

EARLY TERTIARY POLLEN OF PROBABLE DROSERACEAN AFFINITY FROM CENTRAL AUSTRALIA

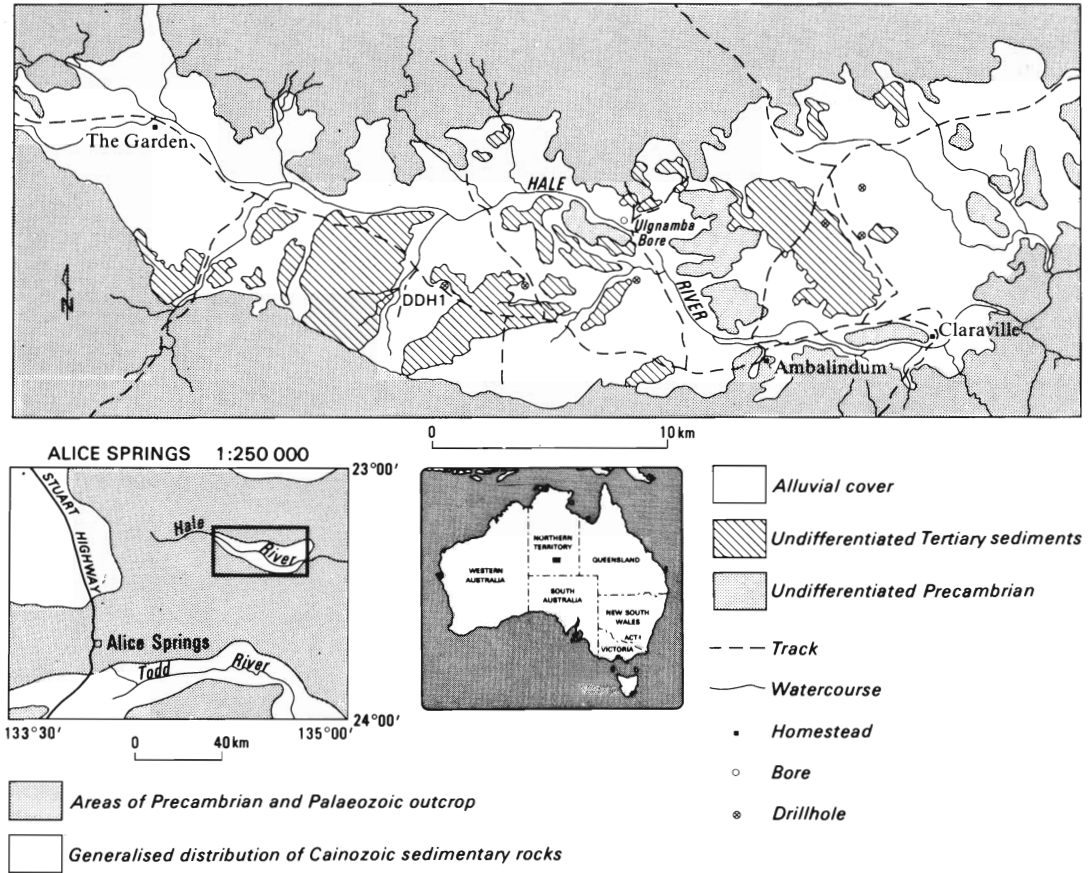
by E. M. TRUSWELL *and* N. G. MARCHANT

ABSTRACT. *Fischeripollis halensis* sp. nov. is described from the Ulgamba Lignite in the Hale River Basin, north-east of Alice Springs, central Australia. This unit, on the evidence of a diverse palynomorph assemblage, with some constraints provided by palaeomagnetic dating of deep-weathering profiles, is probably of Middle to Late Eocene age. Abundant rainforest taxa in the pollen spectrum suggest high, uniformly distributed rainfall. The similarity of *F. halensis*, which occurs either in single grains or in tetrads, to pollen of extant Droseraceae is evident in the proximo-equatorial ring of large apertures, and in the grain wall, which bears processes in two distinct size classes. The strongest resemblance is to pollen of extant *Dionaea*, the Venus Fly Trap, which occurs today only in the south-eastern United States. The presence of pores which penetrate directly into the main body of the grain, rather than into a system of radiating channels on the proximal face, suggests relationship with the *Dionaea* lineage rather than with that of *Drosera*. *F. halensis*, however, differs in detail from the pollen of extant *Dionaea muscipula*. This record is the oldest occurrence of this pollen morphotype.

DURING recent palynological examination of Tertiary sequences in the Hale River Basin of central Australia, a distinctive pollen type was observed in assemblages of pollen and spores from the Ulgamba Lignite. This deposit is a thin unit of probable Eocene age, which forms part of the predominantly sandy Hale Formation. The fossil pollen is characterized by a ring of large pores situated just proximally of the grain equator, and so bears a marked resemblance to pollen of extant Droseraceae, a family of carnivorous annual or perennial herbs occurring today on all continents except Antarctica. Extant Droseraceae include four genera: *Drosera*, the sundews, of cosmopolitan distribution; *Dionaea*, the Venus Fly Trap, confined to the south-eastern United States; *Drosophyllum*, occurring in the Iberian Peninsula; and *Aldrovanda*, which occurs in Eurasia, tropical Africa and Australia. All genera except *Drosera* are monotypic. Many are plants of moist, boggy, or seasonally wet habitats, but only *Aldrovanda*, which has submerged leaves, is a true aquatic.

In the classificatory system of Cronquist (1981), which has been followed in the current *Flora of Australia* (see Marchant *et al.* 1982), the Droseraceae has been grouped with the Nepenthaceae into a single order, Nepentales; similarities in pollen morphology between the two families supports such an arrangement. In other classificatory systems Droseraceae has been included within Rosales, and other families of carnivorous plants, such as the Nepenthaceae and Sarraceniaceae, have been assigned to separate orders (Heywood 1978).

In Australia, Droseraceae is most abundantly represented today by *Drosera*. Of the ninety-odd species of the genus known world-wide, fifty-four are known from Australia, where there is a notable richness of species in the south-west, with forty-two species present there (Marchant *et al.* 1982). In the central Australian region, three species of *Drosera* occur now (Marchant 1981). These are *D. indica* L., which is widespread in the Old World tropics, *D. burmanni* Vahl, which has a south-east Asian and Australian distribution, and *D. petiolaris* R.Br., which ranges through northern Australia, New Guinea, and Indonesia. Of the other genera within the Droseraceae, only *Aldrovanda* is represented in Australia today; *A. vesiculosa* L. occurs in shallow, freshwater localities in northern and coastal eastern Australia (Marchant *et al.* 1982).



TEXT-FIG. 1. Locality map showing the position of the borehole DDH-1 within the Hale River Basin, Northern Territory.

