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CHALLENGES IN RECONSTRUCTING THE VEGETATION ASSOCIATED WITH A LATE EOCENE MAMMAL FAUNA FROM WESTERN EUROPE

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Abstract: Bed TB33, a lacustrine unit within the late Eocene (early Priabonian) How Ledge Limestone, Headon Hill, Isle of Wight, UK, contains a rich mammalian fauna. The previously reconstructed food web included mammalian predators and prey (ground dwelling, scansorial and arboreal; insectivores, frugivores, herbivores and carnivores) and two inferred owls. Unfortunately, the extensive bulk sediment sampling and sieving used to obtain the vertebrate fauna had not yielded any plant fossils other than charophyte gyrogonites. This new work has focused on plant mesofossils and palynofacies in the uppermost horizons of the vertebrate-rich bed aiming to reconstruct the vegetation that hosted the mammals. Other than cysts of Zygnemataceae, phytoplankton are absent. The presence of the aquatic plants *Azolla* and *Salvinia* on the lake is documented by megaspores and microspore massulae. The palynomorphs are dominated by algal cysts, *Azolla* microspore massulae fragments and two morphologies of trilete fern spores. These data document a depositional setting in a lake with abundant free-floating *Azolla* or *Salvinia* and with a margin vegetation dominated by ferns. The data support one of our previous inferences that the arboreal mammals were brought to the site from some distance away by predators. However, the challenge to fully reconstruct the mammalian habitats remains.

Key words: Eocene, mammal, primate, plant mesofossils, resin, algal cyst, pollen, spore, seed, megaspore, microspore massulae, *Azolla*, *Salvinia*

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Introduction, geological context and mammalian fauna

The mammalian fauna, whose ancient environment is investigated here, occurs in the silty clay sediments of bed TB33 within the How Ledge Limestone of SW Headon Hill, UK. The How Ledge Limestone is an unranked lithostratigraphic unit at the top of the Totland Bay Member of the Headon Hill Formation (Late Eocene) of Hampshire and western Isle of Wight. At SW Headon Hill, Isle of Wight, it consists of two limestone units (beds TB31 and TB34) separated by a silty clay (bed TB33), which transitions upwards from a very shelly, partially indurated silty clay (bed TB32). Bed TB34 is capped by a grey marl. Bed TB33 is green in its lower part and becomes darker upwards, terminating in a very thin lignite (Text-fig. 1; Hooker 2021, Vasileiadou et al. 2022). Freshwater gastropods, bones and teeth of fish, ostracods and charophytes (Bristow et al. 1889, Keen 1977, Riveline 1984, pers. obs.) co-occur throughout with terrestrial tetrapods (Rage and Ford 1980, Klembara and Green 2010, Hooker 2021). Using this evidence, the depositional environment has been inferred to have been a lake margin, which, during deposition of bed TB33, dried out seasonally (Vasileiadou et al. 2022).

At SW Headon Hill, collecting by means of screen-washing of bulk sediment samples (Bosma 1974, Hooker 2021) over several decades has yielded a rich mammalian fauna. This collecting has focused mainly on bed TB33, the fauna totalling 41 species (Vasileiadou et al. 2022, Hooker 2024). Small mammals (marsupials, nyctitheres, primates and rodents) predominate and are represented by isolated teeth, jaws and postcranial bones, which inform about their dietary and locomotor adaptations. Most range from semiterrestrial to scansorial, with a few terrestrial, but eight are fully arboreal in their foraging habits. The latter include primates and apatemyids. There are five species of primates: the adapids *Magnadapis* sp. and *Adapis stintoni* Gingerich, 1977 (leaf eaters) and the omomyids *Pseudoloris parvulus* (Filhol, 1890) (insect eater), *Vectipithex smithorum* Hooker et Harrison, 2008 and *Microchoerus erinaceus* Wood, 1844

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(fruit eaters) (Ramdarshan et al. 2011). They demonstrate their arboreality by the ability to grasp branches with curved finger and toe bones and a prehensile hallux (big toe) (Godinot 1991, Hooker 2024). *Microchoerus* Wood, 1844 was also nocturnal (Ramdarshan and Orliac 2015).

Arboreal mammals are highly adapted to life in the trees and most are reticent about descending to the ground, except in dire circumstances, such as needing to drink during a drought (Harrison 1962, Andrews et al. 1979, Eisenberg 1981). Their presence in bed TB33 therefore implies the existence of their forested habitat nearby, unless they have been transported post-mortem to the site of deposition. Bed TB33 is fine-grained and indicates a low energy depositional environment. The close association of disarticulated bones and teeth of single individuals (notably a primate leg, a partial skeleton of a small carnivoran and several cases of upper and lower or left and right apatemyid and rodent tooth rows – Vasileiadou et al. 2022, Hooker 2024) argues strongly against hydraulic transport to the site of deposition; there is also little evidence of weathering of the bones, indicating rapid burial (Vasileiadou et al. 2022). Evidence for predation by mammalian (*Paramiacis* Mathis, 1987 and *Amphiperatherium* Filhol, 1879) and avian predators, however, is widespread, as interpreted from tooth etching by digestive juices and bite marks on bones together with characteristic breakage patterns, and was inferred to be a source of potential transport to the site of deposition (Vasileiadou et al. 2022).

The aim of this paper is to evaluate the likelihood that the arboreal mammals were living either close to or distant from the lake. In the absence of plant macrofossils, we use palynofacies and plant mesofossil analysis of samples from bed TB33 for this study. These data will also be used to provide new information about the lake itself and the local vegetation.

Materials and methods

Samples

The upper part of Bed TB33 was subdivided into three units based on a combination of colour and lithology. All three units have a very fine-grained matrix. The uppermost unit 3 (Text-fig. 1) is a dark brown to black lignitic lithology up to 5 mm in thickness which easily detaches from the underlying bed TB33 unit 2 (Text-fig. 1) but does not easily separate from the overlying Bed TB34. Unit 3 is rich in fragments of freshwater shells as well as containing some complete small shells of freshwater gastropods. At field scale, the junction between bed TB33 and the overlying TB34 appears sharp but in thin section it is undulating and gradational across 1 to 2 mm of thickness (Text-fig. 1).

Laboratory subsampling of sediment from field collections carefully avoided any areas with evidence of modern weathering, oxidation, cracking, rootlet penetration and also contamination from adjacent units where boundaries are gradational. Hence the small sample weights used which are stated below.

Only the middle 2–3 mm of thickness of unit 3 was sampled with a dry weight of 2 grams. The underlying silty clay lithology (Text-fig. 1) was separated into a darker upper unit 2 ca. 20 mm in thickness and a paler lower unit 1 ca. 25 mm in thickness. Both these units contain fragments of freshwater shells but in far less abundance than in unit 3 (e.g., no shells are visible in the thin section; Text-fig. 1). There is a gradational junction between units 2 and 1 and the subdivision for sampling was based on a personal judgement of colour tone. Four random samples were studied from each of unit 2 and unit 1. Individual sample dry weights ranged from 0.7 to 2 grams.

Samples of five grams dry weight were processed for the lower part of bed TB33 and the underlying beds TB32, TB31 (three samples), and TB30 of Hooker (Hooker 2021). These yielded no useful material and are not considered further in this paper.

Figured specimens

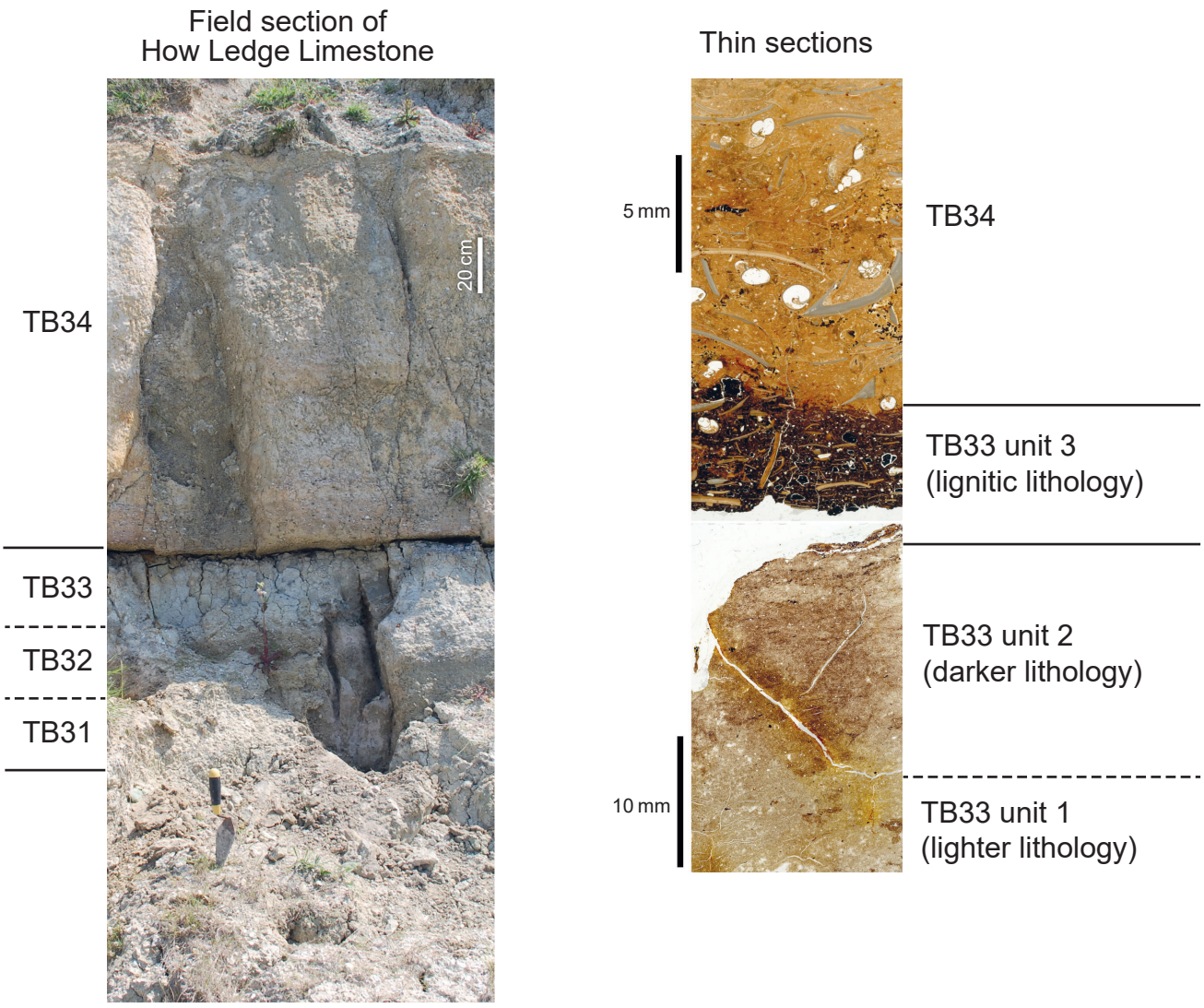
Figured specimens are housed at NHMUK (Natural History Museum United Kingdom) in London, UK. Specimens on three light microscope slides have numbers in this format NHMUK PM FM (where PM = Micropalaeontology and FM = Fossil Miospores) see Tab. A1. All other specimens on slides and plant mesofossils mounted on SEM stubs have numbers in this format NHMUK V XXXXX(X) where V stands for Vegetabilis. These numbers are listed in Tabs A1 and A2 and are stated in the Text-figure captions.

