1400×.
Fig. 5. *Ginkgo huttoni* (Heer) Sternberg, slide V.27499a, mag. 1400×.

Pl. X. Ginkgoales
Fig. 1. *Leptostrobus cancer* Harris, slide V.28580, mag. 500×.
Fig. 2. *Ginkgo huttoni* (Heer) Sternberg, slide Yor–72, mag. 1400×.
Fig. 3. *Leptostrobus cancer* Harris, slide V.28580, mag. 700×.
Fig. 4. *Ginkgo biloba* L., slide 236, colpus and exine, mag. 1200×.
Fig. 5. *Tsugaepollenites lucidus* Pocock, mag. 700×.
Fig. 6. *Ginkgo biloba* L., slide 236, surface, mag. 1200×.

Pl. XI. Coniferales
Fig. 1. *Brachyphyllum mamillare* Brgt. slide V.27554a, mag. 800×.
Fig. 2. *Brachyphyllum mamillare* Brgt. slide Yor–21, nexine attached to sexine, mag. 600×.
Fig. 3. *Brachyphyllum mamillare* Brgt. slide Yor–21, sexine and nexine attached and clearly visible, mag. 800×.
Fig. 4. *Brachyphyllum mamillare* Brgt. slide Yor–21, trilobate, mag. 650×.
Fig. 5. *Brachyphyllum mamillare* Brgt. slide Yor–21, sexine and nexine separated, mag. 1500×.
Fig. 6. *Brachyphyllum mamillare* Brgt. slide Yor–21, trangular "inner body", mag. 700×.

Pl. XII. Coniferales
Fig. 1. *Araucaria araucana*, slide 2523, scalloped sexine and tetrad scar, mag. 700×.
Fig. 2. *Araucaria araucana*, slide 2523, scalloped sexine, mag. 600×.
Fig. 3. *Araucaria araucana*, slide 2523, sexine and nexine attached, mag. 700×.
Fig. 4. *Araucaria araucana*, slide 2523, unfolded sexine, nexine slightly shrunk, mag. 650×.
Fig. 5. *Araucariacites australis* Cookson, 700×.
Fig. 6. *Applanopsis trilobatus* (Balme) Goubin, Taugourdeau et Balme, mag. 600 ×.

Pl. XIII. Coniferales
Fig. 1. *Applanopsis dampieri* (Balme) Döring, mag. 800×.
Fig. 2. *Tsugaepollenites sp.A* Muir, mag. 800×.
Fig. 3. *Elatides williamsoni* (Brgt) Sew., slide V.28481, porus with a weak annulus, mag. 1000×.
Fig. 4. *Elatides williamsoni* (Brgt) Sew., slide V.28481, mag. 1000×.
Fig. 5. *Speripollenites* (= *Exesipollenites*) *subgranulosus* Couper, mag. 1500×.
Fig. 6. *Perinopollenites elatoides* Couper, mag. 1000×.

Pl. XIV. Coniferales

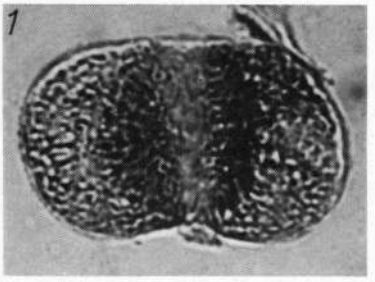
Fig. 1. *Cunninghamia lanceolata* (Lambert) Hook, mag. 650×.
Fig. 2. *Elatides williamsoni* (Brgt) Sew., slide Yor–19, "inner body", mag. 850×.
Fig. 3. *Brachyphyllum crucis* Kendall, slide Yor–80, striae, mag. 1300×.
Fig. 4. *Brachyphyllum crucis* Kendall, slide Yor–79, rimula and tetrad scar, mag. 1000×.
Fig. 5. *Brachyphyllum crucis* Kendall, slide Yor–79, part of tetrad, mag. 750×.
Fig. 6. *Brachyphyllum crucis* Kendall, slide Yor–80, rimula and no exine ornamentation, mag. 1000×.
Fig. 7. *Brachyphyllum scotti* Kendall, slide Yor–77, tetrad, mag. 750×.

Pl. XV. Coniferales

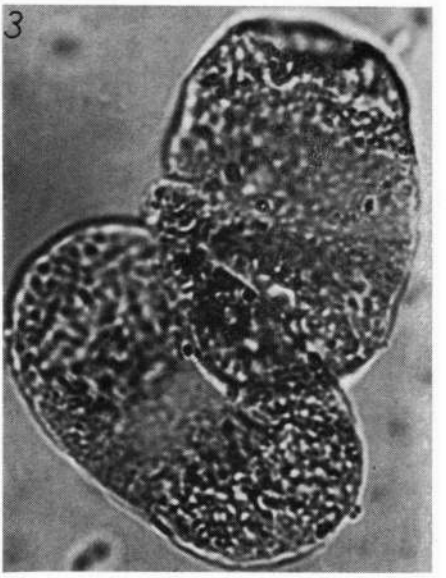
Fig. 1. *Brachyphyllum crucis* Kendall, slide Yor–78, cuticle of microsporophyll with stoma, mag. 650×.
Fig. 2. *Brachyphyllum crucis* Kendall, slide Yor–80, scarious margin of cuticle of microsporophyll, mag. 500×.
Fig. 3. *Circulina parva* Brenner, mag. 1500×.
Fig. 4. *Brachyphyllum crucis*, Kendall, slide Yor–80, striae, mag. 1300×.
Fig. 5. *Classopollis classoides* Pflug, mag. 1300×.

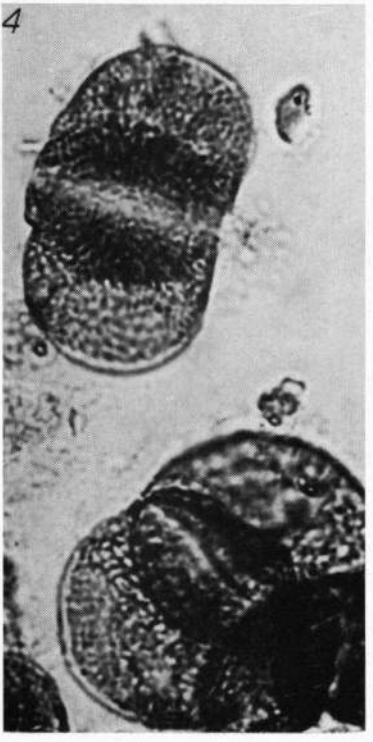
Pl. XVI. Coniferales

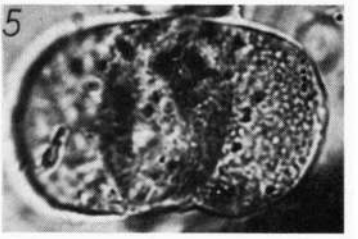
Fig. 1. *Brachyphyllum crucis* Kendall, slide Yor–80, pollen sac, mag. 500×.
Fig. 2. *Pagiophyllum connivens* Kendall, slide V.29562a, mag. 1200×.
Fig. 3. *Pagiophyllum connivens* Kendall, slide V.29561c, mag. 1200×.
Fig. 4. *Pityanthus scalbiensis* sp. nov., slide Yor–73, trisaccate?, mag. 600×.
Fig. 5. *Masculostrobus harrisii* sp. nov., slide Yor–69, mag. 900×.
Fig. 6. *Pityanthus scalbiensis* sp. nov., slide Yor–73, disaccate pollen grain, mag. 700×.