THE GEOLOGICAL SETTING

The Hale River Basin and its sedimentary sequence

The palynomorphs described in this paper come from the Ulgnamba Lignite, at 42.2 m depth in the borehole DDH-1, drilled by the Northern Territory Geological Survey in the Hale River Basin. This basin is located about 80 km to the north-east of Alice Springs (text-fig. 1). It underlies the Hale Plain, between Claraville and The Garden homesteads, and is one of a number of small, sediment-filled depressions lying on the eroded surface of Precambrian and early Palaeozoic rocks. The Hale River Basin forms an arcuate depression approximately 45 km long and 12.5 km wide at its widest point. At least on its southern margin it may be fault-bounded, and its formation may have been influenced by late Mesozoic or Tertiary subsidence. Basement rocks are formed largely of metamorphics and granites of the Arunta Inlier (Shaw and Wells 1983).

Sediments within the basin are dominantly fluvial and lacustrine clastics (Clarke 1975; B. R. Senior in Shaw *et al.* 1982; Shaw *et al.* 1984). Their spatial and temporal distribution remains poorly understood, and published information is scarce. At the base, overlying the deeply weathered metamorphics of the basement complex, is the Hale Formation (Stewart *et al.* 1980; Shaw *et al.* 1984), a unit of kaolinic quartzose sandstone, siltstone, and mudstone, which grades into coarser sediments at the basin margins. Within the Hale Formation (text-fig. 2) the sequence begins with the informally named Ambalindum Sandstone member, consisting of argillaceous, poorly sorted sandstone, with intercalations of granule and pebble conglomerates. Overlying this is the Ulgnamba Lignite, formally designated by Stewart *et al.* (1980), a unit of lignite and carbonaceous shale which is 4 m thick

in its type section in the BMR Corehole Alice Springs 2. The lignite crops out, in a much weathered state, in a mesa 3 km west-north-west of Claraville Homestead. It occurs as lenses in several of the drillholes penetrating the Hale Plain. Sometimes the lignites are associated with pockets of oil shale. Locally, olive-green mudstones and siltstones lie immediately below.

Above the lignite the uppermost part of the Hale Formation has been referred to informally as the Arltunga member, a succession of poorly consolidated, fine-grained silty sandstone, sandy siltstone, and clay interbeds. There is some confusion about the nomenclature of this sedimentary unit, as the name Arltunga beds has been used for arenaceous limestones which may be more appropriately grouped with the overlying Waite Formation equivalents (Shaw and Wells 1983; Shaw *et al.* 1984). The Hale Formation is considered to record a progressively flooding, slowly subsiding basin (Clarke 1975): the basal sandstones reflect a relatively high energy fluvial environment, the Ulnamba Lignite a marsh or swamp habitat, and the Arltunga member a phase of relatively low energy fluvio-lacustrine sedimentation.

The formation of silcrete, presumably by groundwater movements, and another interval of deep weathering preceded deposition of the lacustrine sediments—siltstones and clays—which overlie the Hale Formation. This fine-grained unit is equated with the Waite Formation, best known from the Alcoota 1:250 000 Sheet Area, to the north of Alice Springs. In the Cainozoic Waite Basin in that area (Shaw *et al.* 1982), vertebrate fossils from the Waite Formation are thought to indicate a Late Miocene to Early Pliocene age (Woodburne 1967).

