

UPPER PALAEOCENE SALVINIACEAE FROM THE WOOLWICH/READING BEDS NEAR COBHAM, KENT

by A. R. H. MARTIN

ABSTRACT. A sample from near the base of a section through organic lacustrine deposits exposed in a road cutting near Cobham, Kent, contained abundant megaspore and microspore massulae of *Azolla anglica* sp. nov. and *Salvinia cobhamii* sp. nov. The former is described as a new member of the subgenus *Florschuetzia* and is compared with several more or less contemporaneous species. The latter is described and compared with *S. boveyana* Chandler.

The environment in which the Salviniaceae existed at the site has been interpreted from a histogram of the section. It is suggested that the climate was warm temperate and that the lake was subsequently invaded by reeds and possibly tree growth, under which conditions the Salviniaceae locally died out.

POLLEN and spores were first recorded in Palaeocene-Eocene sediments of southern England by Ma Khin Sein (listed in Chandler 1964). More recently Gruas-Cavagnetto (1970) has recorded pollen and spores from the Woolwich and Reading Beds at Swanscombe, Kent.

Improvements to the A2 road close to its junction with the M2 motorway (grid ref. TQ/6730 6980) near Cobham, Kent, in 1964, made fresh exposures of the Upper Palaeocene deposits of the Woolwich and Reading Beds at Shorne Wood, some 10 km from the site described by Gruas-Cavagnetto. The stratigraphy at this site has been figured by Chandler (1923), and includes a prominent organic horizon, originally described as lignite, though it seems not to contain macroscopic wood and is better described as a lake mud. Four equally spaced samples, each representing 15 cm in vertical extent, from a 60 cm exposure of the seam were generously submitted to me for pollen study by Professor W. G. Chaloner.

Samples given to me by Professor Chaloner from an already-existing exposure of the organic band, contained a rather disappointing pollen flora. These samples were no doubt somewhat weathered. The new samples, besides a rich angiosperm flora, also contained megaspore remains of the two salvinaceous water ferns *Azolla* and *Salvinia*, as well as abundant microspore remains of the latter.

Subsequent cutting back of the exposure revealed 120 cm thickness of the lake deposit (Chaloner, pers. comm.) and samples of this were independently examined by Professor L. V. Hills, who reported (in correspondence, 1970) the occurrence of *Azolla*, *Salvinia*, and *Minerisporites*. *Minerisporites* appears to be absent from the material seen by the author (even after a careful re-examination) and none of these genera is recorded by Gruas-Cavagnetto. Nor, at the time of writing, have Salviniaceae been found in further sampling of the same site by Miss L. Allen (in correspondence, 1974). Such very local distribution of megaspores suggests the profitability of a more three-dimensional study of this site. Such is beyond the scope of the present communication which is of necessity confined to a study of those samples originally submitted. Within these bounds, it was thought useful to make a simple

pollen diagram to reveal as much as possible of the ecological conditions round the site at the time when Salviniaceae grew there. It is felt, too, that subsequent weathering or further destruction of the site may have made future comparisons difficult, without recording of these data. This analysis immediately follows the taxonomic part of the paper.

METHODS

Clean hand-picked pieces of the sediment were washed in distilled water, crushed to a coarse powder, and treated with 5% KOH for 24 hours. This was enough to disintegrate all samples. They were then diluted, washed several times with distilled water, and transferred to 50% glycerol. Thirty seconds treatment with a sonic probe at 15 000 cycles helped to disperse superficial dirt from the pollen. Only the basal sample, R1434, required HF treatment, which was given after KOH disintegration.

Massulae and megaspores of Salviniaceae were present only in R1434, from which they were quite easily isolated and concentrated by decanting the pollen suspension. Once observed, more were obtained by further macerations, specimens being collected by pasteur pipette under a low-power binocular microscope. A total of 40 megaspore and 400 microspore massulae of *Salvinia* were obtained from one sample of 5 gm. Eighteen megaspore massulae and a number of microspore massulae of *Azolla* were obtained in this way from the same sample, but the ratio of the two types could not be assessed as the microspore massulae tend to be attached to the megaspores, often in groups, while free ones remain suspended longer and are more easily lost in decanting. Some of these were recovered later on slides prepared for pollen counting, forming the bulk of the described material of the microspore massulae.