Sediment processing

Sediment samples were broken into small pieces a few mm in size. These were placed in polypropylene containers and treated at room temperature in a fume cupboard with 10% HCl followed by 37% HCl then 40% HF. Gentle stirring using a plastic rod was used to mix the sample during treatment. When HF reaction was judged to be complete the HF was replaced with 37% HCl for 24 hours (to bring any calcium fluoride into solution). During processing, acids were decanted after settling and repeated treatments with each acid were used until no reaction occurred. Final acid treatment was followed by multiple (usually 5 or 6) changes of distilled water until the fluid was neutral. When neutral, samples were sieved first through 125 micron mesh and then 15 micron mesh.

The size fraction >125 microns for each sample was stored in distilled water in a refrigerator in a large sterilin plastic tube and was used for the mesofossil study. All of the residue from each sample was studied.

After initial observations were made two samples of the size fraction >125 microns received further treatments. The sample from unit 3 was treated for 1 minute with HNO_3 with the aim (successful) to remove tiny lignite particles from surfaces and make it easier to recognise mesofossils. One of the most abundant residues from unit 2 was re-sieved through 125 microns and the material passing through that sieve was sieved again through 15 microns and the residue held on the 15 microns sieve was examined. This was to determine if very small mesofossils were present amongst the >125 micron residue but were being missed during sample study. The only mesofossils in the resieved 15–125 microns size fraction were *Azolla* Lam. (see below)



Text fig. 1. Field section at left showing bed TB33 in context of other beds with thin sections at right showing details of TB 33 units 1 to 3 lithologies. A very thin portion of unit 3 partially attached to unit 2 at the right side shows continuity of the units.

which had already been recognised from many specimens after the first sieving.

For all samples the size fraction (residue) between 125 microns and 15 microns was stored in distilled water in a refrigerator in sterilin plastic tubes and used to prepare dilutions to make palynofacies slides. Different dilutions were used with the aim to produce an approximately comparable amount of organic particles on all slides. For some samples from Unit 1, that weighed 2 grams or less, the residue was stored in 5ml of water and 100 µl of that residue was used to prepare the palynofacies slides. For other samples the residues were stored in 10 ml of water and a known volume (either 200 µl or 100 µl) of that was dispersed in 200 µl to 900 µl of water and used to prepare the palynofacies slides.

An Eppendorf pipette was used to transfer 100 µl of the final residues onto a coverslip resting on a warm plate at 25 °C. Approximately 2 drops of PVA emulsion were then mixed with the residue using a dissecting needle and the mixture was dispersed across the coverslip. The coverslip was then left for 30 minutes to dry. Coverslips were then mounted onto glass slides using Petropoxy 154 resin (available from Burnham Petrographics, USA). Laboratory record slide names and slide numbers were etched onto the slides using a diamond pen and are related to the units (1, 2 or 3) of Bed TB33 for each figured specimen in the Appendix (Tab. A1).

Mesofossil analysis

The residues were studied using a Schott KL 1500 fibre optic light under a Zeiss Stemi SV8 binocular microscope with a Plan Apo WD70 X1 objective and zoom magnification range. Specimens of interest were picked using a fine (00000 or 0000) paint brush, allowed to dry naturally in air and mounted on stubs for SEM study. In some cases specimens were mounted onto stubs using a Leit adhesive carbon tab 12 mm diameter (available from Agar Scientific, Stanstead, UK). Other stubs were prepared by attaching a 13 mm diameter coverglass to the stub using Bostik (Bostik Ltd, Leicester, UK) adhesive and then mounting each specimen onto the coverslip with a very small droplet of Bostik diluted in acetone. This latter method is preferred because it will allow easy later removal of a specimen by dissolving the glue in acetone if necessary. However, it is also more time consuming and requires controlled handling and dexterity to

avoid specimens becoming partly covered in glue. Mounting used for each stub is stated in the Supplementary material of SEM stub layouts. Stubs were studied uncoated and specimens photographed under a Hitachi SU3900SEM using the back scatter detector, 15 Kv, low vacuum of 30 pa and 6 mm working distance. Figured specimens are indicated and their positions labelled on each of the eight stubs using LM photographs of the stubs provided in the Supplementary material of SEM stub layouts. Those photographs also indicate unfigured specimens of the figured taxa. A table listing all specimens figured by SEM and their stub and specimen numbers is provided in Appendix (Tab. A2).

Palynofacies analysis

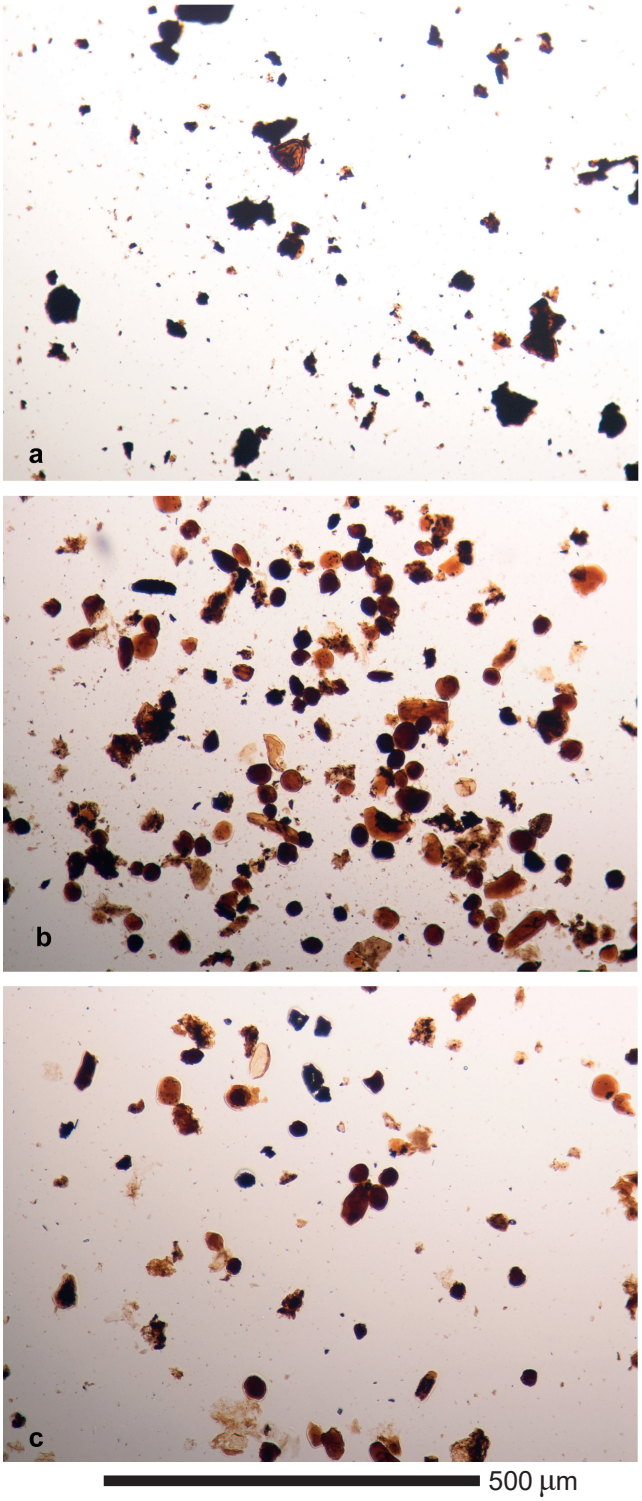
Two slides were studied for each sample. Any relative abundance quoted uses a simple ACFOR (abundant, common, frequent, occasional, rare) domin scale and relates to how frequently specimens were encountered on the slides. Slides were studied and specimens were photographed under a Nikon Microphot-FX microscope with a Nikon FX35A DATA camera linked to image capture software system and using the X10 and X40 objectives. A Nikon stage adaptor added to the standard rotating stage allowed the slides to be mounted to enable use of an England Finder. With this arrangement the arrows on the England Finder faced towards the user and the diamond etched laboratory slide label was on the right of the user. Slide details and England Finder co-ordinates for specimens illustrated are listed in Appendix (Tab. A1).

Results

Palynofacies and palynomorphs results

Palynofacies

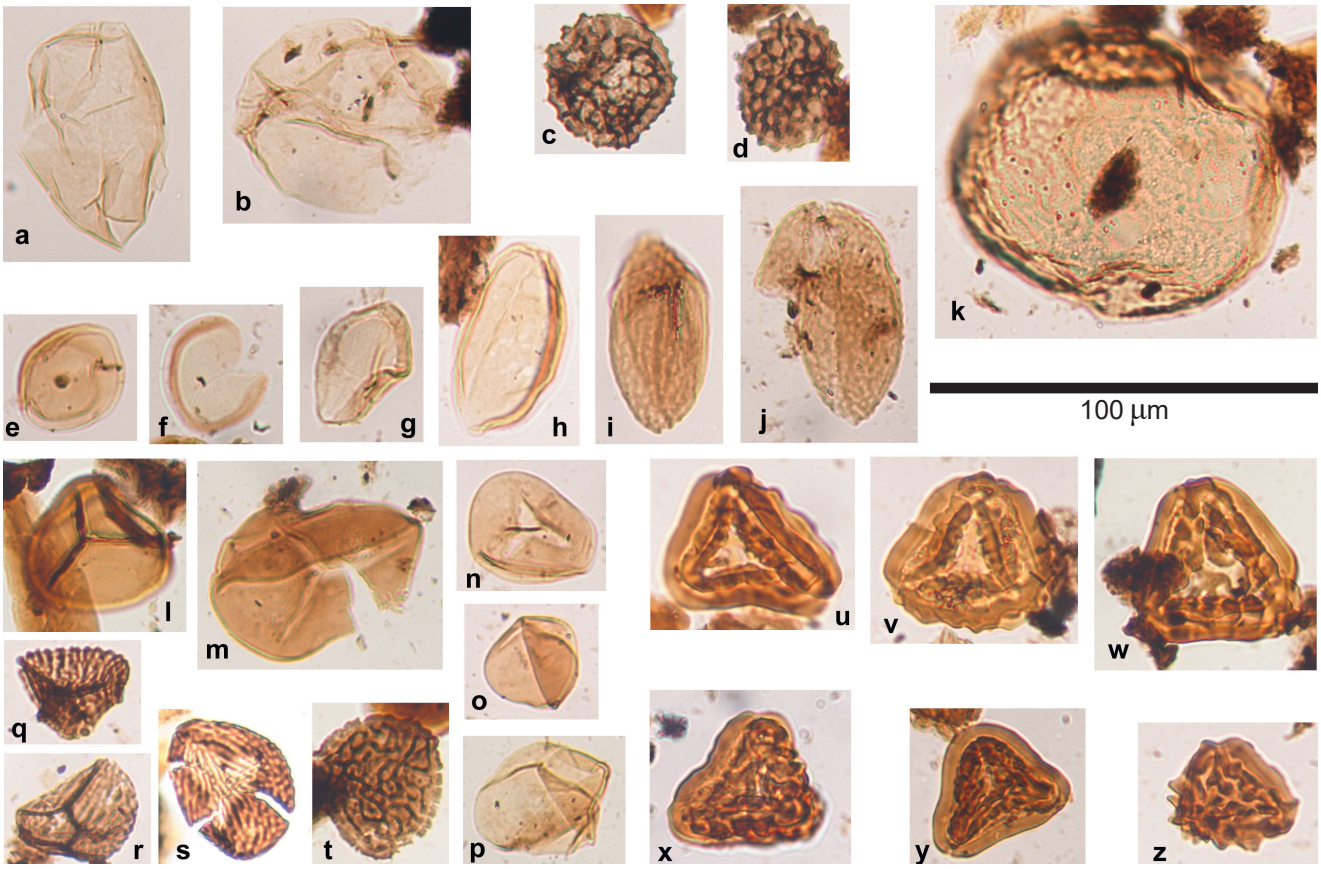
The palynofacies of units 1 and 2 is dominated by resin particles (Text-fig. 2b, c). These occur as globules or rodlets and range from opaque and dark brown to translucent and orange brown. In the representative fields of view illustrated it is obvious that palynomorphs are very rare by comparison. There is one algal cyst type 2 in Text-fig. 2c (near top right of upper left quadrant) and one folded smooth trilete spore near top of the lower right quadrant of Text-fig. 2b. The palynofacies of unit 3 (Text-fig. 2a) is dominated by small structureless dark particles (assumed lignite fragments) and again palynomorphs are very rare. There is one ornamented trilete spore in upper centre of the figure.