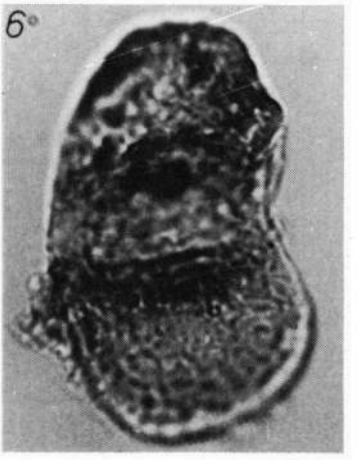




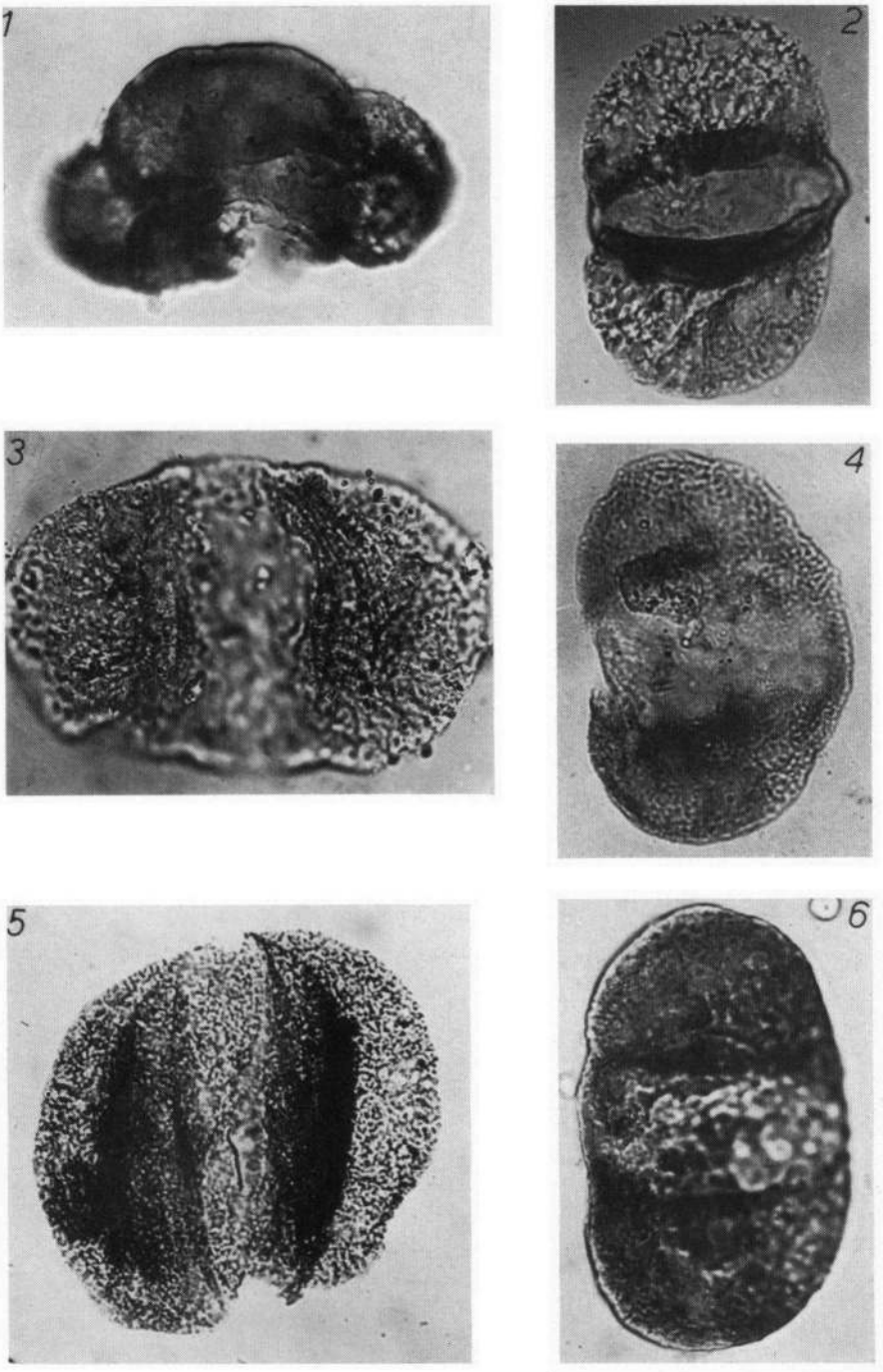






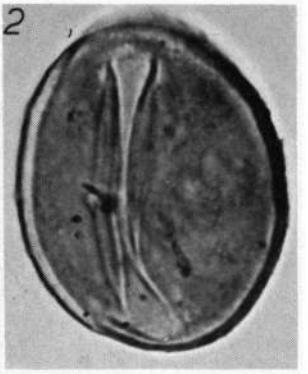


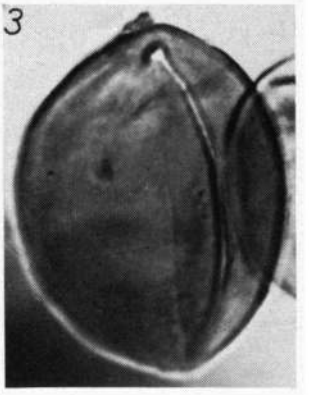
Pl. I. Caytoniales



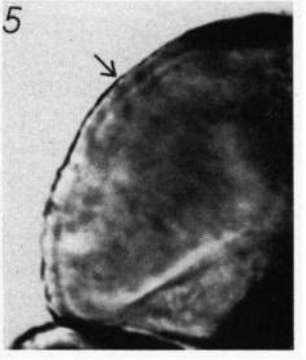
Pl. II. Pteridospermae



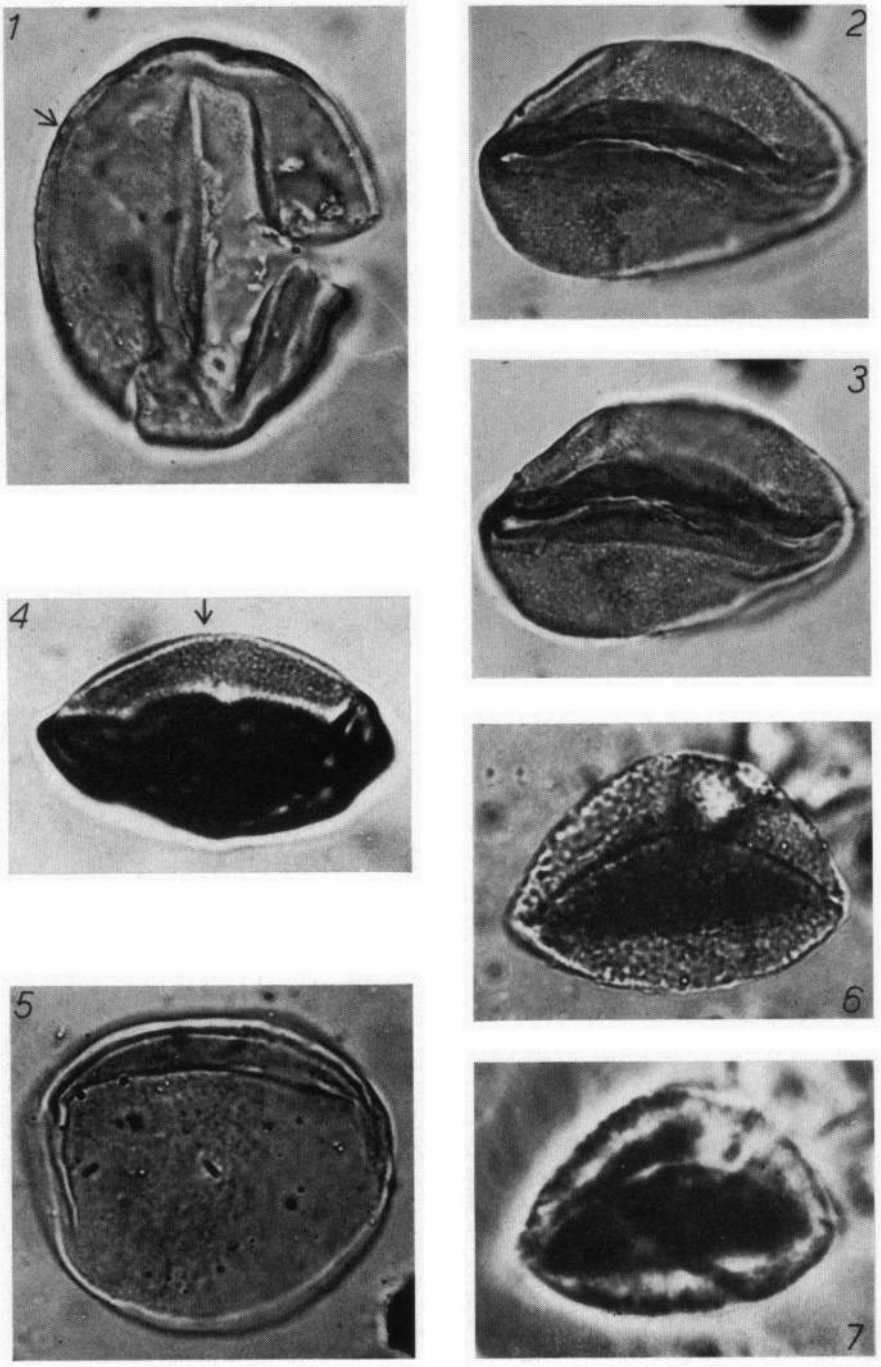




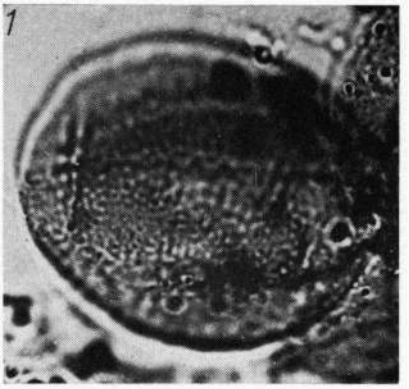


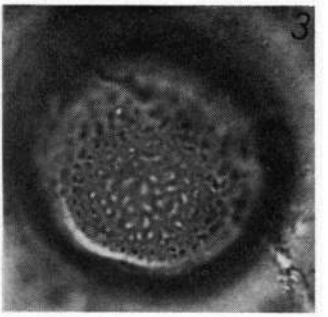


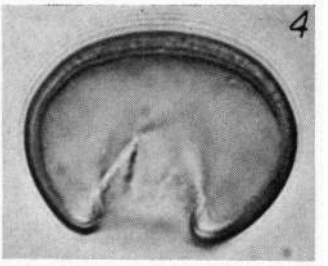
Pl. III. Cycadales