Material for sectioning was prepared according to the method described by Hughes *et al.* (1962), sections being cut at *circa* 0.5 μm . Despite difficulties, some short serial sequences were achieved.

Spores for scanning electron microscopy were stored in 98% ethanol and when required were pipetted on to a clean microscope slide and the ethanol allowed to evaporate. The specimens were oriented on the slide without picking them up. An SEM stub coated with double-sided adhesive tape was then lowered gently on to the spores and usually all of them adhered at once. By this method handling with forceps was avoided. Once attached, the spores cannot be handled but can be detached with xylol, washed carefully, and re-attached.

SYSTEMATIC DESCRIPTIONS

SALVINIACEAE Dumort
Genus AZOLLA Lamarck, 1783
Subgenus FLORSCHUETZIA Kempf, 1968

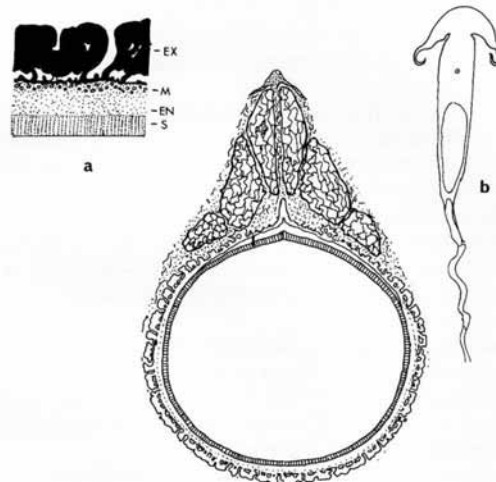
Type species. *A. teschiana* Florschütz, 1945.

Azolla anglica sp. nov.

Plate 27, figs. 1-3, 6; Plate 28, figs. 1, 2; text-fig. 1

Description. Megaspore massula with up to twenty-four floats in three tiers; diameter

of spore with perispore coat 324–413 μm (mean 355 μm , 10 specimens); polar length of spore 308–364 μm , total length with floats 446–599 μm (mean 531 μm , 10 specimens); upper third of spore covered by floats of lower tier; trilete mark not obvious, sporoderm 3–4 μm thick, usually firmly attached to perine at base and detached and often appearing collapsed apically but laesurae not easily separating; total thickness, including perine wall, *circa* 15–18 μm ; surface of perispore regularly foveolate, lumina of foveae *circa* 1.0–2.5 μm diameter, width of muri *circa* 3–5 μm , surface lacking excrescences but thinly hairy, diameter of hairs *circa* 1.0–1.5 μm ; column solid and narrow in section, *circa* 9 μm wide at the base and 30 μm in maximum length; maniculæ occurring on alveolate ridges *circa* 9 μm high, 16 μm wide, about 50 μm from column and between inner ends of lower two tiers of floats; maniculæ short, *circa* 2 μm long, spicate, rarely hooked; upper tier of floats somewhat longer than two lower ones, all externally densely hairy.



TEXT-FIG. 1. Scale reconstruction of sectional view of *Azolla anglica* ($\times 125$). a = interpretation of sporoderm-perispore stratification ($\times 1000$); b = glochidium; EX = exoperine; M = mesoperine; EN = endoperine; S = sporoderm (*Sens. str.*).

Microspore massulae more or less circular to elliptical in outline, 103 \times 103–137 \times 233 μm (mean 118 \times 153 μm , 10 specimens); number of microspores, 4, 8 or 12; diameter of microspores 20–29 μm (mean 24 μm , 20 measurements), laesurae 7–9 μm , wall thickness *circa* 0.7 μm ; glochidia 30–40 μm , of which upper 10–15 μm usually wide and solid, with a single small central bubble 0.5–2.0 μm diameter, attenuated and gyrose towards base, alveolate with at least one septum, maximum width at barbs 9–12 μm ; width 3.5–5.0 μm below barbs, 1–2 μm at base, barbs sometimes 3 in number.

Holotype. Slide V58333, Plate 27, fig. 1; repository: B.M. (N.H.).

Paratypes. Slide V58334, Plate 28, fig. 1; repository: B.M. (N.H.). Slide V58335, Plate 27, fig. 2; repository: B.M. (N.H.). SEM stub V58336, Plate 28, fig. 2; repository: B.M. (N.H.).