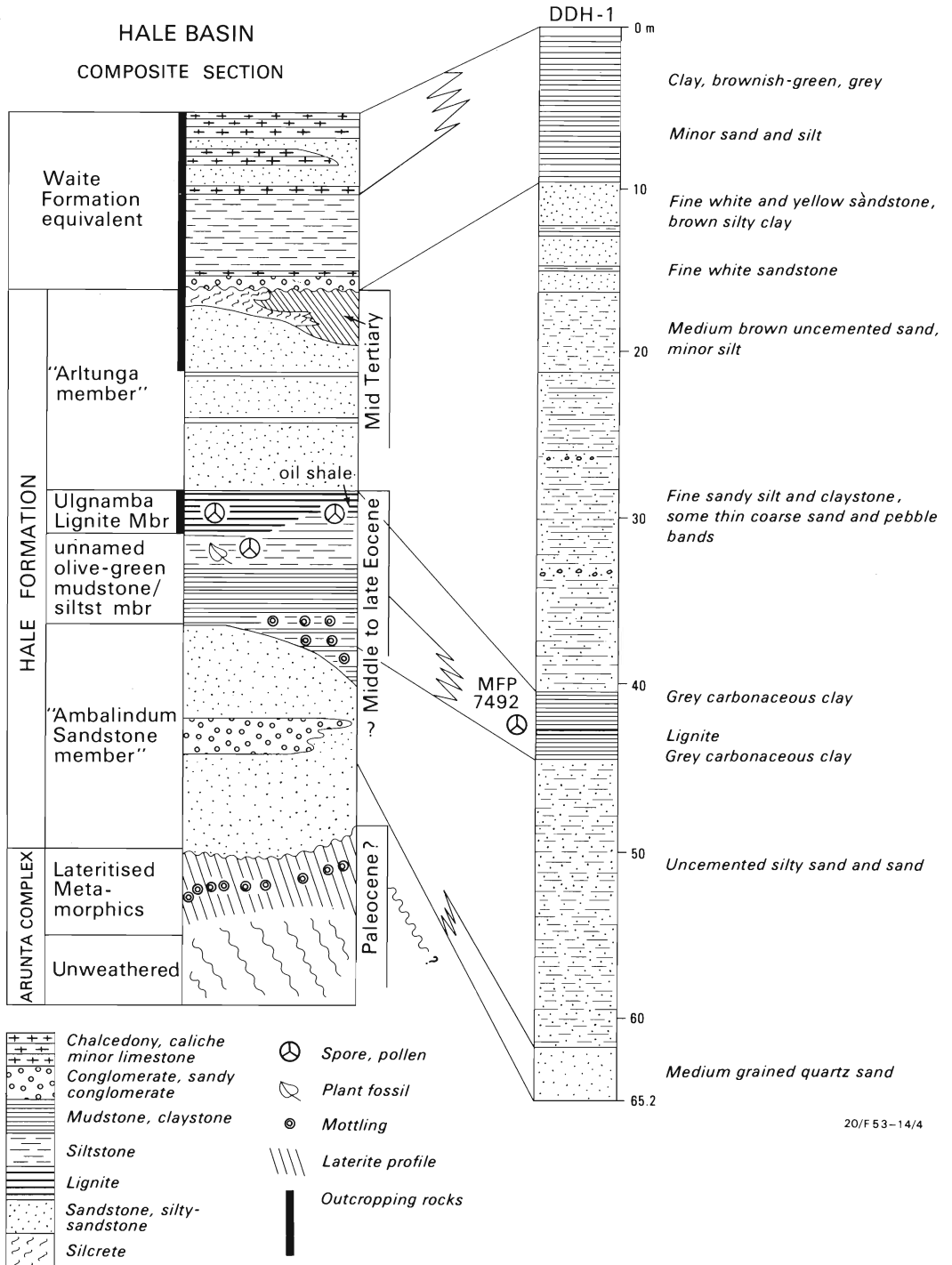
The age of the Ulnamba Lignite

Dating the relatively thin sequences in the Cainozoic basins of inland Australia continues to present a major problem. The difficulties of setting up a time framework within these basins were outlined by Truswell and Harris (1982): the sequences are entirely non-marine, and frequently deeply weathered; there are no intercalated volcanics that would allow radiometric dating; and the sequences are for the most part too thin to permit the use of magnetic reversal stratigraphy as a dating tool. Palaeomagnetism does, however, offer another dating technique that is potentially useful, involving the fitting of palaeomagnetic directions obtained from iron-enriched weathered profiles to the apparent polar wander curve; the latter is derived from the succession of palaeopole positions relative to Australia. This technique, which is still being developed, has been used to establish tentative Palaeocene/Eocene and Miocene ages for deep-weathering profiles in south-west Queensland (Idnurm and Senior 1978).

Palaeontology continues to offer the best potential for establishing a chronology in these small inland basins, and both palynology and fossil vertebrates have already provided broad ages for some sequences (Truswell and Plane 1983). For palynology the major problem is that key biostratigraphic schemes based on the distribution of spores and pollen have been erected only in south-eastern Australia, in the Gippsland and Otway Basins (Stover and Evans 1973; Stover and Partridge 1973; Harris 1971). It is there that Tertiary sequences are thickest and most complete, and the presence of marine sediments has enabled the palynological zones to be independently dated through their relationship with planktic foraminiferal zones. In inland Australia the identification of these coastally based palynological zones is hazardous, as it involves the assumption that the Tertiary vegetation was relatively uniform from the coast to the continental centre, and that the migration of taxa did not involve geologically significant time intervals. Both of these assumptions are open to serious challenge, with the result that the palynological zones defined in the southern coastal basins can only be used very tentatively as dating tools in the small inland basins.

In the Hale River Basin, age limits for the Ulnamba Lignite are cautiously suggested here on the basis of both palaeomagnetic and palynologic data. The Hale Formation is both underlain and overlain by deep-weathering profiles. The climatic event that produced a lateritic profile on the basement Arunta rocks is likely to have occurred in the Late Cretaceous to early Eocene, if the chronology of laterite formation in central Australia is similar to that in the Eromanga Basin of south-west Queensland. The second, younger, weathering event, which affected the top of the Hale Formation, was suggested by Senior (in Shaw *et al.* 1983) to be of late Oligocene age, on the assumption that this event correlated with the younger of the two weathering events in the Eromanga Basin. However, a recent revision of the apparent polar wander curve for Australia (Idnurm, *in press*) has led to increased caution in the interpretation of the age of this younger weathering event. Dr M. Idnurm (*pers. comm.* 1985) now prefers to assign a broader, 'mid-Tertiary' age to this event, suggesting that an Oligo-Miocene age for it is possible. The palaeomagnetic data currently available thus serve only to establish a general early Tertiary age for the Hale Formation and its included Ulnamba Lignite Member.

Palynological dating offers somewhat greater precision—with the qualifications already expressed. The fossil spore and pollen species recorded to date in the Ulnamba Lignite are listed in Table 1. Most species on the list occur with the droseraceous pollen described here from sample MFP7492 in DDH-1 (text-fig. 2); others have been observed during work in progress on the same lignitic interval in other bores penetrating the Hale Plain.



TEXT-FIG. 2. Stratigraphic column for DDH-1, with position of the pollen-rich sample MFP7492 indicated. The lithostratigraphic units in DDH-1 are correlated with a generalized section for the Hale River Basin, compiled by B. R. Senior (in Shaw *et al.* 1982). DDH-1 did not reach basement, but terminated in sands interpreted as Ambalindum Sandstone member. The ages shown next to the composite section are derived from both palynology and from palaeomagnetic dating of deep-weathering profiles.

TABLE 1. List of palynomorphs recovered from the Ulgnamba Lignite in the Hale River Basin. Included are species from DDH-1 and from other boreholes within the basin.

?Bryophytes	<i>M.</i> sp. cf. <i>M. incerta</i> (Thomson and Pflug) Krutzsch
<i>Herkosporites elliotii</i> Stover	<i>Myrtaceidites parvus</i> Cookson and Pike
Pteridophytes	<i>Nothofagidites brachyspinulosus</i> (Cookson) Harris
<i>Gleicheniidites</i> sp.	<i>N. deminutus</i> (Cookson) Stover and Evans
Gymnosperms	<i>N. emarcidus</i> (Cookson) Harris
<i>Araucariacites australis</i> Cookson	<i>N. falcatus</i> (Cookson) Stover and Evans
<i>Dacrycarpites australiensis</i> Cookson and Pike	<i>N. heterus</i> (Cookson) Stover and Evans
<i>Dacrydiiumites florinii</i> Cookson and Pike	<i>N. vansteenisii</i> (Cookson) Stover and Evans
<i>Parvisaccites catastus</i> Partridge	<i>Periporopollenites demarcatus</i> Stover
<i>Podocarpidites ellipticus</i> Cookson	<i>Polycolpites esobalteus</i> McIntyre
<i>Podocarpidites</i> spp.	<i>P. reticulatus</i> Couper
<i>Phyllocladidites</i> sp.	<i>P. oblatu</i> Martin
Angiosperms	<i>Propylipollis annularis</i> (Cookson) Martin and Harris
<i>Arecipites</i> sp.	<i>P. latrobensis</i> (Harris) Martin and Harris
<i>Banksieaidites arcuatus</i> Stover	<i>P. parvus</i> (Cookson) Martin and Harris
<i>Beaupreaidites elegansiformis</i> Cookson	<i>P.</i> sp. cf. <i>P. adenanthoides</i> Cookson
<i>B. verrucosus</i> Cookson	<i>P. confragosus</i> Harris
<i>Cranwellia</i> sp.	<i>P. pachypolus</i> Cookson and Pike
<i>Cupaneidites orthoteichus</i> Cookson and Pike	<i>P. reticulatus</i> Cookson
<i>Cyperaceaeipollis</i> sp.	<i>P.</i> sp. cf. <i>P. sinulatus</i> Dudgeon
<i>Dicotetraidites</i> sp. cf. <i>D. meridionalis</i> (Harris)	<i>Proteacidites</i> spp.
<i>Dilwynites granulatus</i> Harris	<i>Psilodiporites</i> sp. cf. <i>P. redundantis</i> Gonzalez Guzman
<i>Ericipites</i> sp.	<i>Rhoipites alveolatus</i> (Couper) Pocknall and Crosbie
<i>Echiperiporites</i> sp. (cf. <i>Micrantheum</i>)	<i>Santalumidites cainozoicus</i> Cookson and Pike
<i>Graminidites</i> sp.	<i>Sapotaceoideaepollenites rotundus</i> Harris
cf. Gyrostemonaceae	<i>Sparganiaceaeipollenites</i> spp.
<i>Haloragacidites harrisi</i> (Couper) Harris	<i>Tetracolporites</i> sp.
<i>Ilexpollenites</i> sp.	<i>Tricolpites reticulatus</i> Cookson
<i>Liliacidites</i> spp.	<i>Tricolporites paenestriatus</i> Stover
<i>Malvacipollis diversus</i> Harris	<i>Tricolporites</i> spp.
<i>M. subtilis</i> Stover	<i>Triporopollenites</i> sp. cf. <i>T. ambiguus</i> Stover
<i>Milfordia</i> sp. cf. <i>M. homeopunctata</i> (McIntyre) Partridge	