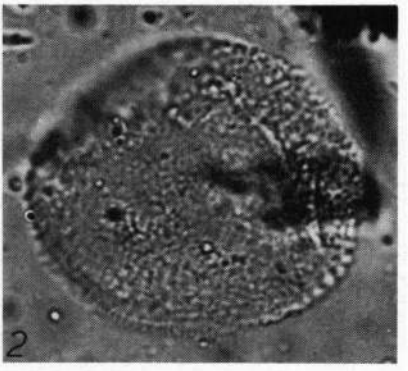


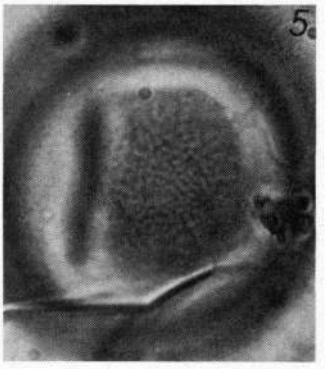
Pl. IV. Cycadales

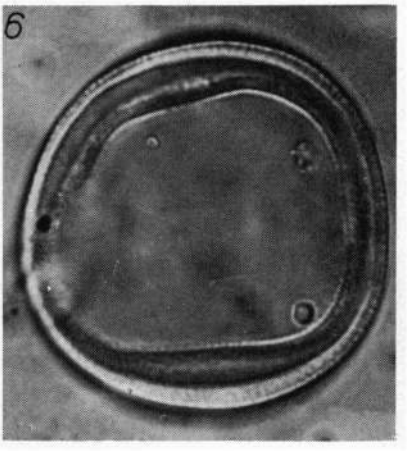


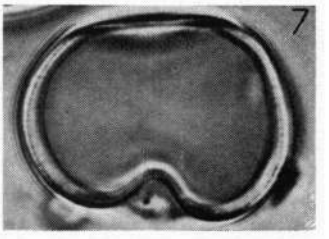




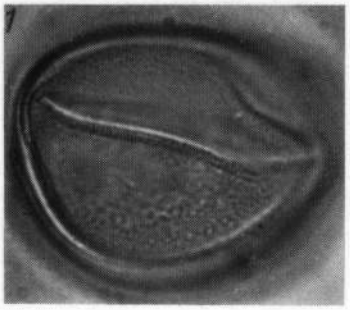


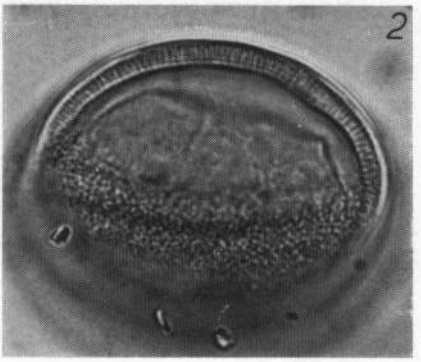


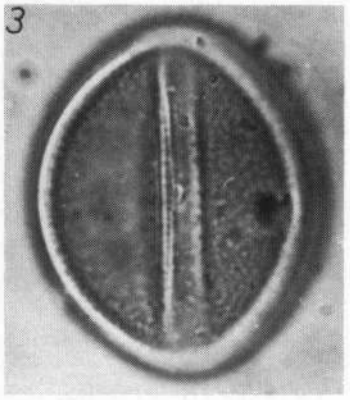


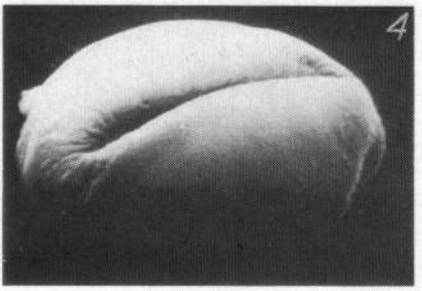


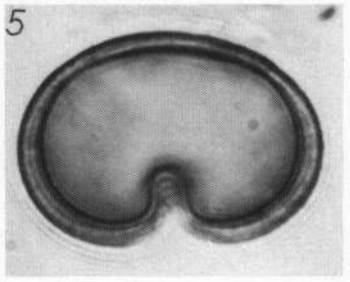
Pl. V. Cycadales

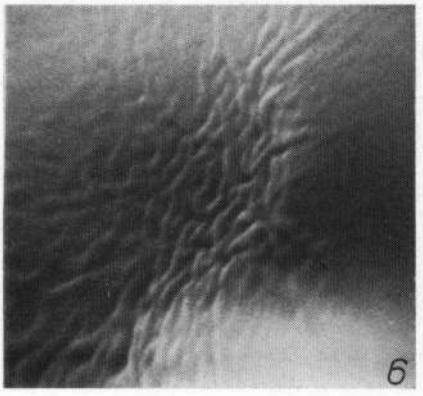