Locality. Shorne Wood, near Cobham, Kent: from drainage ditch connected with road widening. Ordnance Survey 1:50 000 2nd Series East London Sheet No. 177 (1-74); Nat. Grid. ref. TQ/6730 6980.

Horizon. Woolwich/Reading Beds, base of exposure of 60 cm of organic lacustrine sediment (nekron mud).

Sample. Chaloner palynological sample collection; sample No. R1434, Botany Department, Birkbeck College, London.

Remarks. *A. anglica* has a very thin apical region to the perispore, only *circa* 1.5 μm thick with a seemingly discontinuous exoperine resembling the layer of small globules below the tectum (Pl. 27, figs. 2, 3). This may explain why a large part of the population has lost the float apparatus and gapes open at the apex. The distinction between mesoperine and endoperine cannot be made out at the apex. Around the sides and base of the spore, on the other hand, the wall structure is well defined and reminiscent of some angiosperms in having a close semblance of a perforate tectum (Pl. 27, fig. 3). The sporoderm is rather thin.

A. anglica differs from *A. teschiana* Florschütz (Dijkstra 1961) in its regularly foveolate exoperine without excrescences (Pl. 28, figs. 1, 2). The outline of the whole structure with floats is more ovoid, with a lower length to breadth ratio, the floats being lower placed laterally, but they are less distinct individually, possibly because of a thicker coating of hairs (text-fig. 1). The maniculae are less well developed, though the column is almost identical (Pl. 27, fig. 2). The stratification of the perispore (Kempf 1969) is more regular in *A. anglica* with a uniform layer of small rods *circa* 1-2 μm in diameter and length, comparable to columellae (= bacula). *A. teschiana* has a thicker sporoderm (5-6 μm).

The differences between *A. anglica* and *A. schopfii* Dijkst. (1961) are more marked. The shape is not dissimilar and the column of *A. schopfii* is described as small, but the number of floats is described as only fifteen and the exoperine pattern as papillate. Sweet and Chandrasekharam (1973) consider *A. extincta* Jain to be conspecific with *A. schopfii*. If so, it was heterosporangiate as well.

A. velus (Dijkst.) Jain and Hall (1969) is distinguishable in section (Martin, in press)

EXPLANATION OF PLATE 27

Fig. 1. *Azolla anglica* sp. nov. Entire megaspore, in section ($\times 290$). Holotype, slide V58333. col = column; f = float; h = hair mass; ma = ridge with maniculae; p = perispore; s = sporoderm.