Text-fig. 2. Palynofacies representative of each unit of bed TB33. a: Unit 3; V 68942. b: Unit 2; V 68943. c: Unit 1; V 68944. Units 1 and 2 are dominated by resin particles whilst unit 3 is dominated by small lignitic fragments and lacks resin particles. Scale applies to all images.

Algal cysts

Up to five types of algal cysts have been recorded (Text-fig. 3a, b, e–k). Two of these (Types 2 and 4, Text-fig. 3g–j) can be identified as resting spores of the filamentous alga *Spirogyra* Link (Zygnemataceae) and are very similar to material illustrated and described by Van Geel and Van der Hammen (1978: figs 34–48 and other references there cited). These are characterised by an elongate ovoid shape, smooth or pitted surfaces and a longitudinal split. The pitted morphology type 4 (Text-fig. 3i, j) is rare and occurs in unit 2 whilst the smooth morphology type 2 (Text-fig. 3g, h) is common to abundant and occurs in all three units. The other three types do not closely match any genera of Zygnemataceae but their overall simple morphologies suggest algal cysts. Type 1 (Text-fig. 3a, b) is common to abundant, and occurs in all units. Type 3 (Text-fig. 3e, f) is rare but occurs in both units 1 and 2. Type 5 (Text-fig. 3k) is represented only by a single specimen in unit 2.



Text-fig. 3. Palynomorphs – algal cysts, spores and unidentified. a, b: Algal cyst type 1 – large, thin walled, irregularly folded, no obvious split; a – PM FM 31345(1), b – V 68945(3). c, d: Unidentified reticulate palynomorph, possibly fungal; no apertures or laesurae, greyish brown colour as in (c) is typical; c – PM FM 31346(1), d – V 68945(8). e, f: Algal cysts type 3 – small, round, thick-walled, some (as in f) have simple gaping split; e – V 68945(5), f – V 68945(6). g, h: Algal cysts type 2 – elongate oval, often with longitudinal split; g – V 68945(4), h – V 68944(3). i, j: Algal cysts type 4 – elongate oval with pitted texture and longitudinal split; i – V 68946(2); j – V 68945(7). k: Large globose algal cyst; V 68943(2). l–p: Smooth trilete spores often characteristically folded as in (o) and (p); l – V 68945(9), m – V 68945(10), n – V 68943(3), o – V 68943(4), p – V 68945(11). q–s: Ribbed palynomorph, possibly with trilete laesurae, some ribs bifurcating and others anastomosing; q – V 68943(5), r – V 68943(6), s – V 68945(12). t: Unidentified palynomorph with irregular rugulae and no obvious laesurae; V 68945(13). u–z: Ornamented rugulate and tubercled trilete spores with equatorial zona; u – V 68943(7), v – V 68943(8), w – V 68945(14), x – V 68945(15), y – V 68945(16), z – V 68943(9). Scale applies to all images.

Spores

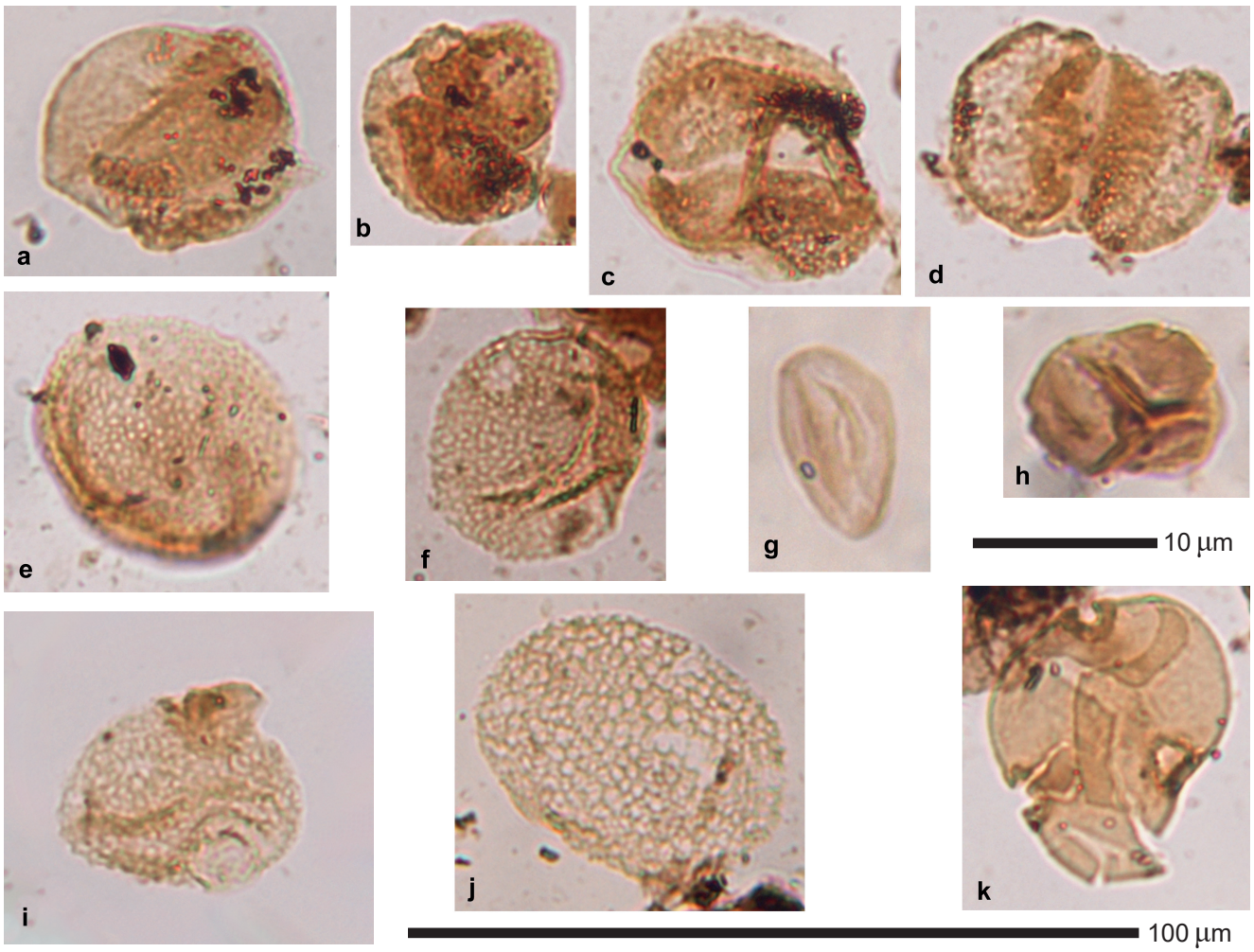
Two types of obviously trilete spore are abundant in the samples. One is smooth trilete (Text-fig. 3l–p) and one is highly ornamented with rugulae and tubercles and has an equatorial zona (Text-fig. 3u–z). Each of these morphologies exhibits some variation as shown in the figures and here they are interpreted as having been produced by at least two different taxa of herbaceous ferns of the Pteridaceae. These occur in all three units. There is a third probable trilete spore (Text-fig. 3q–s) with an ornamentation of narrow rugulae, sometimes branching and anastomosing. None of the three specimens seen (all from unit 2) shows convincing trilete laesurae but all show suggestions of those namely in Text-fig. 3q, r the narrow dark raised ridges and in Text-fig. 3s the wide open pale triangular area.

Unidentified, possibly fungal

Two palynomorphs are quite distinctive but their biological affinity is not clear. They both lack any obvious apertures or laesurae. The morphology in Text-fig. 3c, d (total three specimens, all in unit 2) has a reticulate ornament and an equatorial profile with pointed protrusions whilst that in Text-fig. 3t (total three specimens, all in unit 2) has a rugulate ornament and flat-topped equatorial protrusions. The greyish brown colour tone, as seen well in Text-fig. 3c, might suggest a fungal affinity. No other fungal material has been encountered in any of the slides.

Pollen of conifers

One type of bisaccate pollen has been recorded (Text-fig. 4a–d). This was initially not recognised as a bisaccate when seen laterally compacted (e.g., Text–fig. 4a) and all slides were subsequently re-examined after it was recognised. Seven specimens have been recorded in total, one in unit 1 and six in unit 2. This is the only representative of coniferous trees and is inferred to represent Pinaceae. *Inaperturopollenites* Potonié types (representing Taxodiaceae/Cupressaceae), which might be expected in a lake margin setting of Eocene age in the UK, have not been found in any samples.



Text-fig. 4. Palynomorphs – pollen. a–d: Bisaccate pollen compressed in various orientations; a – V 68943(10), b – V 68944(4), c – V 68943(11), d – V 68945(17). e, f, i, j: Reticulate pollen, round to slightly oval, possibly monoporate, possible pore lacking annulus and best displayed in (f); e – V 68943(12), f – PM FM 31347(1), i – V 68945(18), j – PM FM 31347(2). g: Unique specimen small tricolpate pollen; V 68943(13). h: Unique specimen small triporate pollen; V 68943(14). k: Unique specimen large triporate pollen *Intratriporopollenites*-type morphology; V 68943(15). Scale at base applies to all except (g) and (h). Scale beneath (h) applies to (g) and (h).