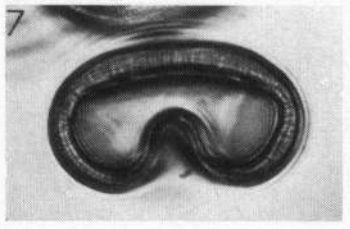




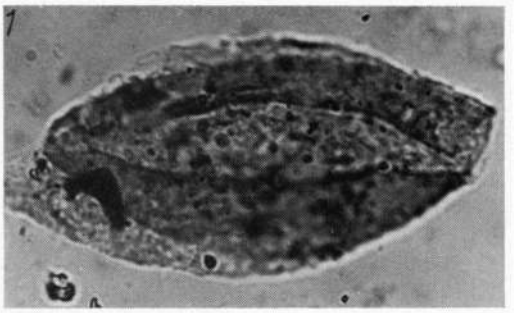


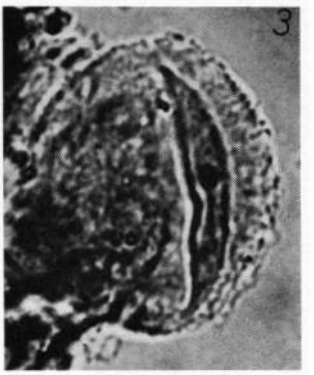


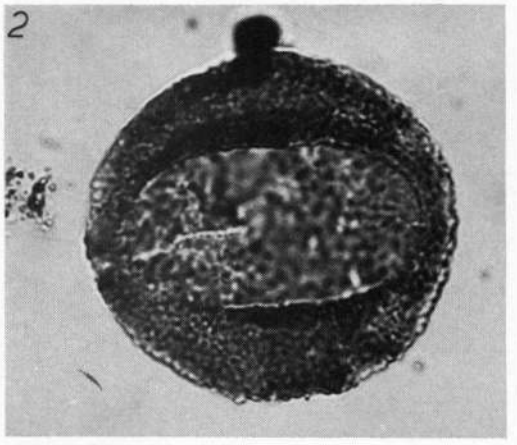




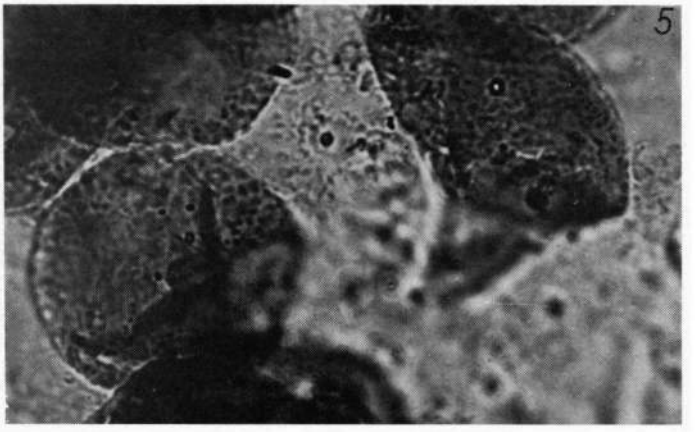
Pl. VI. Cycadales



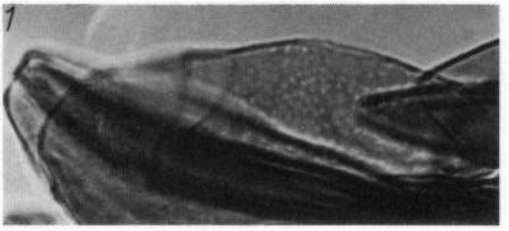


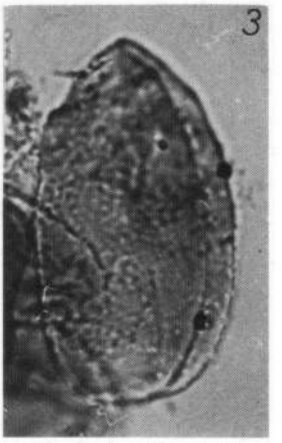


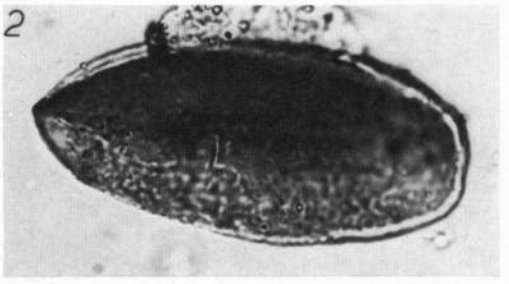


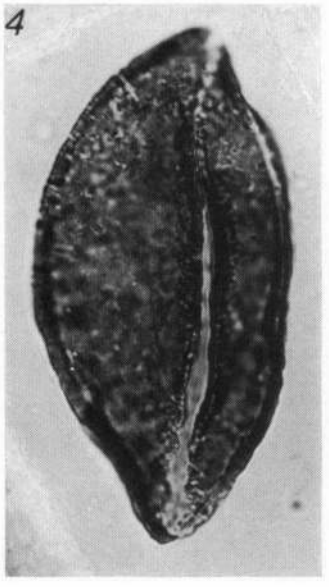


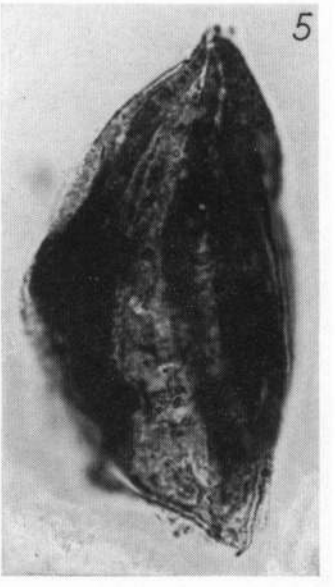