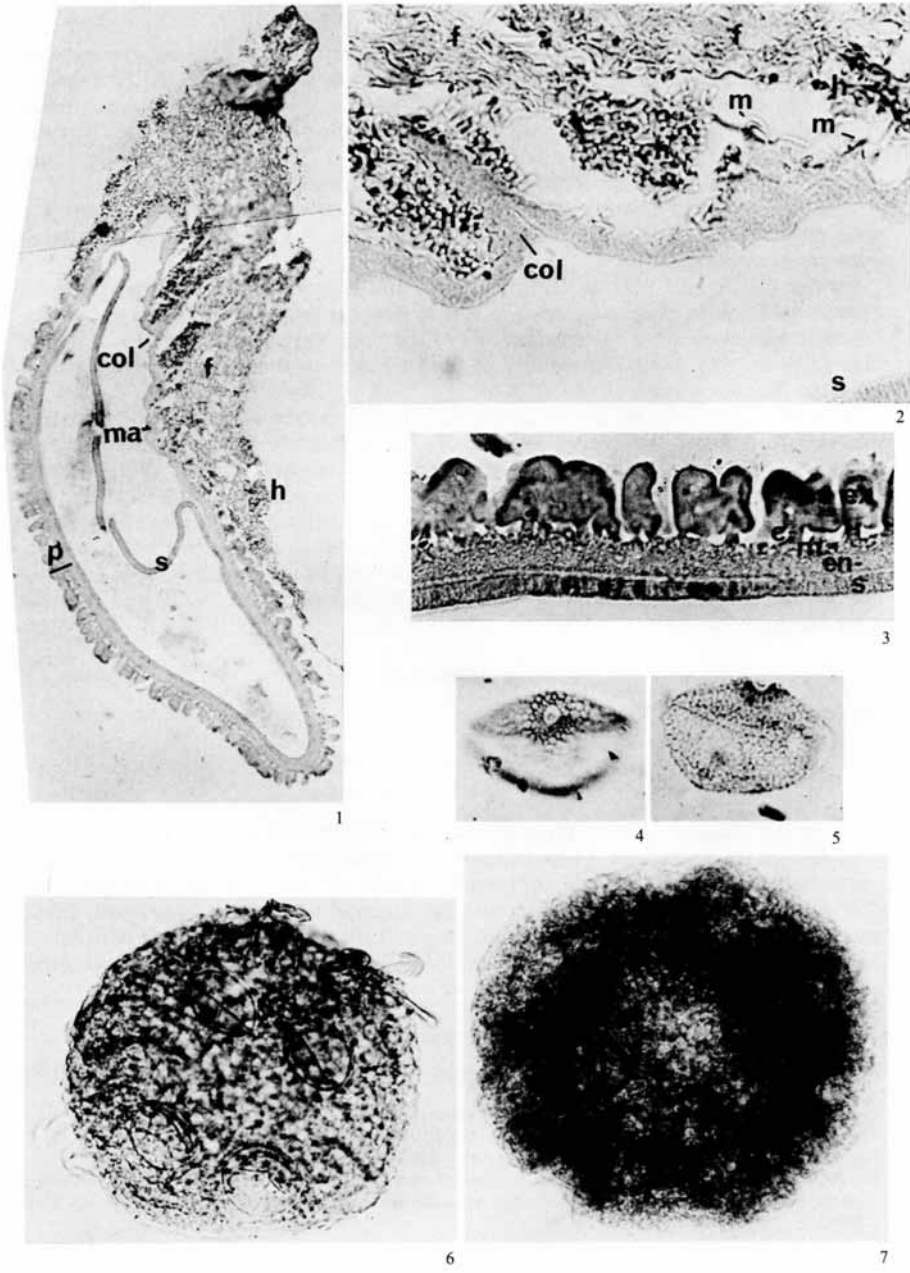
Fig. 2. *Azolla anglica*. Section through perispore apex ($\times 1150$). col = column; f = float; h = hair mass; m = manica; s = sporoderm. The very thin perispore wall should be compared with the appearance in fig. 3. Paratype, slide V58335.

Fig. 3. *Azolla anglica*. Microtome section of perispore and sporoderm. ex = exoperine; m = mesoperine; en = endoperine; s = sporoderm; c = columella ($\times 1250$).

Figs. 4-5. Undescribed monoporate pollen grain associated with Salviniaceae in sample R1434. It shows resemblance to *Aglaeoreidia* and to *Sparganiaceapollenites* but appears distinct from both ($\times 1000$).

Fig. 6. *Azolla anglica*. Small microspore massula showing four microspores and short glochidia ($\times 550$).

Fig. 7. *Salvinia cobhamii*. Microspore massula ($\times 290$). The light area in centre is typical of all the microspore massulae examined. Paratype, slide V58339.



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by its very different float apparatus in two tiers connected to the long column by well-developed manuculae. The exospore stratification is rather similar in the two species and the external pattern though reticulate rather than foveolate, could be confused. As the float apparatus of both species is likely to be obscured by hairs, there is a real possibility of confusion unless it is carefully examined. The size range overlaps considerably though *A. velus* is some 80 μm smaller in mean over-all length.

A. prisca Reid and Chandler (1926) is smaller than *A. anglica* in all dimensions and with only nine floats should be easily distinguishable. It is, in any case, very much younger in age (Oligocene).

Fowler (1975, and pers. comm.) proposes the separation of *A. prisca* from its present position in Sect. *Rhizosperma* into a new subgeneric Section of the genus, based in the main on a re-examination of the float apparatus. Such a systematic change in no way alters the validity of float number as a distinguishing character between the two species.