Pollen of flowering plants

Only four pollen types referrable to flowering plants have been encountered (Text-fig. 4e–k). Three of those (Text-fig. 4g, h, k) are each represented by only a single specimen all from unit 2. One of these (Text-fig. 4k) can be assigned to *Intratriporopollenites* but, owing to poor preservation and single specimens, identification of the other two has not been attempted. The fourth (Text-fig. 4e, f, i, j) is represented by a total of four specimens all in unit 2. This latter has microreticulate to reticulate ornament and is tentatively interpreted as monoporate. The feature that resembles an annulate pore in Text-fig. 4i is not a pore. However, the break in the reticulum in Text-fig. 4f (upper left) may be a pore which is certainly lacking an annulus. It is tentatively suggested that this pollen might belong to Sparganiaceae.

Plant mesofossil results

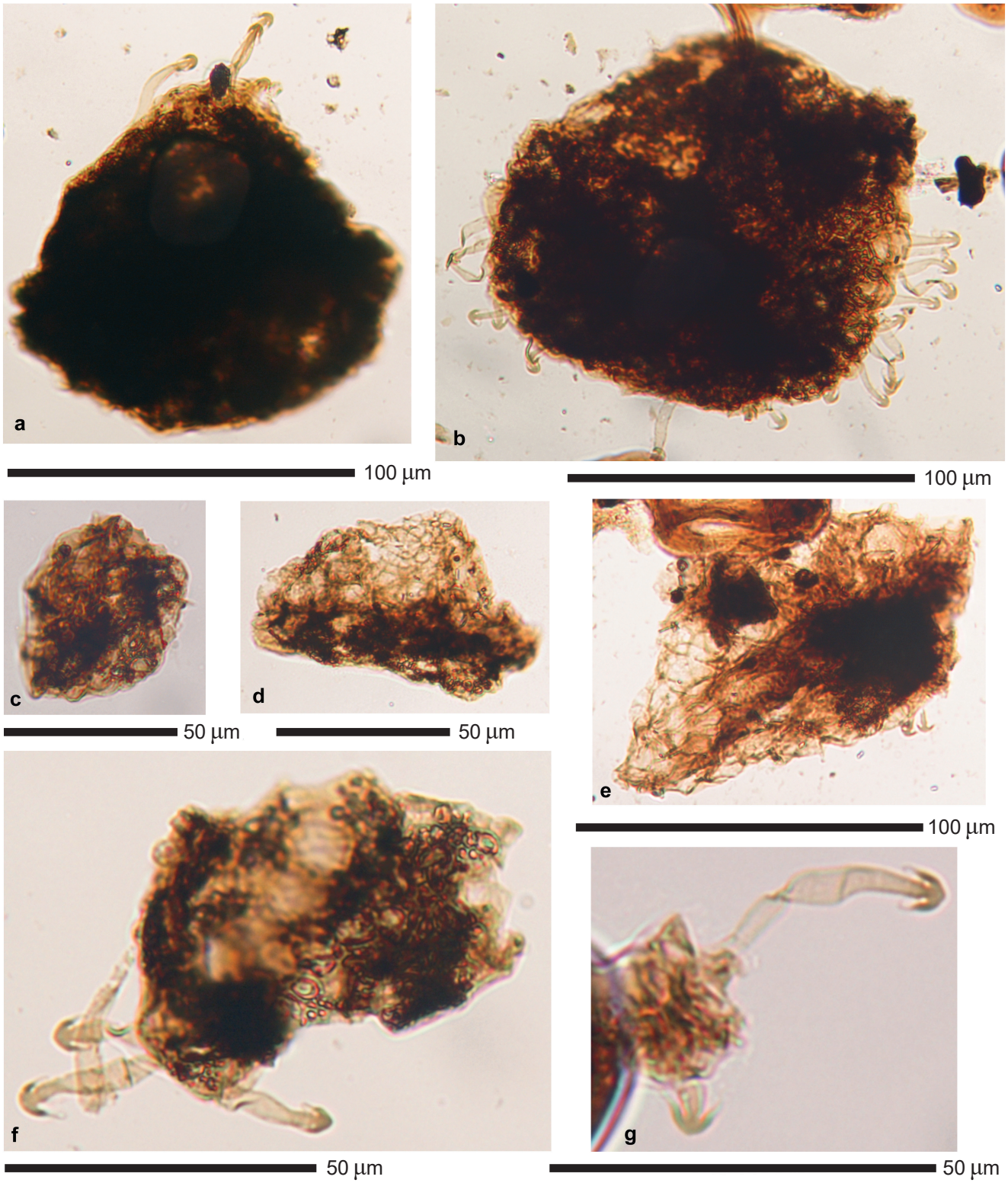
TB 33 unit 1 yielded no useful mesofossils.

In the text to follow abundance is indicated by stating number of specimens documented.

Azolla and Salvinia

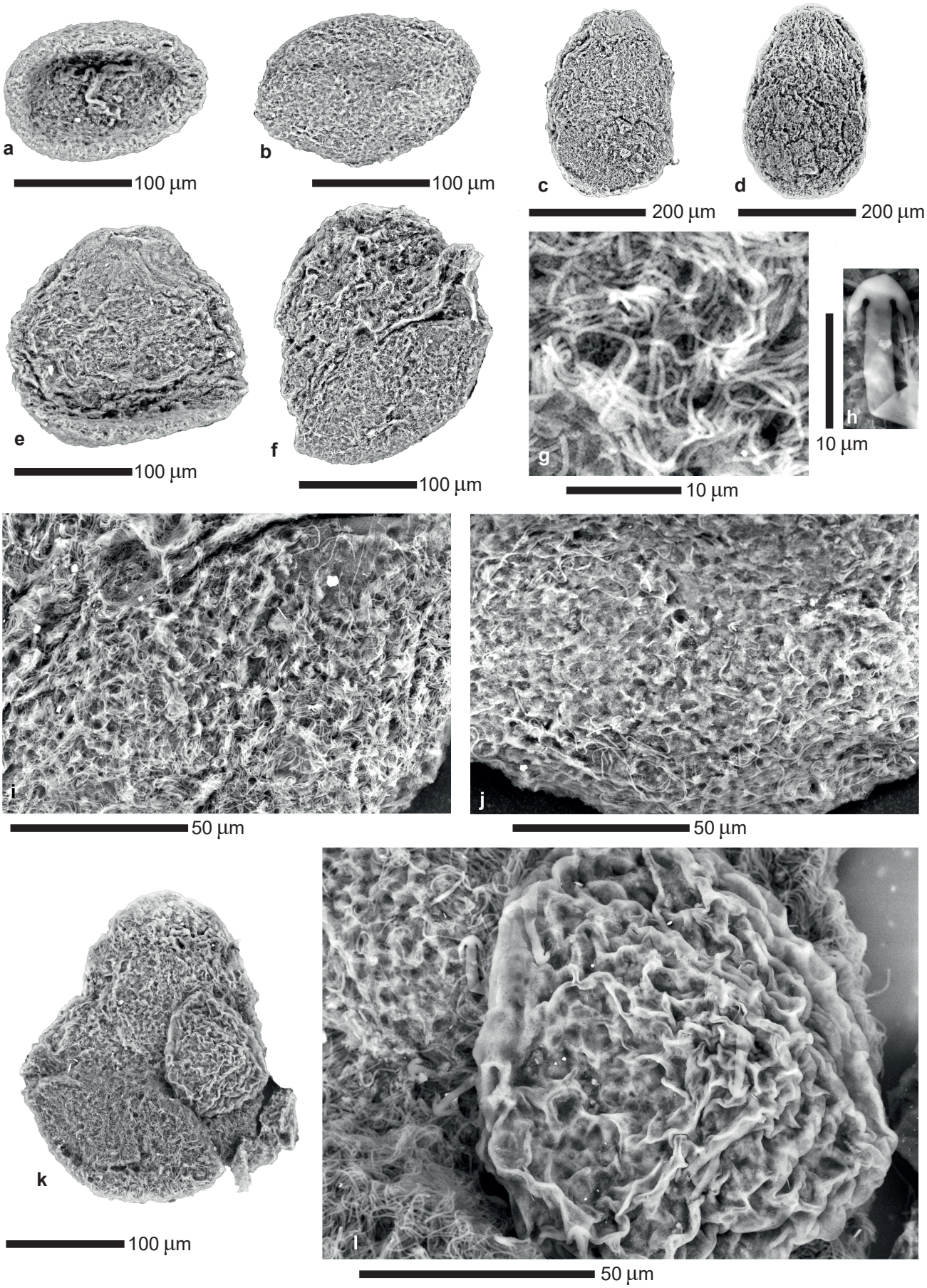
Two genera of freshwater free-floating heterosporous ferns, *Azolla* Lam. and *Salvinia* L., occur in bed TB33.

Complete specimens of *Azolla* microspore massulae occur in palynofacies slides from unit 2. Rare examples are immediately recognisable owing to attached glochidia (Text-fig. 5a, b). Specimens with a 'meshwork' texture (Text-fig. 5c–e) are frequent and some of these show glochidia and hence confirm their identification as *Azolla* (Text-fig. 5e). Fragments of *Azolla* microspore massulae (Text-fig. 5f, g) also occur in the palynofacies slides from unit 1. *Azolla* megaspore apparatus (one with a microspore massula attached; Text-fig. 6k) occur in the mesofossils from unit 2 but not in unit 1. 42 megaspore apparatus specimens have been obtained. Some are compressed laterally (Text-fig. 6c, d, k) whilst others are dominantly lateral but slightly oblique (Text-fig. 6e, f) and some are in apex/base compressions (Text-fig. 6a, b). Several of the unusual planes of compression were found in the re-sieved sample (see methods) which is mounted on SEM stub V 68949 (see Supplementary material of SEM stub layouts). Unfortunately, although there is a suggestion of multiple