Pl. VII. Cycadales and Bennettitales



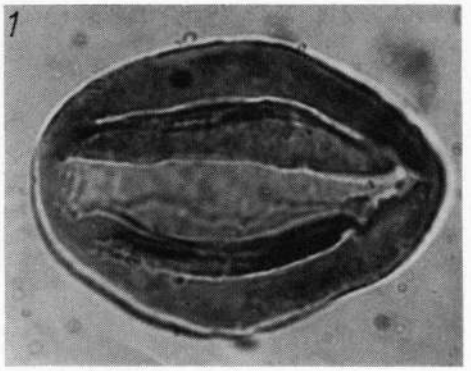




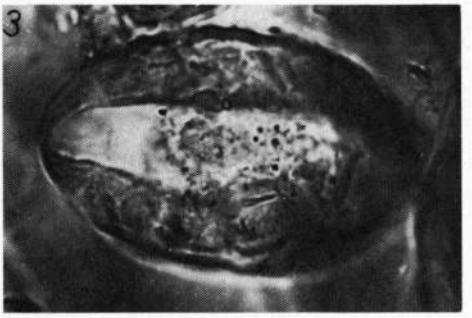




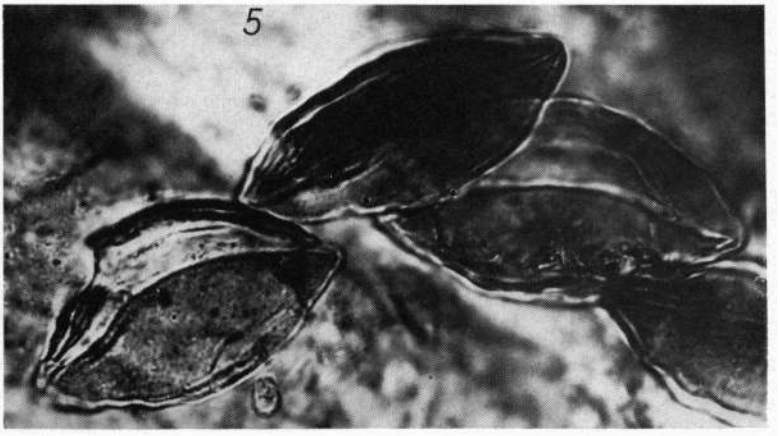
Pl. VIII. Bennettitales



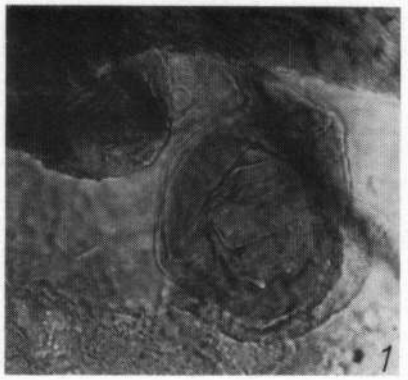




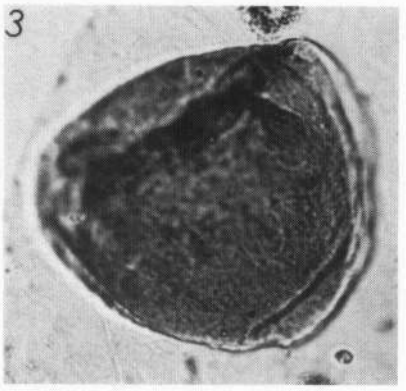


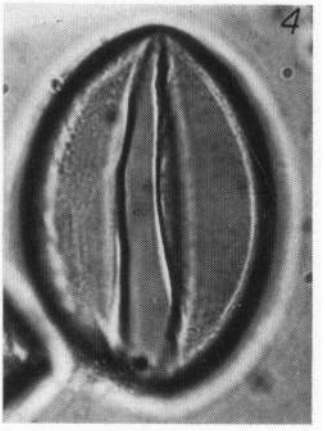


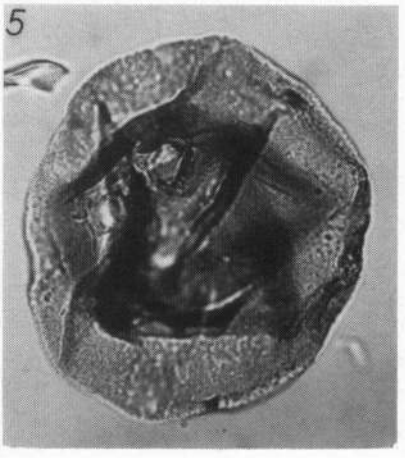
Pl. IX. Cycadales and Ginkgoales

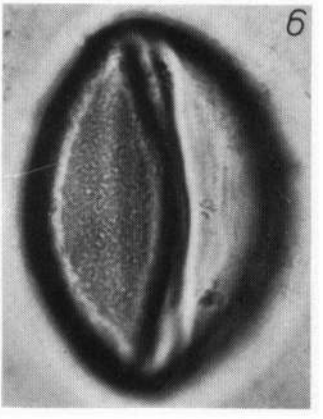