It is probably futile to try to distinguish *Azolla* species on microspore massula characters. Among the earlier species of *Azolla*, septate glochidia are perhaps uncommon (they are only recorded in *A. indica* Trivedi and Verma, 1971), though small alveoli often appear in the shafts which may simulate a septum (text-fig. 1c). Occasional three-barbed glochidia are not unusual among these species. Possibly some reliance can be put on glochidial length. Those of *A. prisca* are 45–52 μm long, *A. teschiana* 25–55 μm long (measured from photograph), *A. anglica* 30–44 μm long (Pl. 27, fig. 6), *A. schopfi* 30 μm (Sweet and Chandrasekharam 1973), and *A. velus* only 18 μm .

Genus SALVINIA Seguiet

Type species. *S. natans* (L.) All., 1785.

Salvinia cobhamii sp. nov.

Plate 27, fig. 7; Plate 28, figs. 3–5

Description. Megaspores with three-lipped convoluted perispore, equatorial diameter 292–405 μm (mean 345 μm , 13 measurements); axial length 340–380 μm ; diameter of contained megaspore 220–267 μm (mean 238 μm , 13 measurements), length 210–250 μm (mean 233 μm , 4 measurements), thickness of sporoderm *circa* 6 μm , trilete mark inconspicuous, laesurae 15–20 μm long and *circa* 6 μm wide at base with raised tapering lips; thickness of perispore *circa* 60 μm , surface elaborately convoluted,

EXPLANATION OF PLATE 28

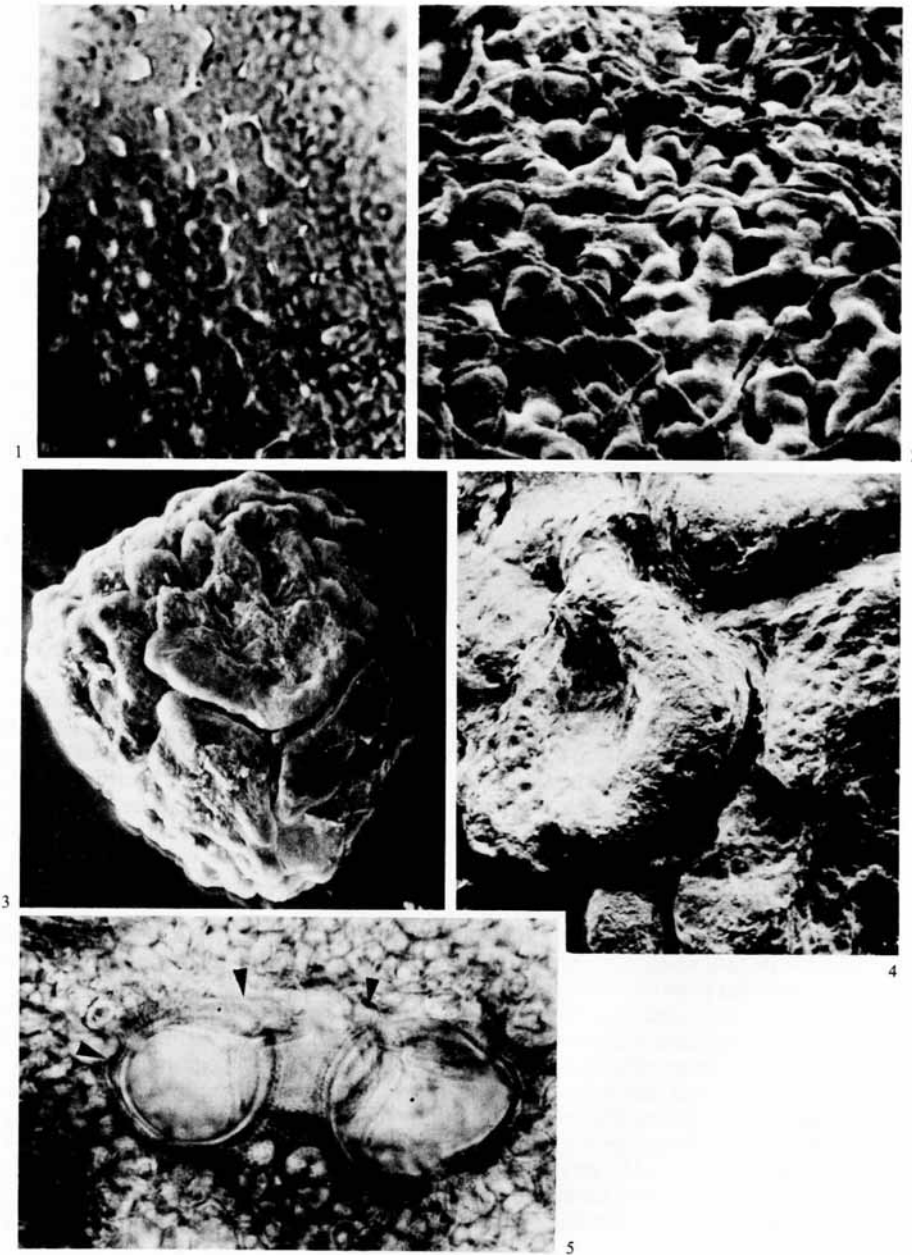
Fig. 1. *Azolla anglica*. Tangential section of perispore showing lumina, muri, and columellae ($\times 1150$). Paratype, slide V58334.