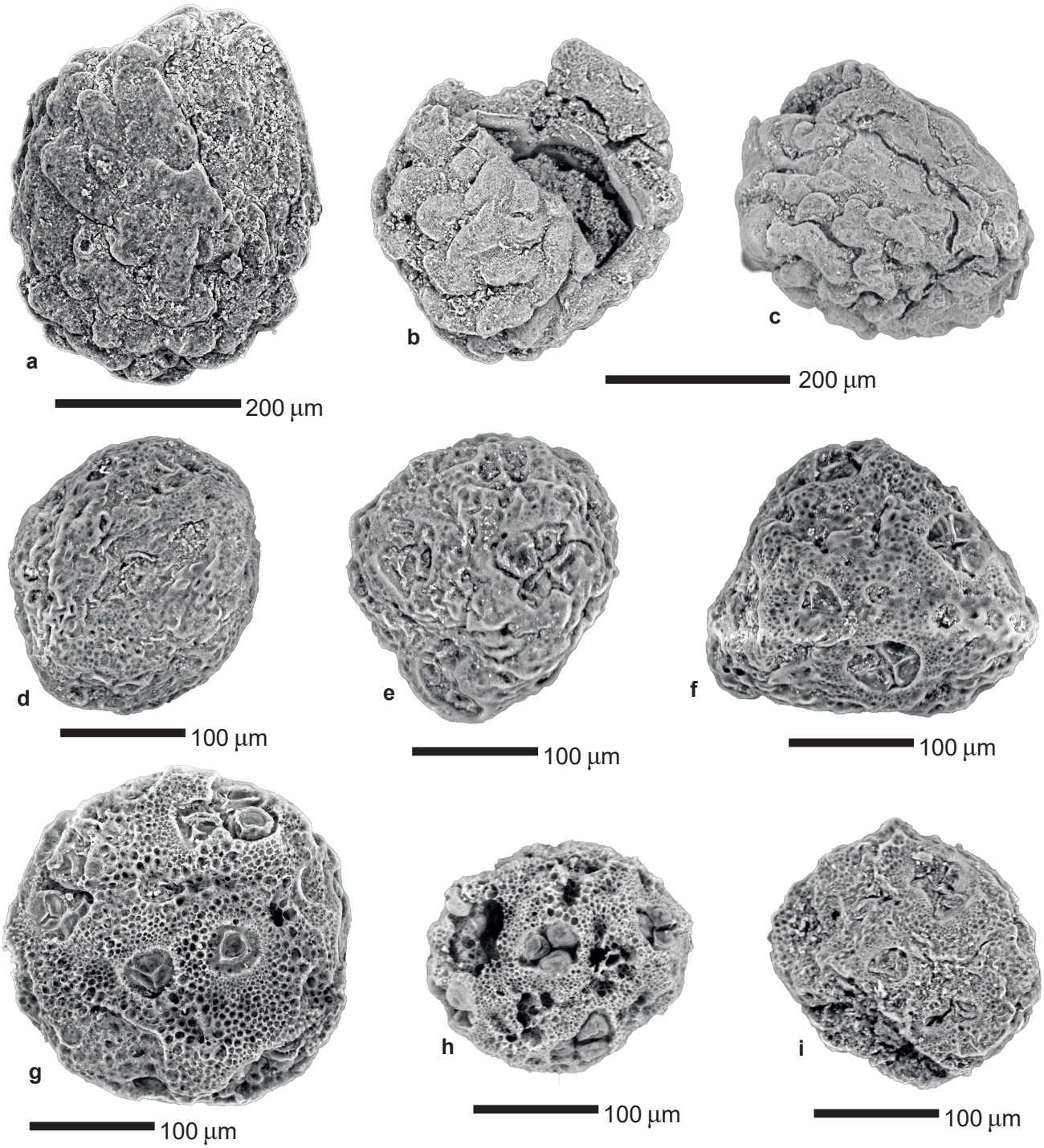


Text-fig. 5. ***Azolla*** **from palynofacies slides. a: Complete microspore massula with a few grapnel-tipped glochidia evident; V 68947(1). b: Complete microspore massula with many grapnel-tipped glochidia evident; V 68945(1). c–e: Complete microspore massulae showing a meshwork-like structure with (e) showing grapnel-tipped glochidia confirming that these are** ***Azolla*****; c – V 68948(1), d – V 68944(2), e – V 68945(2). f, g: Two fragments of microspore massulae showing different degrees of completeness; grapnel-tipped glochidia with recurved hooks and at least one septum in some of the stalks; f – V 68946(1), g – V 68948(2). Individual scales for each image.**

floats on some of the megaspore apparatus (Text-fig. 6e, f), the float number cannot be confirmed. The megaspore is covered with filosum (Text-fig. 6g, i, j) and the ornamentation of the megaspore wall is hard to observe even where the filosum cover is limited (Text-fig. 6j). In the UK Paleogene *A. prisca* E.Reid et M.Chandler, 1926 (Fowler 1975); *A. colwellensis* M.E.Collinson, 1980; *A. anglica* A.R.H.Martin, 1976 (Collinson et al. 2013) and *A.* cf. *teschiana* Florschütz emend. Batten and Collinson (2001) are recorded. The former two are relevant here being from the Solent Group of the Isle

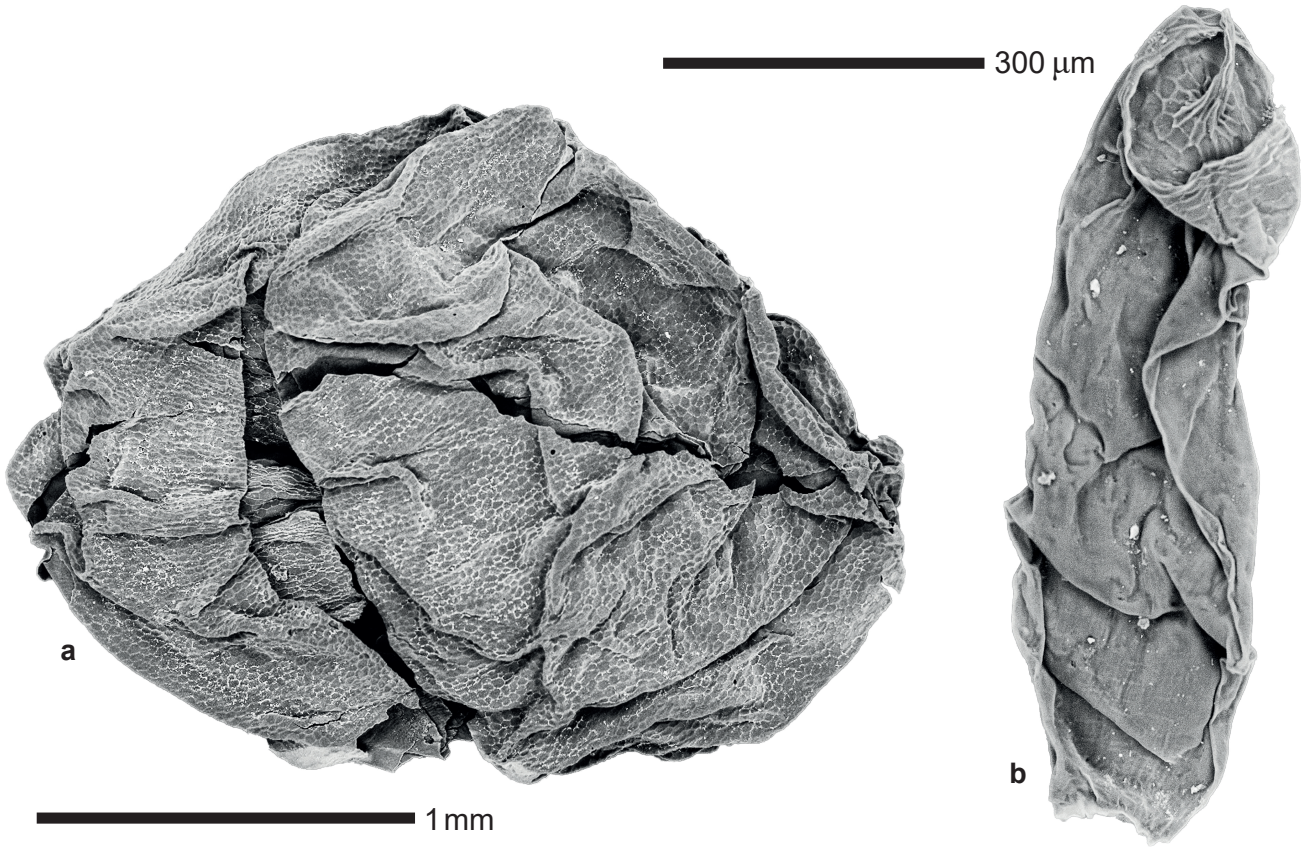


Text-fig. 6. ***Azolla*** **megaspore apparatus by SEM. a: Apical view of specimen from which floats have been lost showing trilete feature; V 68949(1). b: Basal view of specimen; V 68949(2). c–f: Lateral views of specimens showing range of shapes linked to varying compression; c – V 68950(1), d – V 68951(1), e – V 68952(1), f – V 68952(2). e, f: Showing tentative hints of outlines of multiple floats. g: Detail of characteristic filosum from (f); V 68952(2). h: Glochidium tip from upper left of (l) showing grapnel**



Text-fig. 7. ***Salvinia*** **megaspores and microspore massulae by SEM. a–c: Megaspores all with rugulate to tubercled ornament; a – V 68954(1), b – V 68955(1), c – V 68955(2). a: Strongly compressed but complete. b, c: More 3-dimensional but damaged. b: With breakage, showing thick pseudovacuolate perispore and thin inner exine. d–i: Microspore massulae. d: Has no microspores visible. d–i: All show pseudovacuolate structure but overall shapes vary from almost globose in (d), (g), (h) to laterally faceted slightly in (e) and strongly in (f); d – V 68956(1), e – V 68956(2), f – V 68955(3), g – V 68954(2), h – V 68956(3), i – V 68956(4). g: Specimen slightly corroded with loss of outermost layer very clearly displaying pseudovacuolate structure and microspores. h: A very corroded specimen revealing spores whilst (f) and (g) reveal microspore groups most clearly and (e) and (i) are somewhat intermediate.**

shape, distal dilation and recurved hooks; V 68953(1). i: Filosum cover mostly obscuring the megaspore wall, detail from (f); V 68952(2). j: Detail of megaspore surface in an area from (b) with less filosum cover, megaspore ornament of poorly defined fine reticulum with small tubercles; V 68949(2). k: Specimen with attached microspore massula; V 68953(1). l: Detail of microspore massula from k showing glochidia along left margin and in the centre; V 68953(1).