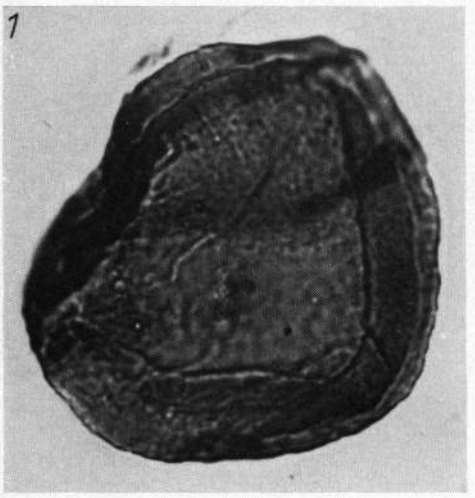


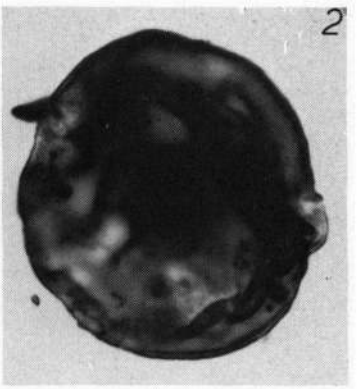


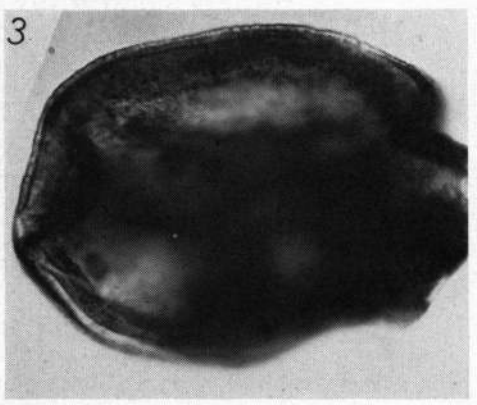


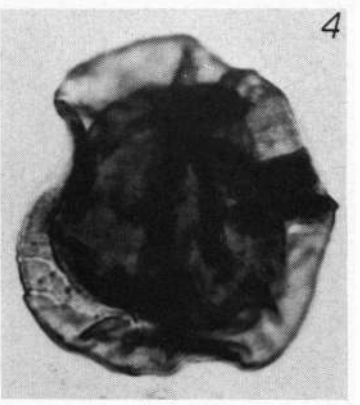


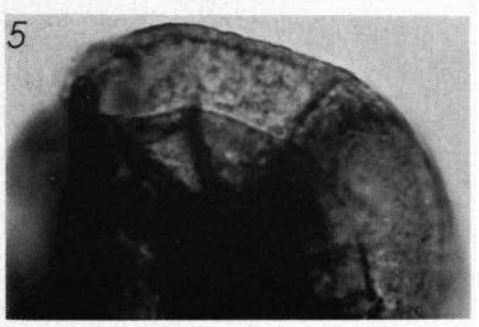
Pl. X. Ginkgoales

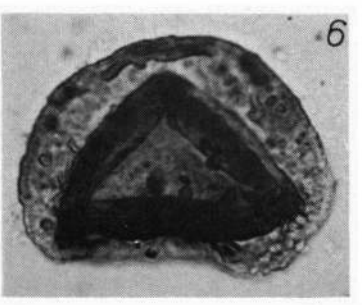




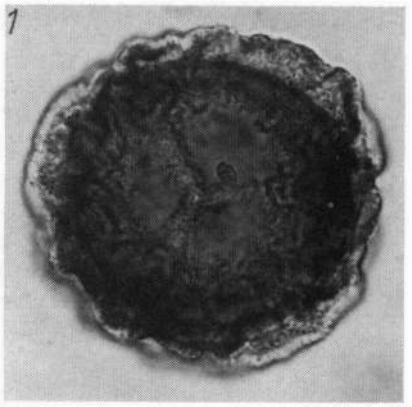


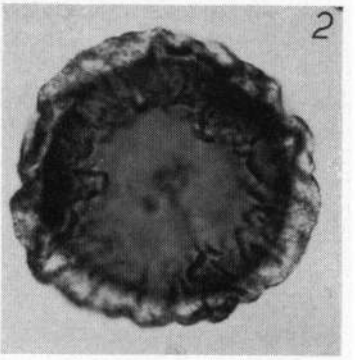


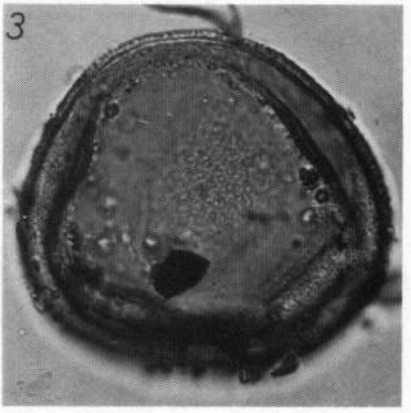


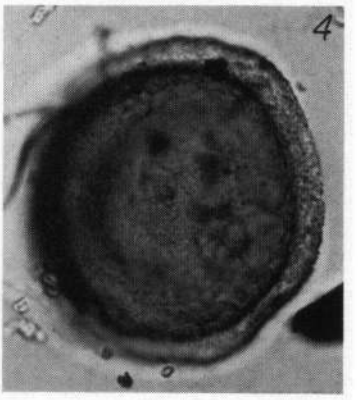