Most of the species shown are long-ranging in the Australian Tertiary. A few, however, have restricted stratigraphic ranges in the sedimentary basins of the south coast.

In its general aspect, with an abundance and diversity of *Nothofagidites* pollen, together with a diversity of form among triporate pollen grains of probable proteaceous affinity, the Ulgnamba Lignite assemblage resembles Eocene pollen suites from south-eastern Australia. In terms of established palynological zones the strongest correlation appears to be with the middle part of the *N. asperus* Zone of the Gippsland Basin (Stover and Partridge 1973, 1982; Partridge 1976), which spans the middle to late Eocene boundary. The suggested correlation rests on such species as *Polycolpites reticulatus* Couper, which in the Gippsland Basin does not appear before the base of the Middle *N. asperus* Zone; and on *Propylipollis latrobensis* (Harris) Martin and Harris, *Proteacidites confragosus* Harris, *P. reticulatus* Cookson, and *Santalumidites cainozoicus* Cookson and Pike, none of which is found above the Middle *N. asperus* Zone in south-eastern Australia. *P. pachypolus* Cookson and Pike was also listed (Stover and Partridge 1973) among species which terminated their ranges within the Middle *N. asperus* Zone; more recent work (summarized in Truswell *et al.* 1985) has shown that this species in fact extends upwards into the Miocene. The list of forms with restricted ranges remains short, and, given the possibility that ranges may differ in inland localities, we hesitate to stress too precise a correlation with southern biozones. A generalized middle to late Eocene age for the Ulgnamba Lignite does however seem acceptable on the basis of the available data.

The only species apparently at odds with such an age assignment is a type comparable with pollen of the fireweed family Gyrostemonaceae; these tricolporate grains with apparently homogeneous exine have not been reported from south-eastern Australia before the mid-Oligocene. Records are confined, however, to one report from the Latrobe Valley (Luly *et al.* 1980) and one from the western Murray Basin (Truswell *et al.* 1985), so that the total range of the form is not fully understood. Periporate pollen types comparable to pollen

of extant *Micrantheum* (Euphorbiaceae) are also unreported before the mid-Oligocene in south-eastern Australia, but again, records are few, and an extension into older sediments is not unreasonable. The form genus *Cyperaceae*pollis has not been reported from south-eastern Australia before the Miocene, but in coastal south Australia it is clearly present in the middle Eocene (Harris *in* Martin 1978); its presence in the middle to late Eocene of central Australia is in line with the time of appearance of the distinctive pseudomonads in Europe (Muller 1981).

PALAEOECOLOGY

Counts of relative frequencies of the major pollen types in the Ulnamba Lignite and the clays underlying it are presently being undertaken for a number of boreholes in the Hale River Basin. Until this work is completed, only generalizations can be made concerning the composition of Eocene plant communities in the area and their palaeoclimatic significance.

Pollen spectra from the Ulnamba Lignite are distinguished by the co-dominance of species of *Nothofagidites* and *Haloragacidites harrisii*, the latter being almost certainly pollen of Casuarinaceae. The *Nothofagidites* pollen consists mainly of the *N. brassi* morphotype, which is today produced by evergreen rainforest taxa growing in highland New Guinea and in New Caledonia. In lesser frequencies are pollen of *Podocarpus*, *Dacrydium*, and *Dacrycarpus*. The inaperturate grains of Araucariaceae occur only rarely. Among the angiosperms, apart from southern beech pollen and Casuarinaceae, there is a diversity of triporate forms of possible proteaceous affinity. Products of the emergent aquatics, Sparganiaceae and Cyperaceae, are locally common. So too are monoporate grains suggestive of Restionaceae, but these could equally well represent pollen of the rainforest family Flagellariaceae. In contrast to most coeval assemblages from southern Australian localities, pollen of Myrtaceae is very rare in the Hale River assemblages. Rare too are fern and bryophyte spores; those ferns represented mainly belong to the Gleicheniaceae.

Residues from sample MFP7492 contain an abundance of *Botryococcus*, rare non-marine dinoflagellate cysts and resting spores of Zygnemataceae, suggesting that deposition at the site occurred under open water conditions in a swamp or lake. Accumulated information concerning the pollen dispersal characteristics of the major extant taxa which are represented in the Australian Tertiary (Luly *et al.* 1980; Sluiter 1984) allows some speculation about possible plant community structure in the area. The Sparganiaceae, Cyperaceae, and perhaps Restionaceae may reflect swamp margin vegetation on the edge of open water. This seems likely also to have been the habitat of the droseraceous parent plants, whose pollen probably had a strictly local distribution. *Gleichenia* may have formed a scrambling ground cover in this zone, or in the forests on higher ground. Pollen of Casuarinaceae, the podocarps, and *Nothofagus* would have been regionally rather than locally distributed. The Casuarinaceae may have been part of the swamp margin vegetation, or have grown on higher ground; the beech and podocarp forests seem likely to have occupied well-drained soils at some distance from the water's edge.

The presence of such mixed forests suggests a high rainfall, with precipitation distributed evenly throughout the year. By analogy with present New Guinea forests, some authors (e.g. Martin 1973) have suggested that a preponderance of *Nothofagus* type pollen is indicative of rainfall of 1500 to 1800 mm per year. Others, such as Luly *et al.* (1980) have cautioned against such direct extrapolation of modern climatic tolerances, noting that the present distribution of rainforest taxa in Australia is determined by complex factors including competition and recurrent stress during Quaternary climatic fluctuations. While it seems likely that the central Australian region was dramatically wetter in the Eocene than it is now (Kemp 1978), with moisture available all year-round, there are some aspects of the pollen spectrum which suggest that this region may have been drier than coeval coastal localities. There is for instance a very low representation of myrtaceous pollen. Much of that present in early Tertiary suites suggests rainforest Myrtaceae, so its near absence from the Hale River Basin may reflect less complex rainforests there. The low frequency of fern spores may also indicate relatively xeric conditions.