Fig. 2. *Azolla anglica*. Perispore surface ($\times 1625$). Paratype, SEM stub V58336.

Fig. 3. *Salvinia cobhamii* sp. nov. Entire megaspore ($\times 230$). Holotype, slide V58337.

Fig. 4. *Salvinia cobhamii*. Part of apex of perispore ($\times 550$). Paratype, SEM stub V58338.

Fig. 5. *Salvinia cobhamii*. Two microspores in alveolar mass. The left-hand arrow indicates the individual perine coat of one spore; the centre and right-hand arrows indicate the perispore apices ($\times 1150$). Slide V58339.



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forming obtusely angled and rounded cushion-like masses up to 100 μm in diameter, often with depressed centres, irregularly foveolate with foveae *circa* 1 μm in diameter; lips of perispore bluntly triangularly lobed in outline, extending about half the width of the entire spore, separated by a trifurcate cleft *circa* 6–10 μm wide, each arm *circa* 100 μm long and bifurcated at the distal end into recurved arms about 50 μm long. Massulae of microspores more or less circular-elliptical 227–306 \times 215–292 μm (mean 271 \times 253 μm , 6 measurements), with dark margin and pale centre, microspores peripheral, in 6–8 clusters (minimum number of spores seen 24, maximum 42), diameter of spores 22–31 μm (mean 27 μm , 32 measurements from 3 massulae), thickness of sporoderm *circa* 1.0–1.5 μm , length of trilete mark 18 μm across, each laesura *circa* 13 μm , each spore enclosed in individual perine coat within the massula.

Holotype. Slide V58337, Plate 28, fig. 3; repository: B.M. (N.H.).

Paratypes. SEM stub V58338, Plate 28, fig. 4; repository: B.M. (N.H.). Slide V58339, Plate 27, fig. 7; Plate 28, fig. 5; repository: B.M. (N.H.).

Locality. Shorne Wood, near Cobham, Kent: from drainage ditch connected with road widening. Ordnance Survey 1:50 000 2nd Series East London Sheet No. 177 (1–74); Nat. Grid. ref. TQ/6730 6980.

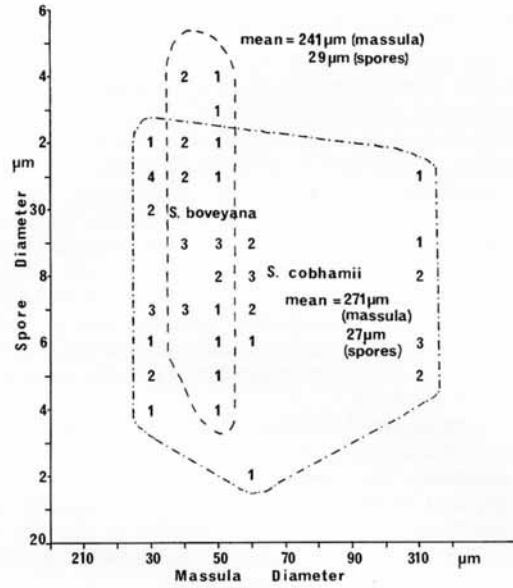
Horizon. Woolwich/Reading Beds, base of exposure of 60 cm of organic lacustrine sediment (nekron mud).

Sample. Chaloner palynological sample collection; sample No. R1434, Botany Department, Birkbeck College, London.