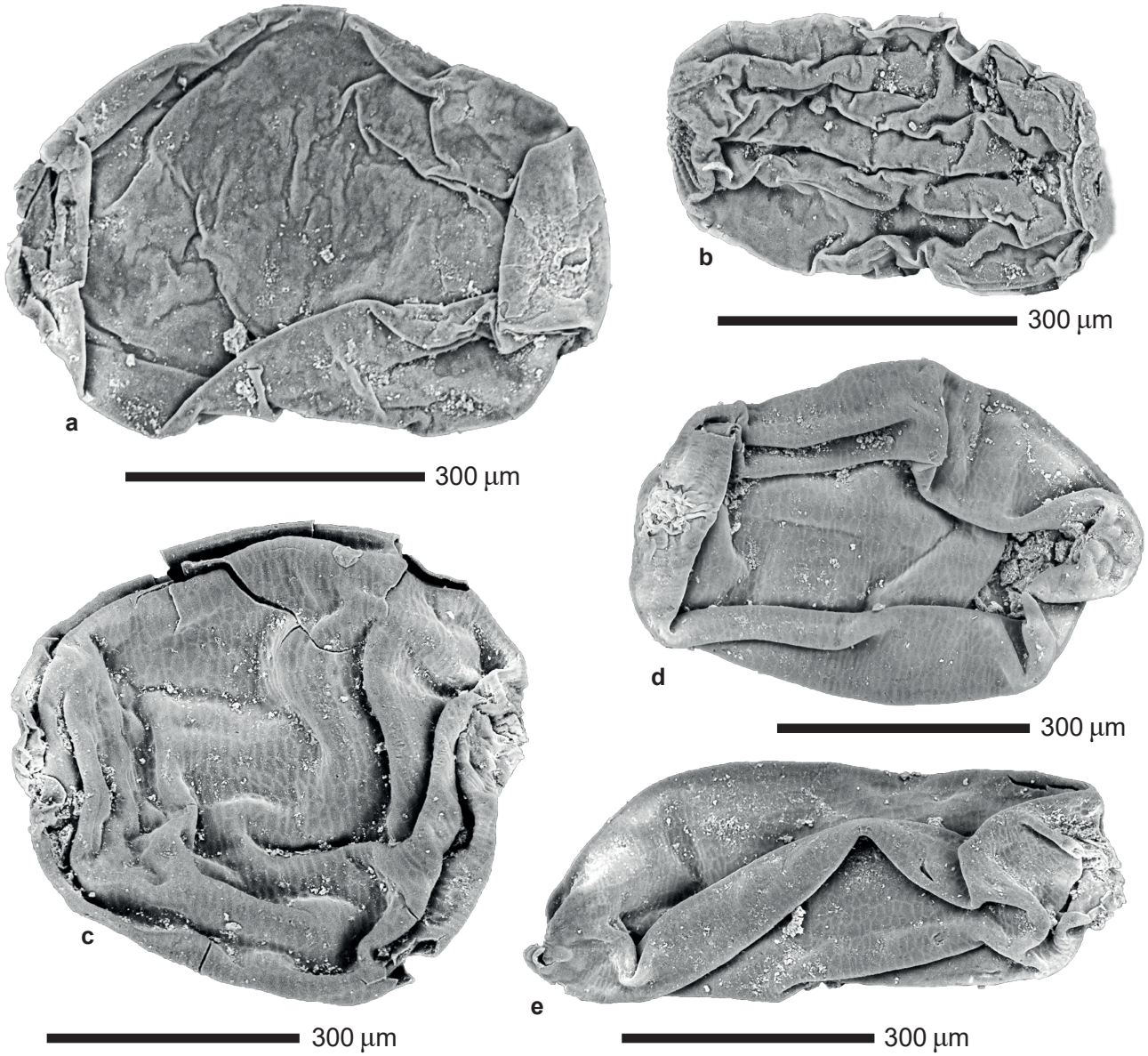
Text-fig. 8. SEM. a: *Rhamnospermum bilobatum* M.Chandler, 1925 interpreted as a seed of unknown botanical affinity; V 68953(2). b: *Typha*-like seed with terminal mucronate operculum characteristic of *Typha*; V 68953(3).

of Wight and of late Eocene age. The glochidia morphology of the material in TB33 (anchor tipped with a distal dilation and recurved tips; Text-fig. 6h) is the same as those of both *A. colwellensis* from the Linstone Chine Member, Headon Hill Formation (previously Upper Headon Beds) at Linstone Chine, Colwell Bay and *A. prisca* from the Insect Limestone, Gurnard Member (previously Bembridge Marls), Bouldnor Formation from western Isle of Wight and Totland Bay Member (previously Lower Headon Beds) at Hordle Cliff (Collinson 1980). However, the lack of information on float number and megaspore wall structure in the TB33 material prevents full comparison with those species and means that the TB33 *Azolla* species cannot be identified.

Salvinia occurs only in unit 3 with eight megaspores (including fragments; Text-fig. 7a–c) and 34 microspore massulae (Text-fig. 7d–i) having being obtained from the mesofossil fraction. Based on the overall shape and ornamentation the megaspores can be assigned to Section Cerebrata sensu Dorofeev (see discussion in Collinson et al. 2002). The megaspores are similar in overall morphology to those of *Salvinia cobhami* A.R.H.Martin as illustrated by Collinson et al. (2013) from the PETM interval at Cobham in the UK. That is the only other record of *Salvinia* megaspores in the UK Paleogene (Collinson et al. 2013) although Chandler (1925) reported *Salvinia* foliage from the Totland Bay Member (formerly Lower Headon Beds) of Hordle Cliff. The microspore massulae of *S. cobhami* are characterised by a stellate feature (Collinson et al. 2013: fig. 1B, C) which has not been seen on any of the TB33 specimens. External surfaces of dispersed specimens from Cobham lack the obvious pseudovacuolate structure so characteristic of the TB33 specimens (Text-fig. 7d–i) but that structure was observed in the TEM thin sections from Cobham (Collinson et al. 2013: fig. 1I). Many of the Cobham *Salvinia* massulae were still contained in sori so that material may be slightly immature, whilst all the TB33 specimens have dispersed and hence would be mature. However, a maturity factor alone seems unlikely to account for the differences. Hence the TB33 specimens may be a new species but it would be premature to name that species here without further study.

Seed cuticles

Seed cuticles (Text-figs 8–10) have been found in units 2 and 3 but are most common in Unit 2. A single specimen of *Rhamnospermum bilobatum* M.Chandler, 1925 has been found in unit 2 (Text-fig. 8a). This taxon occurs throughout most of the UK Paleogene. Key features are summarised by Collinson (1983: 213–214) where it was considered to be a seed of unknown botanical affinity. A single specimen of a *Typha*-like seed has been found in unit 2 (Text-fig. 8b). Features indicative of *Typha* L. include the translucent cuticular structure, the elongate oval shape, hints of cellular pattern at either end, and, especially, the mucronate operculum at the inferred apex (mucro is now slightly damaged by an attempt to physically remove a thin strand of glue, that glue has been removed from the figure digitally by the journal). The operculum is illustrated in an LM image in Collinson (1983: fig. 24) in a specimen from the UK Gurnard Member (formerly Bembridge Marls). However, as shown



Text-fig. 9. SEM. Seed cuticles almost equiaxial allowing for folding, >400 µm in length. a, b: Type 1 no evident cell pattern over central area. c–e: Type 2 clear but faint cell pattern all over specimen.

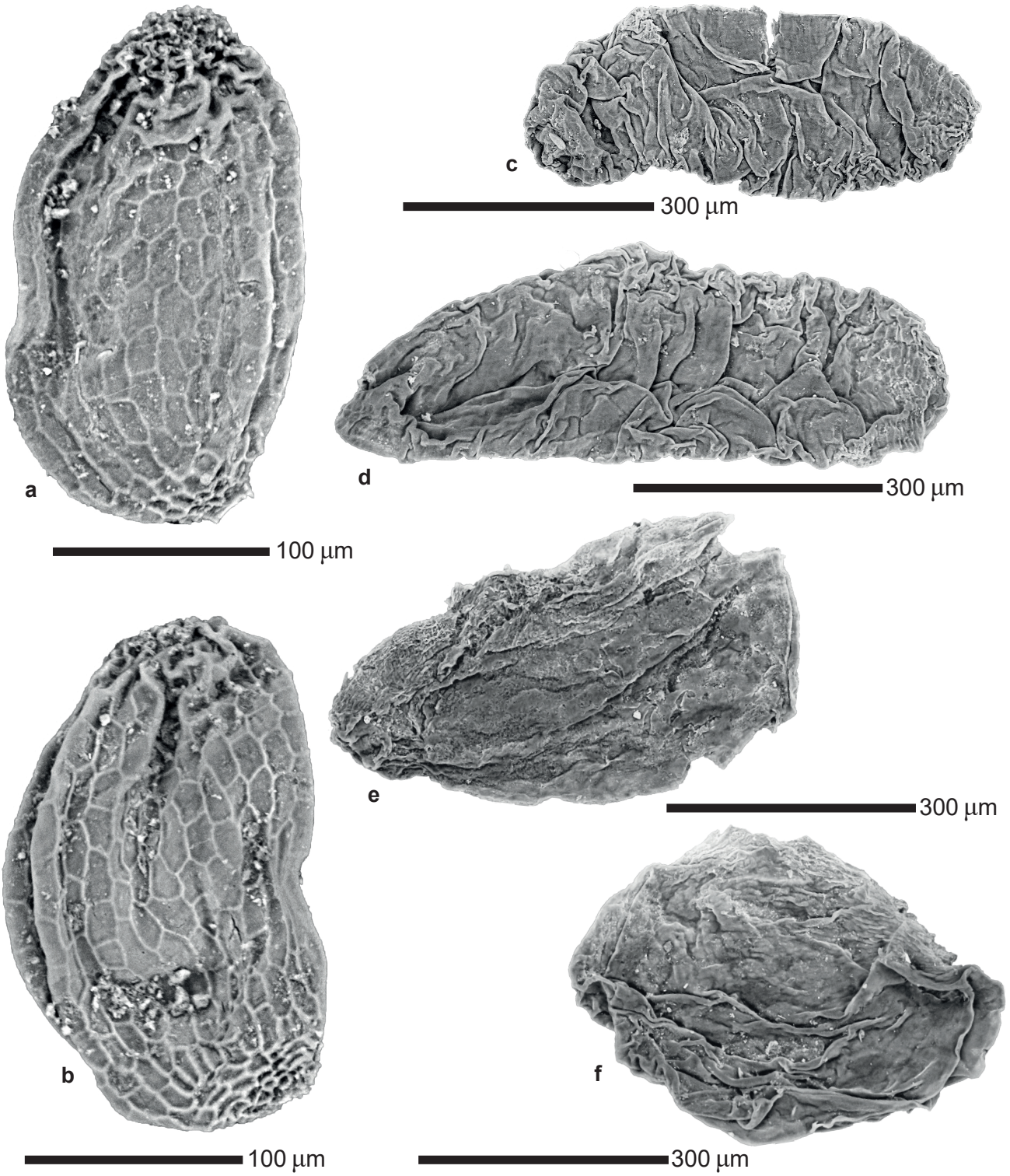
in that figure, specimens usually narrow to a closed rounded point at the base, whereas the TB33 specimen seems to have a truncated and possibly open base.

Five other morphologies (types 1–5, Text-figs 9, 10), each considered to represent a different plant taxon, of seed cuticle have been found in bed TB33 but none of these can be identified to a parent plant. They are illustrated here in the hope that future studies may shed some light on their botanical affinity. All are less than 500 microns in length and hence represent very small seeds which can be termed dust seeds (see Eriksson and Kainulainen 2011). Such seeds could easily be blown some distance from their life setting. As these are all cuticles (mostly translucent under LM) it is possible, and indeed likely, that additional outer seed coat layers were originally present and those would have provided more characters to aid identification. Types 1–4 all have modified structure at either end, likely to represent the positions of one or more of hilum, micropyle and/or chalaza. Types 1 to 4 occur in unit 3 and types 1, 2, 4 and 5 occur in unit 2. It is important to document these dust seeds, even though they cannot be identified, as they should be taken into account in future research which examines the evolution of seed size through time evaluating possible links to climate and environmental change.