MATERIAL AND METHODS

Preparation of the material for palynological examination was carried out using standard techniques. All slides for light microscopy were made with glycerine jelly. The holotype and figured specimens are held in the type collection of the Bureau of Mineral Resources, Canberra, and are prefixed CPC (Commonwealth Palaeontological Collection). Gold-coated specimens examined with the JEOL-JSM2 Scanning Electron Microscope are also held in the collection. Co-ordinates given are for Leitz Orthoplan microscope no. 895191.

SYSTEMATIC PALAEOLOGY

Earlier workers in Tertiary palynology approached problems of taxonomy and nomenclature in a variety of ways. Some used extant genera to accommodate fossil pollen, others used purely morphographic, artificial taxa, while others again used rather arbitrary combinations of the two approaches. These diverse practices have resulted in nomenclatural instability and a failure to achieve a high resolution stratigraphy. To counter these effects, a number of workers in the past decade have advocated or applied new procedures in systematic palaeontology. Hughes's (1975 and earlier) system of 'biorecords' was designed to produce a more finely focussed biostratigraphy and so dispensed with conventional binomial nomenclature and type specimens, which, it was alleged with some justification, had failed to serve stratigraphy. A variant of this system, using informally named morphographic groups at the level of sub-genus, was applied by Wilkinson and Boulter (1980) to solve correlation problems in Oligocene sediments in Britain.

While we have some sympathy for these views, especially as they encourage finer resolution in palynological stratigraphy, we have adhered here to conventional binomial nomenclature, with its attendant type specimens. The purpose of this report is to describe fossil material which may bear on the history of a living plant group, therefore a more formal palaeontological description should, we feel, make this information more readily accessible to taxonomic botanists. Further, the use of such formal nomenclature, provided that it is supported by adequate material from a clearly defined stratigraphic interval, should in no way restrict the stratigraphic usefulness of the material described.

Genus FISCHERIPOLLIS Krutzsch 1970

Type species. Fischeripollis undulatus Krutzsch 1970

Fischeripollis halensis Truswell and Marchant sp. nov.

Plate 27, figs. 1-14; Plate 28, figs. 1-6

Diagnosis. Pollen grains united in tetrads or dispersed singly. Individual grains radially symmetrical, anisopolar, with a strongly arched distal face and a flattened, pyramidal proximal face. Each grain with 10-15 large apertures in a ring proximally situated with respect to the grain equator. Apertures circular to oval, 5-7 μm in diameter, and 5-8 μm apart. Up to 5 additional circular to oval apertures usually present on the proximal face of the grains, when this is visible in specimens freed from the tetrad. Exine intact and obscurely stratified, much thicker on the distal face than on the proximal. Exine is 2-3 μm thick distally, with nexine approximately twice as thick as sexine. Sexine surface with processes of two sizes: the smaller elements, which form a lower level sculpture, are densely packed grana or conia 0.5-1.0 μm in basal diameter and height; the larger elements are spinae or, more rarely, clavae. Larger elements 2-3 μm high, 0.6-1.0 μm in basal diameter, and tapering gently to a blunt point. Some are club-shaped, with their widest diameter about midway up the height of the process. Many elements bent or reflexed. Larger processes are scattered irregularly on the distal face, 2-4 μm apart, rarely present on the proximal face, but irregular granulate elements are usually present on the proximal face and between the apertures in the proximo-equatorial ring.

Dimensions. Tetrad diameter 40 (41) 43 μm ; individual grains 24 (27) 32 μm . Based on 15 specimens from Sample MFP7492.

Holotype. Sample MFP7492/2, 42.1, 100.0 (Plate 27, figs. 1–3). Single grain, orientated proximo-distally. Thirteen or 14 oval to circular apertures in proximo-equatorial ring. Central region of proximal face missing. Exine 2.0 μm thick. Major sculptural elements are spinae, up to 5.5 μm long. Some elements are club-shaped.

Type locality. Northern Territory Geological Survey corehole DDH-1, Hale River Basin, Northern Territory, Australia. Ulgamba Lignite Member of Hale Formation at 42.2 m., middle to late Eocene.

Remarks. Specimens assigned here to *Fischeripollis* show constancy in their basic morphology, but a range of variation in detail. In the sculpture of the exine, there is variation in the density and shape of the larger processes on the distal face and also in the number of apertures present on the proximal face; some specimens have only a single, roughly central pore, while others have as many as five pores.

Assignment to *Fischeripollis* rests on the presence of a subequatorial ring of large pores, and on the relatively thick wall with its sculpture of spinae and grana. The clear absence of any radially disposed ridges on the proximal face precludes assignment to the superficially similar genus *Droserapollis*. The type species, *F. undulatus* is the only fossil species previously described. The Australian species differs from the type species in several respects; it is smaller, thinner-walled, and bears apertures on the proximal face in addition to those in the proximo-equatorial ring; the sculptural elements differ too in that in the Australian species the larger elements are spinae or clavae, in contrast to the broader-based, sturdy conae evident in the type species.

A species of *Fischeripollis* reported by W. K. Harris (pers. comm. 1985) from the Palaeocene to Eocene Eyre Formation of the Frome Embayment in South Australia, differs from *F. halensis*. It is larger and thicker-walled, and has fewer apertures; these are disposed so that the openings of adjoining individuals in the tetrad are opposite, forming large apertures which are continuous from grain to grain. It has not been possible to discern pores on the proximal face. *F. halensis* similarly differs from specimens of *Fischeripollis* from the Gippsland and Otway Basins provided by A. D. Partridge. These have fewer apertures and shorter, spinose processes. All were observed in tetrads, and no proximal apertures could be detected.