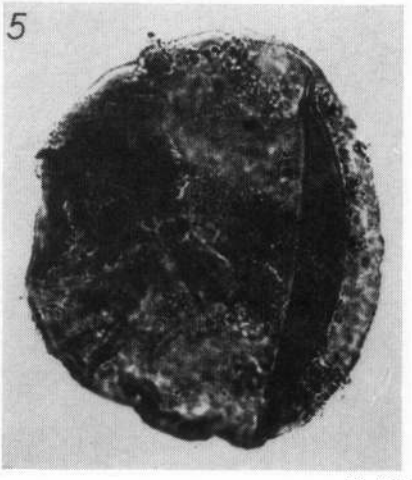
Pl. XI. Coniferales

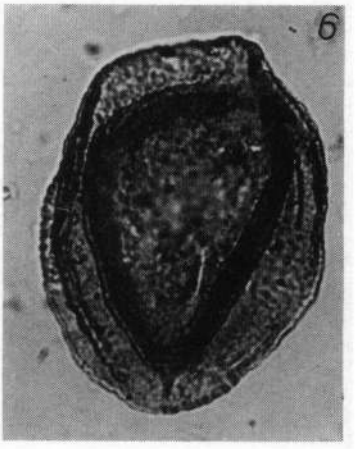




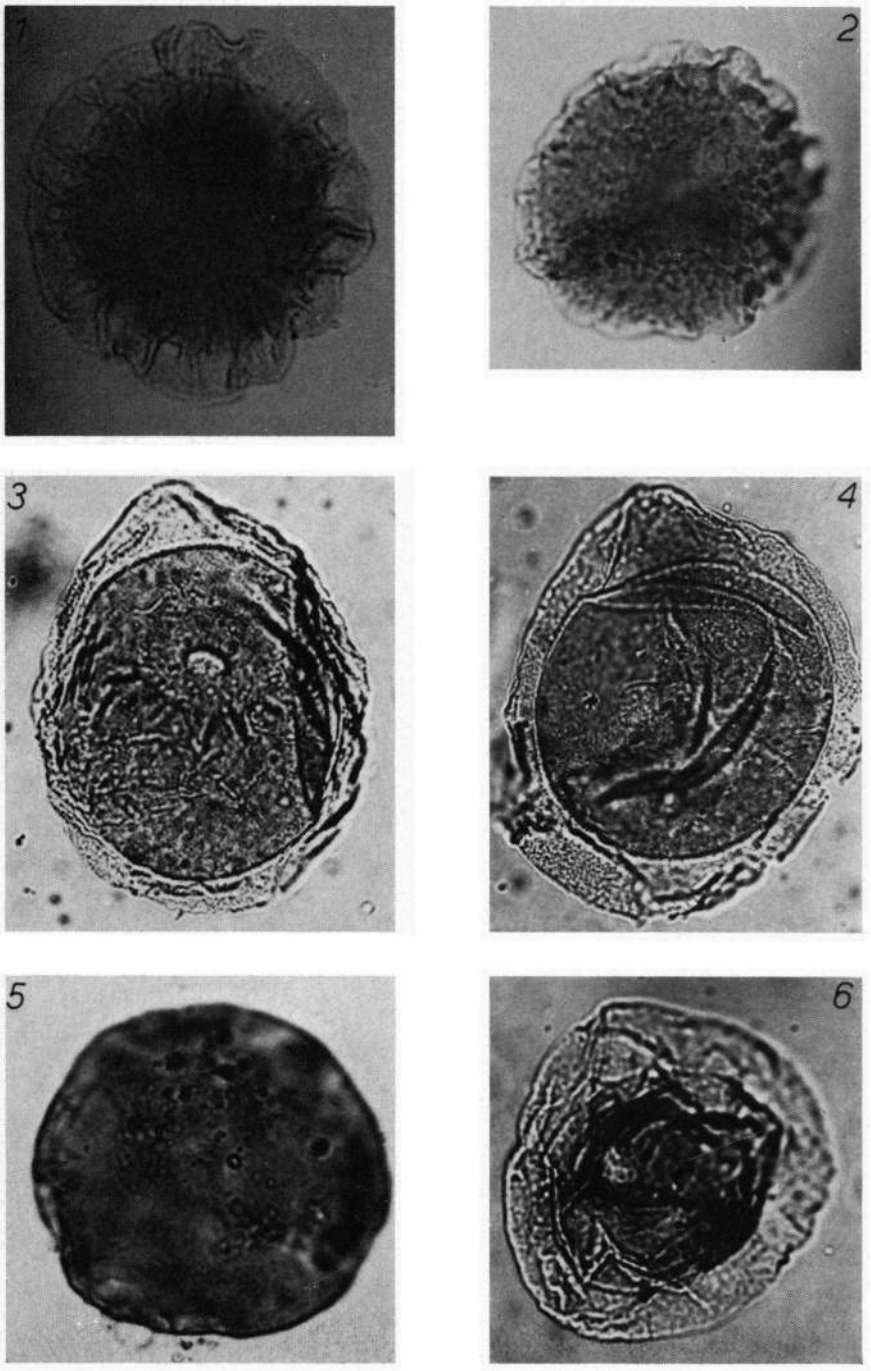




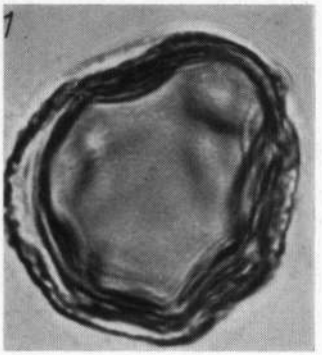




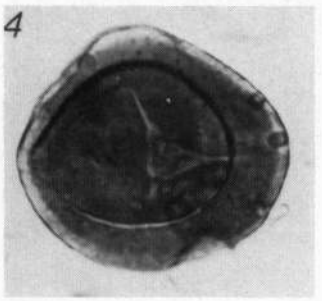
Pl. XII Coniferales

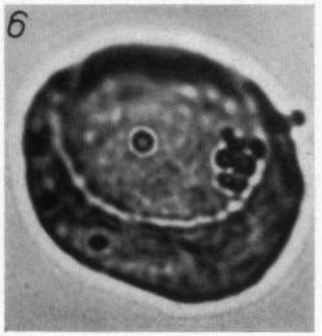


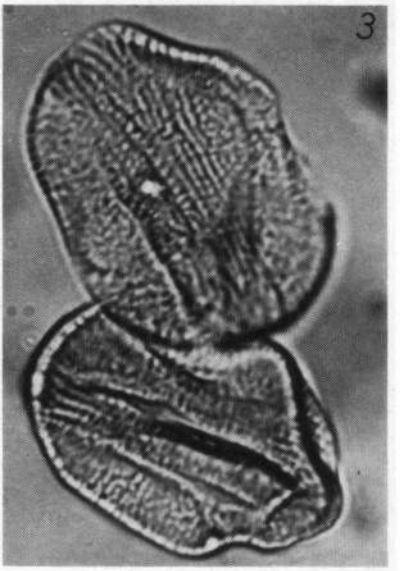
Pl. XIII. Coniferales

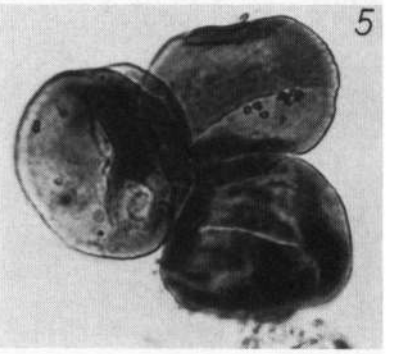


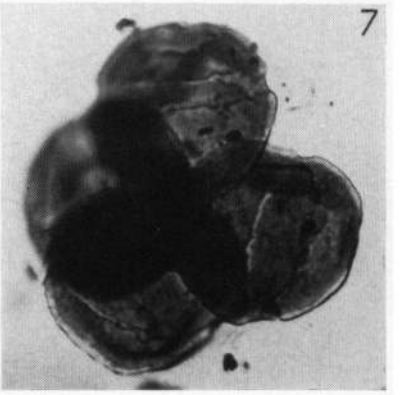