Remarks. *S. cobhamii* appears to be the oldest known species from the British Isles, possibly the oldest from western Europe, though the genus is now known from the Upper Cretaceous of Canada. The classification of fossil *Salvinia* species depends both on the leaves and on the spore bodies. As these are not often found together, the number of species described might exceed the true number. However, the number of early Tertiary species is small. As far as possible this form has been compared with *S. boveyana* Chandler (1957) of the Oligocene. The holotype of *S. boveyana* is a microsporocarp with its contained massulae, and megaspores have not been described. Text-fig. 2 shows that there is no fundamental difference in size between the microspores and massulae of the two species. The slightly more restricted size range of *S. boveyana* may be simply due to both the massulae being from a single sporocarp.

The main objections regarding the new form being *S. boveyana* are that it is much older and there is little evidence that microspore massulae are at all species-diagnostic. Where megaspores are available it seems better to base the species diagnoses on them and not to overweight the similarity of the microspore massulae, though one should keep open the possibility that they may prove to be conspecific.

The only other species of comparable age and sufficiently well described to compare with *S. cobhamii*, are *S. aureovallis* Jain and Hall (1969), and *S. intertrappea* Mahabale (1950). The former, of the United States Eocene, has smaller megaspores, *circa* 240–320 μm in diameter, but large microspore massulae which are described as of the same size as the megaspores. The microspores are small, 20–26 μm with laesurae measuring up to 9 μm . *A. intertrappea*, also of the Eocene, is a silicified fossil and therefore not easy to compare directly; its microspore massulae (originally described as *Massulites coelatus* Sahni and Rao) are hollow, as in modern *S. auriculata*. Those of *S. cobhamii* may have been hollow, but the microspores of all species are probably peripheral and



TEXT-FIG. 2. Scatter diagram for microspores and massulae of *Salvinia cobhamii* and *S. boveyana*. The vertical columns of numbers on the graph refer to the numbers of microspores of each diameter (as measured along the greatest axis) in each massula.

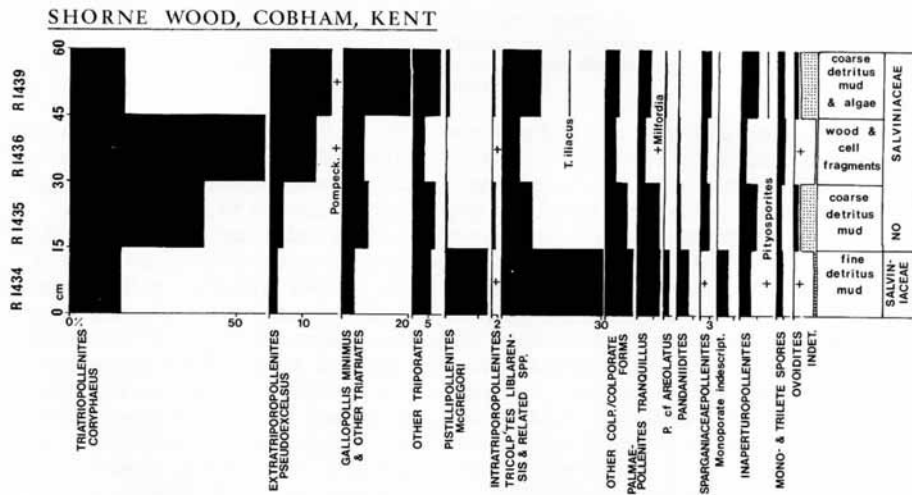
the appearance of a dark ring and pale centre (Pl. 27, fig. 7) would result equally if the centre consisted of large and the surface of small alveoli. The even older *S. stewartii* Jain (1971) of the North American Upper Cretaceous, was a species with very large megaspores up to 950 µm in length and large microspores over 50 µm in diameter.