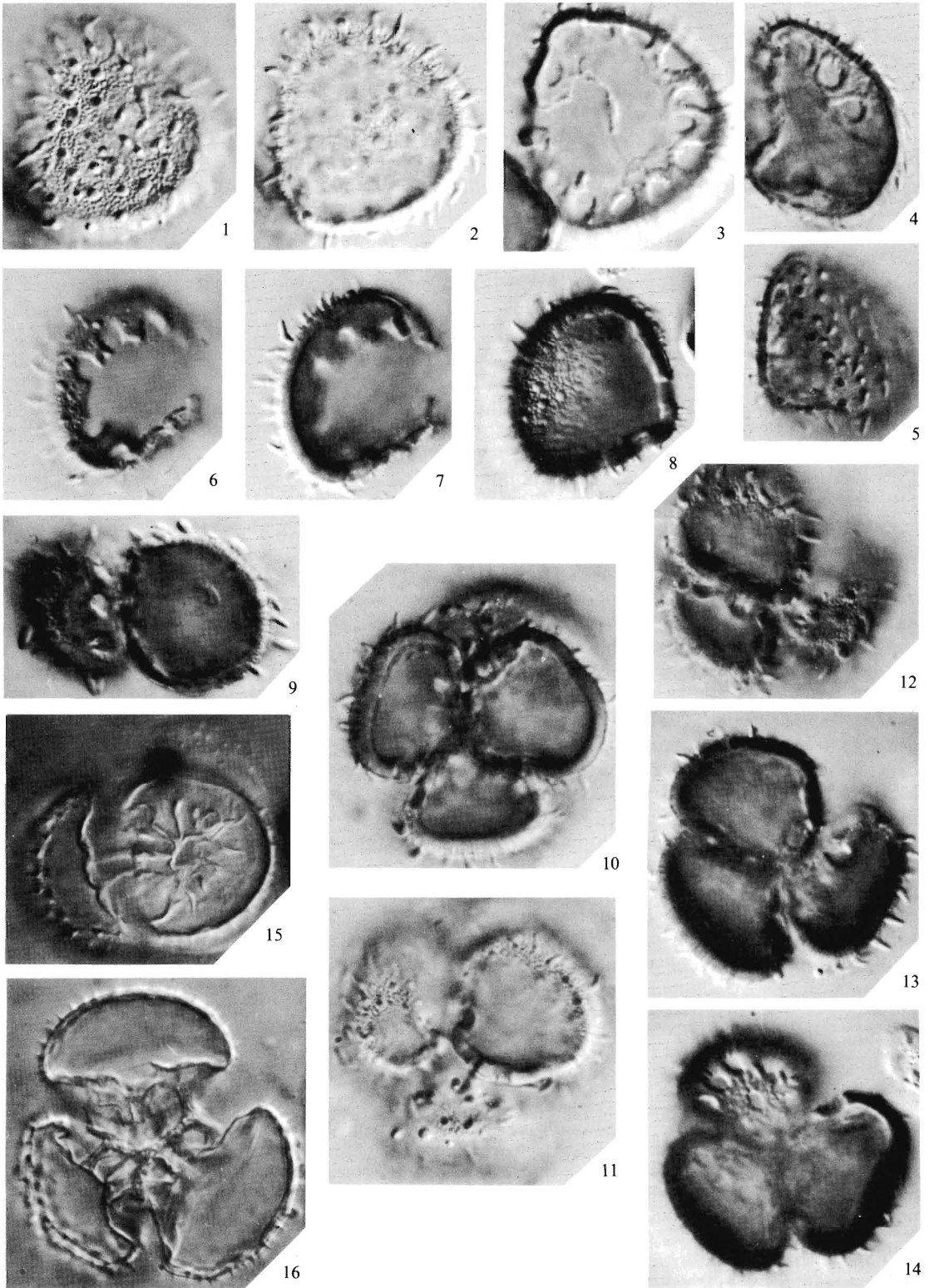
AFFINITY OF THE FOSSIL POLLEN

Hughes (1976, 1977) has constantly warned of the dangers of 'backwards systematics'—of pushing backwards in time taxonomic concepts which rest on a morphological base defined in the present time-plane. The recognition of a modern group—at family level for instance—in the early Tertiary, strictly interpreted, implies the presence then of the same complex of characters that delineate the group today. Such can rarely be established on the basis of fossil evidence. Moreover, to infer the presence of the same character complex some 40 or 59 million years ago would be to deny evolutionary process. In most instances where modern taxa have been identified in the fossil record, the

EXPLANATION OF PLATE 27

Figs. 1–14. *Fischeripollis halensis* Truswell and Marchant sp. nov. All specimens from Preparation MFP7492, 42.2 m in Corehole DDH-1, Hale River Basin. Magnifications $\times 1000$. 1–3, holotype, CPC25537, 7492/3:42.1, 100.0. Focus on distal, equatorial, and proximal grain surfaces. 4 and 5, CPC25538, 7492/4:107.3, 40.0. Proximal and distal foci. 6–8, CPC25539, 7492/4:101.1, 42.0. Proximal, median, and distal foci, much of proximal face missing. 9, CPC25542, 7492/4:95.6, 32.2. Part of tetrad with two grains remaining, one in proximal view. 10 and 11, CPC25541, 7492/3:29.4, 92.3. Tetrad with proximal and distal foci. 12–14, CPC25540, 7492/4:111.5, 39.1. Tetrad showing distal focus on three grains, median focus, then proximal focus on one grain showing proximal apertures.

Figs. 15 and 16. Pollen grains of *Drosera indica* L., West Australian Herbarium no. 9682. Coll. C. A. Gardner. Light micrographs, interference contrast. Magnifications $\times 1000$. 15, high focus on one grain of tetrad, showing radial folds or plaits of proximal exine in plan view. 16, tetrad in optical section showing confluent distal and proximal compartments of individual grains: proximal folds and line of junction between adjoining grains clear.



TRUSWELL and MARCHANT, *Fischeripollis*, *Drosera*

identification has been made on the evidence of a single organ, usually pollen, more rarely fruits and seeds. In the face of inevitably incomplete fossil data, the best working hypothesis, and the one which we have adopted here, is to regard fossil pollen which is similar to that produced by a living taxon as suggestive only of the presence of the lineage which gave rise to the modern group.

As Muller (1981) has pointed out, the probability that a fossil pollen represents a certain taxon increases in relation to its degree of specialization. The pollen of living Droseraceae is a case of extreme specialization. The pollen morphology, at least of three of the four genera in the family, is unique, particularly with respect to the form and position of the apertures and their relation to the retention of the grains in tetrads at dispersal.