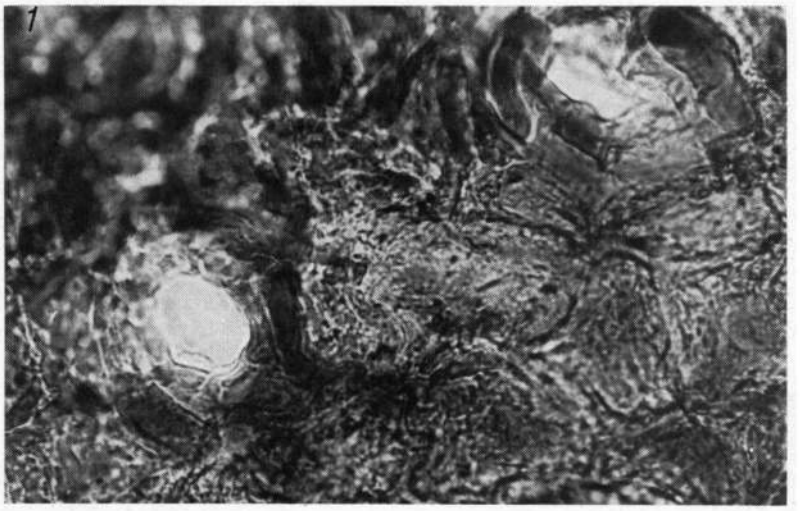


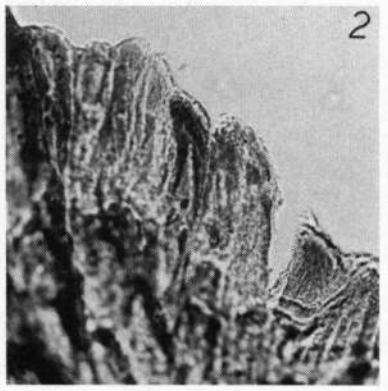


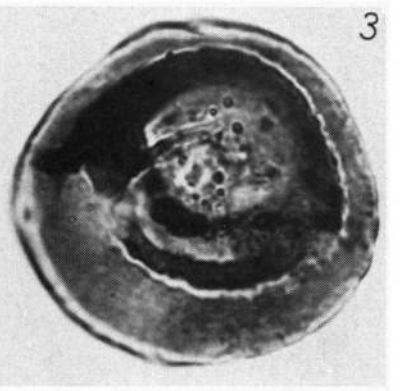


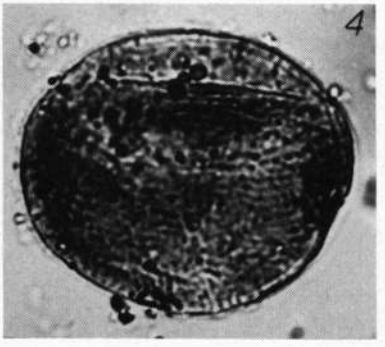


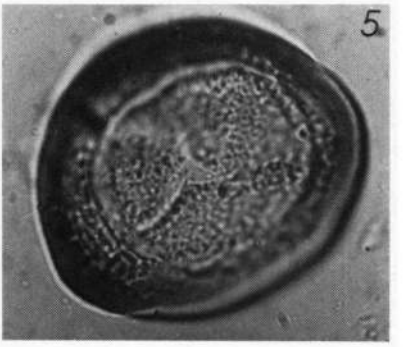
Pl. XIV. Coniferales



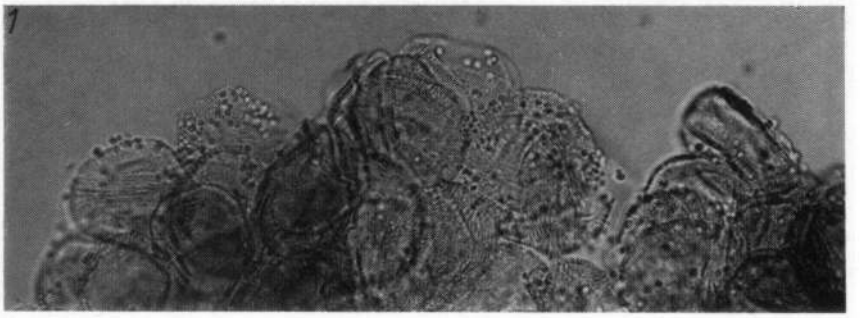




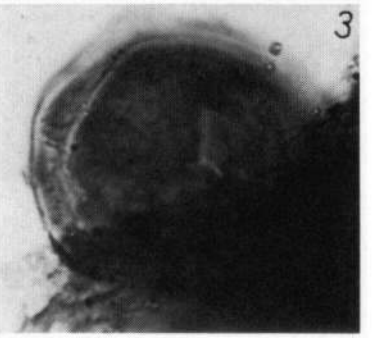


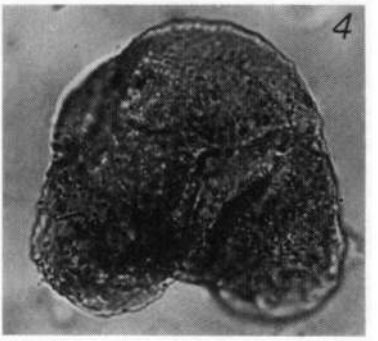


Pl. XV. Coniferales

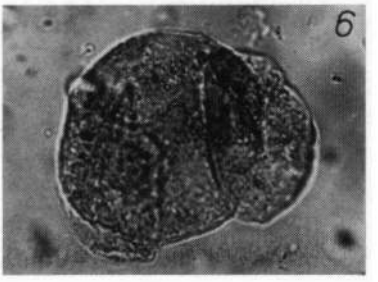












Pl. XVI. Coniferales