It is of interest that *S. cobhamii* microspores have individually distinguishable perines. Kempf (1971) has shown from ultra-thin sections that while microspores in a massula always have a triradiate opening to the exterior preformed in the perine of the massula, the perine of some species is also differentiated into a trizonate layer round each microspore, e.g. *S. cerebrata*. Other species have only slight differentiation of the perine, e.g. *S. rhenana* and the modern species *S. natans*. While direct comparison with the EM-sectioned material is not possible, examination of entire massulae of *S. cobhamii* shows that the microspores have a separate distinguishable perine coat which is patterned inside the massula. The apex of each separate perine has a triradiate opening to the exterior (Pl. 28, fig. 5). It seems that *S. cobhamii* was more like the Lower Miocene species *S. cerebrata* than the Plio-Pleistocene species *S. rhenana* or modern *S. natans*, in this respect.

THE ASSOCIATED POLLEN AND SPORE FLORA

The samples obtained were equally spaced and represent the entire vertical extent of the exposure (60 cm). A simple pollen diagram showing the quantitative variation of the commoner pollen and spore types through this short profile is given in text-fig. 3. The flora contains about forty species, most of which are similar to or identical with forms from the European lower Tertiary or the North American (Wilcox) Palaeocene-Eocene (Fairchild and Elsik 1969). The sample in which *Salviniaceae* occur is distinguished by an abundance of *Pistillipollenites mcgregori*, tricolpate pollen of the *Tricolpopollenites liblarensis*-*T. microhenrici* group, and a small undescribed monoporate grain (Pl. 27, figs. 4, 5) which resembles *Aglaeoreidia* in being elliptical but differs from both described species of *Aglaeoreidia* in being more uniformly reticulate. (I am indebted to Mr. K. Fowler for pointing this distinguishing character out to me.) This species appears unique among monoporate grains of this general description in being operculate. There are also more of the two forms *Palmaepollenites tranquillus* and *Pandaniidites* sp. in this level.

The upper three samples are dominated by *Triatriopollenites coryphaeus*, *Gallopollis*, and species of *Extratropopollenites*. Especially in R1436 and R1439 these forms tend to be corroded. The comparative rarity of Gymnosperms, particularly the bisaccate groups, and of fern spores is interesting. Fairchild and Elsik (1969) comment on the greater abundance of Normapollens in the Wilcox as compared with younger strata. The relative abundance of Normapollens (*Extratropopollenites*



TEXT-FIG. 3. Pollen diagram of Shorne Wood, near Cobham, Kent; profile from which *Azolla anglica* and *Salvinia cobhamii* were isolated. The pollen percentages are based on counts of at least 300 pollen grains in each sample. Pompeck = *Pompeckjoideapollenites* sp. Tricolp'tes = *Tricolpopollenites*.

spp. (up to 18%), and *Pompeckjoideapollenites*), at the Cobham site perhaps helps to confirm the Late Palaeocene–earliest Eocene age of the Woolwich/Reading Beds.

The section seems to record the shallowing of a lake with encroachment of reeds (*Sparganiaceapollenites*) upon a more open phase with floating Salviniaceae, then a possible reflooding. *P. tranquilus* and *P. areolatus* have been equated with *Palmae*, the *Tricolpopollenites liblarensis* group with *Cupuliferae* and *Triatriopollenites coryphaeus* with *Juglandaceae*, while the *Normapolles* and *Pistillipollenites* are of unknown source. The total flora suggests warm temperate, rather than subtropical conditions. The simplest explanation of the diagram might be that *Juglandaceae* and perhaps the *Normapolles* sources formed riparian forest which advanced and was consequently strongly over-represented during the drying phase, while the *Cupuliferae* represent a more long-distance component. The *T. coryphaeus* pollen in R1436 is often clumped as if anthers were falling directly into the supposed reed swamp. *Pistillipollenites*, judging by its striking association with the lake phase, may have been a waterside or even an aquatic plant. Thus the Salviniaceae at this site seem to have died out through a plant succession, or 'verlandung', though in the absence of macroscopic wood remains it would be unwarranted to infer that some kind of swamp forest was the highest stage reached.

Acknowledgements. I wish to thank Professor W. G. Chaloner for offering me this problem to study. Professor Chaloner and Dr. M. Muir are also thanked for their kindness in offering the facilities of their respective departments during periods of leave. The nomenclature of text-fig. 3 has been adopted after discussion with Miss Lynn Allen and Mr. K. Fowler, for which I am very grateful. Mrs. P. Thiem and Mrs. S. Kilkeary are thanked for their technical assistance.

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A. R. H. MARTIN
School of Biological Sciences
University of Sydney
Australia