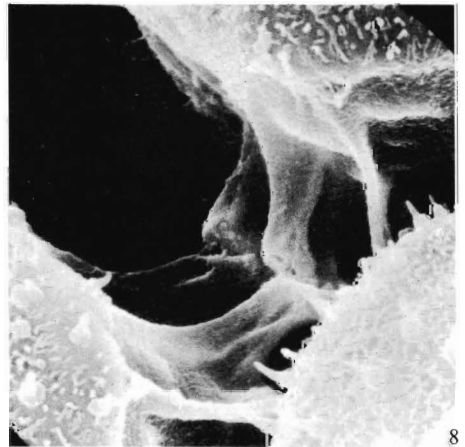
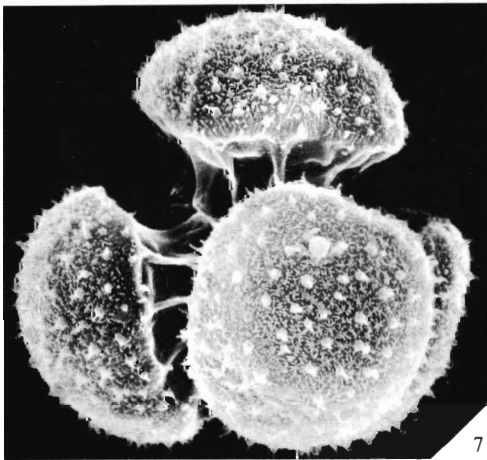
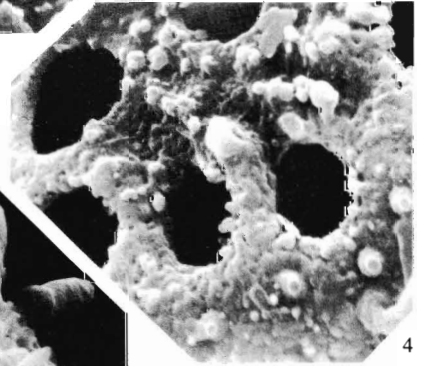
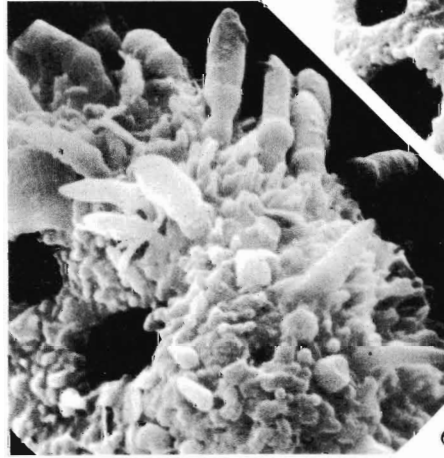
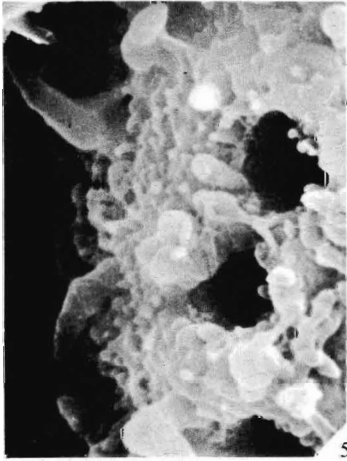
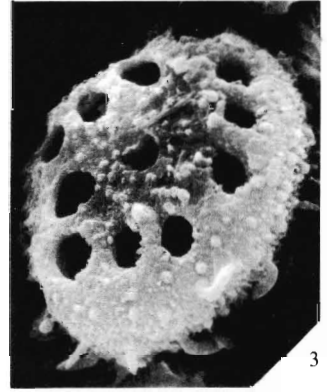
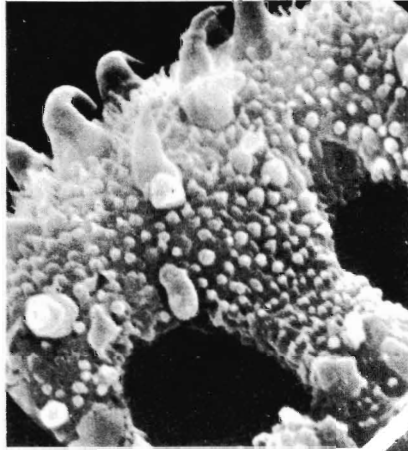
Pollen of Droseraceae was described, at least in part, as long ago as the 1830s; the earlier literature is reviewed by Jones (1964) and Chanda (1965). In spite of this early beginning, there are as yet no comprehensive descriptions of pollen types in the family, and few studies of pollen ultrastructure or development. It was long considered (e.g. in Wodehouse 1935), that pollen in Droseraceae was always shed in tetrads. From more recent studies (Erdtman 1952; Chanda 1965) it is apparent that dispersal as tetrads occurs in *Drosera*, *Dionaea*, and *Aldrovanda*, but not in *Drosophyllum*, where grains are shed as monads. Although the grains in *Aldrovanda* are retained in tetrads, they differ considerably in their basic morphology from those of *Drosera* and *Dionaea* in that they are essentially tricolpate, with widely gaping colpi with poorly defined margins.

In *Drosera* and *Dionaea* individual pollen grains are strongly anisopolar, and the germinal apertures occur as large, near-circular pores distributed in a ring or rings either close to the grain equator or on a much modified proximal face. Such an arrangement of apertures on anisopolar grains is unique to this family. In this paper we have illustrated *Drosera* pollen by reference to two of the species which now grow in central Australia, *D. indica* and *D. petiolaris*. In *Drosera* the grains are divided into two distinct sections, or confluent compartments. The distal, larger section, the 'main body' of the grain, is strongly convex, with a relatively thick ornamented exine. The proximal face of the grain is pyramidal, with a thinner, unornamented exine which is thrown into a series of radially aligned folds or 'plaits', arranged to form a system of hollow channels. The visible pores, which occur in one or more rows, (Pl. 28, figs. 7 and 8; Pl. 29, figs. 2 and 3) are in fact the external openings of these channel-like structures. The folds converge on an opening or larger pore at the proximal centre of the grain as shown in disassociated grains of *D. indica* (Pl. 29, fig. 1). Accounts of the structure and development of *Drosera* pollen have been given by Jones (1964) and Kuprianova (1973); the latter paper clearly shows the microstructure of the grain walls. From these accounts it appears that, at maturity, the cytoplasmic contents fill the 'upper' or distal cavities of the grains, and pass out through the central pore and the radiating channels with their pore-like openings, to protrude at the grain surface. The cytoplasmic protrusions or arms are covered with a layer of intine (Kuprianova 1973, pl. 2, figs. 7 and 8). In each grain a single cytoplasmic arm or papilla gives rise to a pollen tube. The protrusion of arms of cytoplasm from the pores of all grains forms an aggregate mass in the grooves between the grains in the centre of the tetrad; it is this mass which controls volume changes in response to hydration. The whole tetrad in *Drosera* thus functions as a harmomegathus, taking over the function of water-loss control usually performed by the furrows or pores of individual pollen grains.

EXPLANATION OF PLATE 28

Figs. 1–6. *Fischeripollis halensis* Truswell and Marchant sp. nov. SEMs. 1 and 2, 7492/SEM 5. 1, single grain showing apertures in proximo-equatorial ring and on the proximal face, $\times 1550$; 2, detail of exine surface, $\times 5300$. 3 and 4, 7492/SEM 3. Proximal face of grain showing proximo-equatorial and proximal apertures. 3, $\times 1740$; 4, enlarged to show grana and coni between the apertures on the proximal face, $\times 4000$. 5, 7492/SEM 3. Detail of a specimen showing intectate wall in section at apertures. 6, 7492/SEM 5. Detail of proximal and equatorial region on a specimen in which club-shaped processes predominate, $\times 4000$.

Figs. 7 and 8. Pollen grains of *Drosera indica* L., West Australian Herbarium no. 9682. Coll. C. A. Gardner. SEMs. 7, tetrad, showing distal sculpture and exine folds in proximal region, with apertures formed by the open ends of the exine folds or channels. $\times 1340$. 8, detail of proximal region between adjacent grains, $\times 3600$.