Discussion

Taxonomic identifications of mesofossils and palynomorphs have only been possible at the genus or family level. In most cases this could probably not be improved upon by further work, either on the existing specimens or on new collections. Fortunately, specific identifications are not necessary to test our hypothesis.

The uppermost unit 3 of TB 33 is notable for the presence of *Salvinia* with both megaspores and microspore massulae having been obtained from the mesofossil fraction. The underlying units 1 and 2 do not contain *Salvinia*. By contrast, unit 2 contains abundant *Azolla*, both megaspores in the mesofossil fraction (one with an



Text-fig. 10. SEM. Seed cuticles. a, b: Type 3 less than 250 µm in length, slightly elongate, very clearly defined cell pattern with raised anticlinal walls and smaller cell sizes at both ends; a – V 68956(5), b – V 68956(6). c, d: Type 4 narrowly elongate >400 µm in length and strongly folded across the short axis, slight hints of cell pattern at one end (right of images); c – V 68951(2), d – V 68953(4). e, f: Type 5 >400 µm in length, slightly wrinkled but not strongly folded, lacking any clear cell patterns and having generally thicker structure, no clear terminal features; e – V 68953(5), f – V 68953(6).

attached microspore massula) and microspore massulae (complete and fragmentary) in the palynofacies slides. Unit 1 lacks informative mesofossils but contains *Azolla* in the palynofacies slides. The *Azolla* rich unit 2 samples have a palynofacies assemblage with abundant resin globules and rodlets. However, that resin is lacking in the *Salvinia*-rich unit 3 sample. Nevertheless, the most common palynomorphs of TB33 (smooth and ornamented trilete spores and algal cysts types 2 and 4) do all occur in unit 3. The mesofossil and palynomorph data do not provide any clear indication of the source for this very abundant resin in unit 2. The dominant palynomorphs in all samples are spores (ornamented and smooth) of two types of herbaceous ferns and algal cysts. The rarer palynomorphs provide

little evidence from which to interpret other vegetation but their rarity (e.g., of bisaccates and flowering plant pollen) suggests that their parent plants grew a significant distance away from the lake. Wood fragments, cuticle fragments with stomata (such as those that would be derived from leaves) and charcoal fragments have not been recognised in the palynofacies slides or the mesofossil samples. Apart from two examples of very rare palynomorphs that might be derived from fungi (Text-fig. 2c, d, t) no fungal spores have been encountered in the palynofacies slides. These results, together with sediment features, imply a lake succession with the free-floating water fern *Azolla* later being replaced by its close relative the free-floating water fern *Salvinia* accompanied by increasing sediment organic content and lake shallowing. Rare pollen with some similarity to that of Sparganiaceae and one specimen of a *Typha*-like seed provide tantalising hints, but not conclusive evidence, of a lake marginal vegetation. The abundance and consistent occurrence of spores from two types of herbaceous ferns indicates a fern-dominated vegetation near the lake. There is no evidence for other vegetation near the lake. The rarity of their pollen suggests that the Pinaceae grew some distance away from the lake but even if near the lake such trees would not be appropriate habitat for folivorous and frugivorous primates. There is no evidence for the presence of suitable habitats for the arboreal primates anywhere near the lake.

Conclusions

Apart from the previously recorded charophytes this study provides the first evidence for the vegetation in and around the lake in which bed TB33 was deposited and the vertebrate biota, including mammals, accumulated. In the later stages of its existence the lake surfaces were populated by free-floating heterosporous water ferns, initially *Azolla* later replaced by *Salvinia*. Filamentous algae of the Zygnemataceae lived in the lake alongside the previously reported charophytes but phytoplankton (e.g., *Pediastrum*, *Botryococcus*, freshwater dinoflagellates) were lacking. At least two types of herbaceous ferns of the Pteridaceae grew nearby the lake. The lack of evidence for suitable vegetation for the arboreal primates to inhabit, coupled with the low-energy sedimentary context, supports one of our previous inferences, based on mammalian taphonomy, that these mammals lived some distance away and were brought to the exposed lake margin by predators.

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References

Andrews, P., Lord, J. M., Nesbit Evans, E. M. (1979): Patterns of ecological diversity in fossil and modern mammalian faunas. – Biological Journal of the Linnean Society, 11: 177–205. https://doi.org/10.1111/j.1095-8312.1979.tb00034.x

Batten, D. J., Collinson, M. E. (2001): Revision of species of *Minerisporites*, *Azolla* and associated plant microfossils from the deposits of the Upper Palaeocene and Palaeocene/Eocene transition in the Netherlands, Belgium and the USA. – Review of Palaeobotany and Palynology, 115: 1–32. https://doi.org/10.1016/S0034-6667(00)00071-3

Bosma, A. A. (1974): Rodent biostratigraphy of the Eocene-Oligocene transitional strata of the Isle of Wight. – Utrecht Micropaleontological Bulletins, 1: 1–128.

Bristow, H. W., Reid, C., Strahan, A. (1889): The Geology of the Isle of Wight, 2nd ed. –Memoirs of the Geological Survey, England and Wales. The Lords Commissioners of Her Majesty's Treasury, London, xiv + 349 pp., 5 pls. https://doi.org/10.5962/bhl.title.35238

Chandler, M. E. J. (1925): The Upper Eocene Flora of Hordle, Hants. Part I. Pages 1–32; Plates I–IV. Monographs of the Palaeontographical Society, 77(360): 1–32. https://doi.org/10.1080/02693445.1925.12035595

Collinson, M. E. (1980): A new multiple floated *Azolla* from the British Eocene with a brief review of the genus. – Palaeontology, 23: 213–299.

Collinson, M. E. (1983): Palaeofloristic assemblages and palaeoecology of the Lower Oligocene Bembridge Marls, Hamstead Ledge, Isle of Wight. – Botanical Journal of the Linnean Society, 86: 177–225. https://doi.org/10.1111/j.1095-8339.1983.tb00725.x

Collinson, M. E., Kvaček, Z., Zastawniak, E. (2002): The aquatic plants *Salvinia* (Salviniales) and *Limnobiophyllum* (Arales) from the Late Miocene flora of Sosnica (Poland). – Acta Palaeobotanica 41: 253–282.

Collinson, M. E., Smith, S. Y., Van Konijnenburg-van Cittert, J. H. A., Batten, D. J., Van Der Burgh, J., Barke, J., Marone, F. (2013): New observations and synthesis of Paleogene heterosporous water ferns. – International Journal of Plant Sciences 174: 350–363. https://doi.org/10.1086/668249

Eisenberg, J. F. (1981): The Mammalian Radiations. An Analysis of Trends in Evolution, Adaptation, and Behaviour. – University of Chicago Press, Chicago, xx + 610 pp.

Eriksson, O., Kainulainen, K. (2011): The evolutionary ecology of dust seeds. – Perspectives in Plant Ecology, Evolution and Systematics 13: 73–87. https://doi.org/10.1016/j.ppees.2011.02.002

Fowler, K. (1975): Megaspores and massulae of *Azolla prisca* from the Oligocene of the Isle of Wight. – Palaeontology, 18: 483–507.

Godinot, M. (1991): Approches fonctionnelles des mains de primates paléogènes. – Geobios Mémoires Spéciales, 13: 161–173. https://doi.org/10.1016/S0016-6995(66)80021-9

Harrison, J. L. (1962): The distribution of feeding habits among animals in a tropical rain forest. – Journal of Animal Ecology, 31: 53–63. https://doi.org/10.2307/2332

Hooker, J. J. (2021): The Mammals of the Late Eocene – Early Oligocene Solent Group, Part 1, Introduction and

Euarchonta: Nyctitheriidae. – Monographs of the Palaeontographical Society, London, 175(659): 1–147, pls 1–48. https://doi.org/10.1080/02693445.2021.1928440

Hooker, J. J. (2024): The Mammals of the Late Eocene – Early Oligocene Solent Group, Part 2, Euarchonta (Nyctitheriidae and Primates), Lipotyphla, Chiroptera, Pseudorhyncocyonidae, Pantolesta, Apatotheria. – Monographs of the Palaeontographical Society, London, 177(667): 148–290, pls 49–122. https://doi.org/10.1080/02693445.2023.2339592

Keen, M. C. (1977): Ostracod assemblages and the depositional environments of the Headon, Osborne, and Bembridge Beds (upper Eocene) of the Hampshire Basin. – Palaeontology, 20: 405–445.

Klembara, J., Green, B. (2010): Anguimorph lizards (Squamata, Anguimorpha) from the Middle and Late Eocene of the Hampshire Basin of southern England. – Journal of Systematic Palaeontology, 8: 97–129. https://doi.org/10.1080/14772011003603531

Rage, J.-C., Ford, R. L. E. (1980): Amphibians and squamates from the Upper Eocene of the Isle of Wight. – Tertiary Research, 3: 47–60.

Ramdarshan, A., Merceron, G., Marivaux, L. (2011): Spatial and temporal ecological diversity amongst Eocene primates of France: evidence from teeth. – American Journal of Physical Anthropology, 147: 201–216. https://doi.org/10.1002/ajpa.21638

Ramdarshan, A., Orliac, M. J. (2015): Endocranial morphology of *Microchoerus erinaceus* (Euprimates, Tarsiiformes) and early evolution of the Euprimates brain. – American Journal of Physical Anthropology, 159: 5–16. https://doi.org/10.1002/ajpa.22868

Riveline, J. (1984): Les gisements à charophytes du Cénozoique (Danien au Burdigalien) d'Europe occidentale. Lithostratigraphie, biostratigraphie, chronostratigraphie. – Bulletin d'Information des Géologues du Bassin de Paris, Mémoire hors série, 4: 1–523.

Van Geel, B., Van der Hammen, T. (1978): Zygnemataceae in Quaternary Colombian sediments. – Review of Palaeobotany and Palynology, 25: 377–392. https://doi.org/10.1016/0034-6667(78)90021-0

Vasileiadou, K., Hooker, J. J., Collinson, M. E. (2022): Taphonomy of an Eocene micromammal assemblage in a lake-margin depositional setting elucidates an ancient food web. – Palaeontologia Electronica, 25(2): a16 (31 pp.). https://doi.org/10.26879/1214

Supplementary material

Diagrams using LM photographs of the eight SEM stubs to show the positions of the figured specimens with their specimen numbers. Unfigured specimens of the figured taxa are also indicated.

Appendix

Table A1. List of figured LM palynofacies and palynomorph slides with England Finder co-ordinates and NHMUK numbers for figured specimens.

Text-fig, number	Laboratory record slide name etched on slide surface	Item illustrated	England Finder on LM slide	TB 33 Unit	Museum number
Text-fig. 2a	TB33-6 slide 2	Palynofacies lignite fragments	L46/3 / M46/1	3	V 68942
Text-fig. 2b	TB33 black bottom slide 2	Palynofacies resin dominated	O47	2	V 68943
Text-fig 2c	TB33 black pale slide 1	Palynofacies resin dominated	M37	1	V 68944
Text-fig. 3a	TB33 pale slide 1	algal cyst type 1	F29/3	below 1	PM FM 31345(1)
Text-fig. 3b	TB33 black bottom slide 1	algal cyst type 1	J31/H31	2	V 68945(3)
Text-fig. 3c	TB33 black top slide 1	reticulate palynomorph no laesurae	H28	2	PM FM 31346(1)
Text-fig. 3d	TB33 black bottom slide 1	reticulate palynomorph no laesurae	K43	2	V 68945(8)
Text-fig. 3e	TB33 black bottom slide 1	algal cyst type 3	K31	2	V 68945(5)
Text-fig. 3f	TB33 black bottom slide 1	algal cyst type 3	L33	2	V 68945(6)
Text-fig. 3g	TB33 black bottom slide 1	algal cyst type 2	K34/ 2/4	2	V 68945(4)
Text-fig. 3h	TB33 black pale slide 1	algal cyst type 2	M37	1	V 68944(3)
Text-fig. 3i	TB33-3 slide 1	algal cyst type 4	G32/1	1	V 68946(2)
Text-fig. 3j	TB33 black bottom slide 1	algal cyst type 4	H44/1 / G44/3	2	V 68945(7)
Text-fig. 3k	TB33 black bottom slide 2	algal cyst type 5	K49/K50	2	V 68943(2)
Text-fig. 3l	TB33 black bottom slide 1	smooth trilete spore	R43/3	2	V 68945(9)
Text-fig. 3m	TB33 black bottom slide 1	smooth trilete spore	V28/3	2	V 68945(10)
Text-fig. 3n	TB33 black bottom slide 2	smooth trilete spore	E30	2	V 68943(3)
Text-fig. 3o	TB33 black bottom slide 2	smooth trilete spore	W34	2	V 68943(4)
Text-fig. 3p	TB33 black bottom slide 1	smooth trilete spore	Q47/1	2	V 68945(11)
Text-fig. 3q	TB33 black bottom slide 2	rugulate probably trilete spore	U42	2	V 68943(5)
Text-fig. 3r	TB33 black bottom slide 2	rugulate probably trilete spore	H48	2	V 68943(6)
Text-fig. 3s	TB33 black bottom slide 1	rugulate probably trilete spore	Q35	2	V 68945(12)
Text-fig. 3t	TB33 black bottom slide 1	rugulate palynomorph no laesurae	T39/T40	2	V 68945(13)
Text-fig. 3u	TB33 black bottom slide 2	ornamented trilete spore	L41	2	V 68943(7)
Text-fig. 3v	TB33 black bottom slide 2	ornamented trilete spore	H39/1	2	V 68943(8)
Text-fig. 3w	TB33 black bottom slide 1	ornamented trilete spore	Q41/Q42	2	V 68945(14)
Text-fig. 3x	TB33 black bottom slide 1	ornamented trilete spore	P40/2	2	V 68945(15)
Text-fig. 3y	TB33 black bottom slide 1	ornamented trilete spore	F35	2	V 68945(16)
Text-fig. 3z	TB33 black bottom slide 2	ornamented trilete spore	D38/3	2	V 68943(9)
Text-fig. 4a	TB33 black bottom slide 2	bisaccate pollen	J49/1	2	V 68943(10)
Text-fig. 4b	TB33 black pale slide 1	bisaccate pollen	K35/3 / L45/1	1	V 68944(4)

Table A1. continued

Text-fig, number	Laboratory record slide name etched on slide surface	Item illustrated	England Finder on LM slide	TB 33 Unit	Museum number
Text-fig. 4c	TB33 black bottom slide 2	bisaccate pollen	Q31/3 / P31/2	2	V 68943(11)
Text-fig. 4d	TB33 black bottom slide 1	bisaccate pollen	T43/ 3/1	2	V 68945(17)
Text-fig. 4e	TB33 black bottom slide 2	reticulate ?monoporate pollen	T44	2	V 68943(12)
Text-fig. 4f	TB33 black trial sample slide 1	reticulate ?monoporate pollen	E30	2	PM FM 31347(1)
Text-fig. 4g	TB33 black bottom slide 2	small tricolpate pollen	P34	2	V 68943(13)
Text-fig. 4h	TB33 black bottom slide 2	small triporate pollen	S44/4 / S45/3	2	V 68943(14)
Text-fig. 4i	TB33 black bottom slide 1	reticulate ?monoporate pollen	O36/O37	2	V 68945(18)
Text-fig. 4j	TB33 black trial sample slide 1	reticulate ?monoporate pollen	M29/2	2	PM FM 31347(2)
Text-fig. 4k	TB33 black bottom slide 2	large triporate pollen	T37/3	2	V 68943(15)
Text-fig. 5a	TB33-2 slide 1	*Azolla* complete massula few visible glochidia	O39/4	2	V 68947(1)
Text-fig. 5b	TB33 black bottom slide 1	*Azolla* complete massula many visible glochidia	N42/3	2	V 68945(1)
Text-fig. 5c	TB33-4 slide 1	*Azolla* small massula no visible glochidia	M33	1	V 68948(1)
Text-fig. 5d	TB33 black pale slide 1	*Azolla* small massula no visible glochidia, meshwork	L37/3	1	V 68944(2)
Text-fig. 5e	TB33 black bottom slide 1	*Azolla* small massula two visible glochidia, meshwork	J41	2	V 68945(2)
Text-fig. 5f	TB33-3 slide 1	*Azolla* massula fragment with glochidia	B33/4	1	V 68946(1)
Text-fig. 5g	TB33-4 slide 1	*Azolla* very small massula fragment with glochidia	G31/1	1	V 68948(2)

Table A2. List of figured mesofossil specimens on SEM stubs with NHMUK specimen numbers.

Text-fig. number	SEM stub number and specimen number	Item illustrated	TB33 Unit	Museum number
Text-fig. 6a	SEM stub 4014 specimen 12	*Azolla* megaspore apical view lacking floats	2	V 68949(1)
Text-fig. 6b	SEM stub 4014 specimen 11	*Azolla* megaspore basal view	2	V 68949(2)
Text-fig. 6c	SEM stub 4011 specimen 1	*Azolla* megaspore lateral view	2	V 68950(1)
Text-fig. 6d	SEM stub 4007 specimen 8	*Azolla* megaspore lateral view	2	V 68951(1)
Text-fig. 6e	SEM stub 4010 specimen 3	*Azolla* megaspore lateral view, hints of floats	2	V 68952(1)
Text-fig. 6f	SEM stub 4010 specimen 2	*Azolla* megaspore lateral view, hints of floats	2	V 68952(2)
Text-fig. 6g	SEM stub 4010 specimen 2 detail	*Azolla* megaspore filosum detail	2	V 68952(2)
Text-fig. 6h	SEM stub 4006 specimen 10 detail	*Azolla* microspore massula detail of glochidium from Text-fig. 6l	2	V 68953(1)
Text-fig. 6i	SEM stub 4010 specimen 2 detail	*Azolla* detail of megaspore filosum cover from Text-fig. 6f	2	V 68952(2)
Text-fig. 6j	SEM stub 4014 specimen 11 detail	*Azolla* detail of megaspore outer wall and filosum	2	V 68949(2)
Text-fig. 6k	SEM stub 4006 specimen 10	*Azolla* megaspore lateral view with microspore massula attached	2	V 68953(1)
Text-fig. 6l	SEM stub 4006 specimen 10 detail	*Azolla* detail of microspore massula from Text-fig. 6k	2	V 68953(1)
Text-fig. 7a	SEM stub 4008 specimen 9	*Salvinia* megaspore complete lateral view	3	V 68954(1)
Text-fig. 7b	SEM stub 4015 specimen 5	*Salvinia* megaspore lateral view broken showing thick wall	3	V 68955(1)
Text-fig. 7c	SEM stub 4015 specimen 21	*Salvinia* megaspore lateral view slightly broken clear ornament	3	V 68955(2)
Text-fig. 7d	SEM stub 4016 specimen 15	*Salvinia* microspore massula spores not visible	3	V 68956(1)
Text-fig. 7e	SEM stub 4016 specimen 7	*Salvinia* microspore massula one obvious group of spores visible	3	V 68956(2)
Text-fig. 7f	SEM stub 4015 specimen 24	*Salvinia* microspore massula two compact groups of spores clearly visible, massula with unusual triangular shape	3	V 68955(3)
Text-fig. 7g	SEM stub 4008 specimen 13	*Salvinia* microspore massula outer wall eroded, several spore clusters visible and very clear pseudovacuolate texture	3	V 68954(2)
Text-fig. 7h	SEM stub 4016 specimen 25	*Salvinia* microspore massula outer wall very eroded, several spore clusters visible, pseudovacuolate texture and some disintegration	3	V 68956(3)
Text-fig. 7i	SEM stub 4016 specimen 28	*Salvinia* microspore massula initally thought to be debris	3	V 68956(4)
Text-fig. 8a	SEM stub 4006 specimen 1	*Rhamnospermum bilobatum*	2	V 68953(2)
Text-fig. 8b	SEM stub 4006 specimen 15	Typha-ike seed	2	V 68953(3)
Text-fig. 9a	SEM stub 4015 specimen 2	Seed cuticle type 1 not strongly wrinkled	3	V 68955(4)
Text-fig. 9b	SEM stub 4015 specimen 18	Seed cuticle type 1 strongly longitudinally wrinkled	3	V 68955(5)
Text-fig. 9c	SEM stub 4015 specimen 7	Seed cuticle type 2 almost equiaxial, clear cell pattern	3	V 68955(6)
Text-fig. 9d	SEM stub 4015 specimen 1	Seed cuticle type 2 slightly folded longitudinally, clear cell pattern	3	V 68955(7)
Text-fig. 9e	SEM stub 4015 specimen 9	Seed cuticle type 2 strongly longitudinally folded, clear cell pattern	3	V 68955(8)
Text-fig. 10a	SEM stub 4016 specimen 9	Seed cuticle type 3 clear cell pattern, terminal pattern clearer at top of image	3	V 68956(5)
Text-fig. 10b	SEM stub 4016 specimen 21	Seed cuticle type 3 clear cell pattern, terminal pattern clearer at base of image	3	V 68956(6)

Table A2. continued

Text-fig. number	SEM stub number and specimen number	Item illustrated	TB33 Unit	Museum number
Text-fig. 10c	SEM stub 4007 specimen 15	Seed cuticle type 4 transverse folding slightly shrunken specimen	2	V 68951(2)
Text-fig. 10d	SEM stub 4006 specimen 4	Seed cuticle type 4 transverse folding elongate oval chape	2	V 68953(4)
Text-fig. 10e	SEM stub 4006 specimen 2	Seed cuticle type 5 slightly damaged specimen seems to have extra outer layers	2	V 68953(5)
Text-fig. 10f	SEM stub 4006 specimen 3	Seed cuticle type 5 folded specimen but mostly seems to be cuticle	2	V 68953(6)