In *Dionaea*, as represented by its single extant species *D. muscipula* Ell., there is no division of individual pollen grains into distinct sections. The proximal region of exinal folding and channel formation which characterizes *Drosera* is absent and the germinal apertures penetrate directly into the body of the grain (Pl. 29, figs. 6-8). The apertures which, like those of *Drosera*, are large in relation to the grain diameter, occur in a ring proximally situated with respect to the grain equator. The ornament which characterizes the distal exine continues across the equator into the germinal area of the grains.

From the above, we are reasonably confident in deducing that the fossil pollen described here reflects, if not Droseraceae in its modern guise, at least the ancestral line of that family. Within that lineage, we are less confident in assigning relationship to a living genus. However, the fossil form clearly has a much greater resemblance to pollen of *Dionaea* than to that of other living members of the family. The similarity is evident in the proximo-equatorial ring of apertures which penetrate the main body of the pollen grain, and are not associated with infolding and channel formation on the proximal face as in *Drosera*. While showing a basic morphological similarity to pollen of *Dionaea* the fossil species *F. halensis* differs in detail from pollen of living *D. muscipula*. In *D. muscipula* (Pl. 29, figs. 4-8) there are no pores visible on the proximal face of individual grains; the walls are much thicker than in *F. halensis*, and they bear short, sturdy conae rather than slender spinae and clavae.

Pollen of *Nepenthes* (Nepenthaceae), a genus which is represented today in tropical Australia, is very similar to that of Droseraceae, especially *Drosera*; it is shed in tetrads, and has a spinose exine. It differs, however, in being inaperturate, or obscurely aperturate (Basak and Subramanyam 1966). In addition, pollen grains of *Nepenthes* are thin walled, and hence not closely similar to the fossil described here.

PREVIOUS FOSSIL RECORDS OF DROSERACEAE

The known fossil record of the Droseraceae, as evident from pollen records, was summarized by Muller (1981). The oldest records previously published are those of tetrads closely resembling *Aldrovanda*. Krutzsch (1970) described such forms as *Saxonipollis saxonicus* when he recovered them from the Early and Late Eocene of Germany, while Kondratjev (1973) reported the same basic type as *A. kuprianovae* and *A. unica* from the Eocene of the USSR. *Aldrovanda* is the only genus for which a macrofossil record is available. Seeds from the Lower Headon Beds (probably Late Eocene) in the Hampshire Basin of southern England were first described by Chandler (1925) as *Nuphar ovatum*; subsequently, these were reassigned as *A. ovata* by Reid and Chandler (1926). These latter authors also added another seed taxon, *A. intermedia*, from seed floras of the Bembridge Beds, which are probably of Oligocene age.

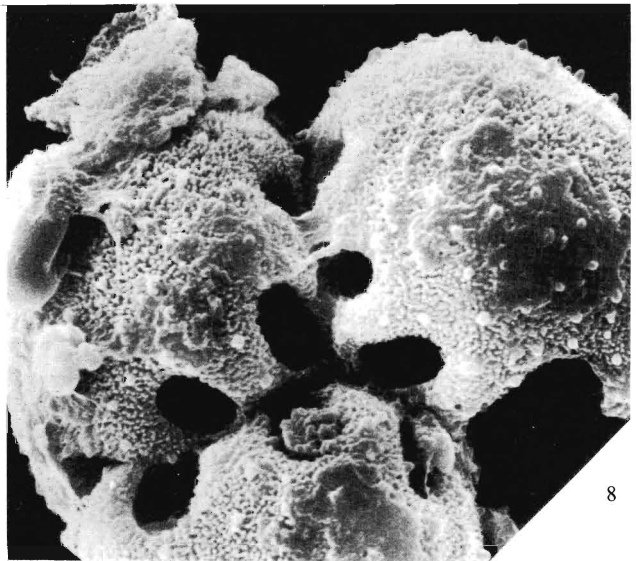
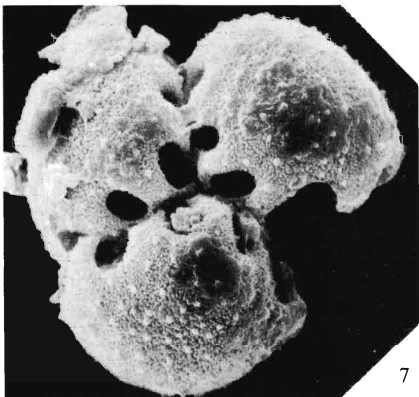
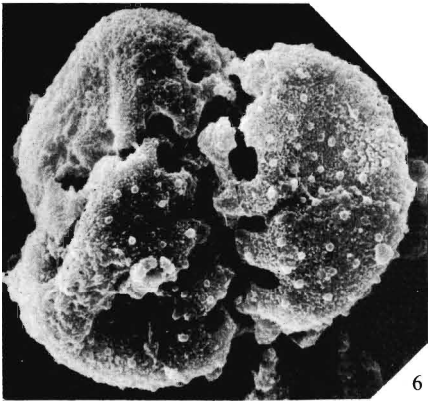
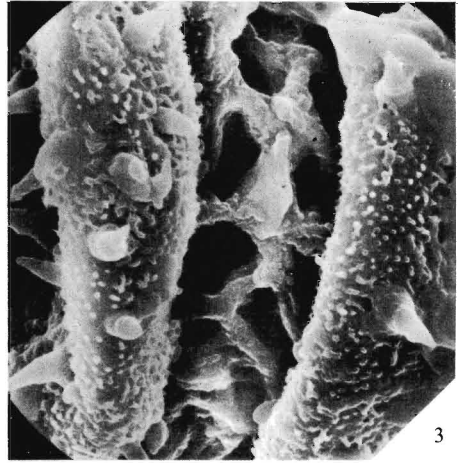
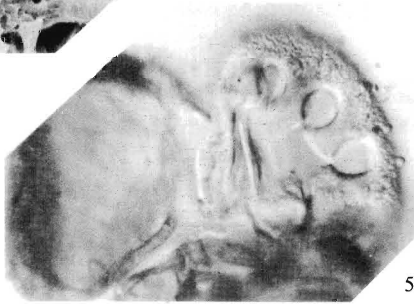
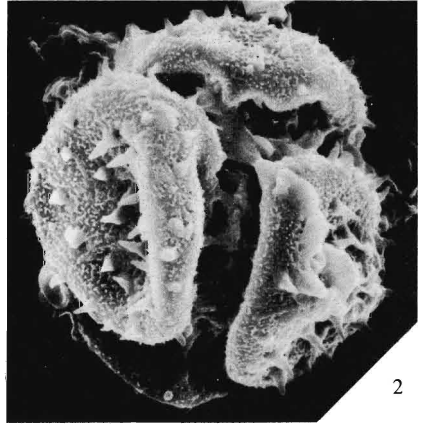
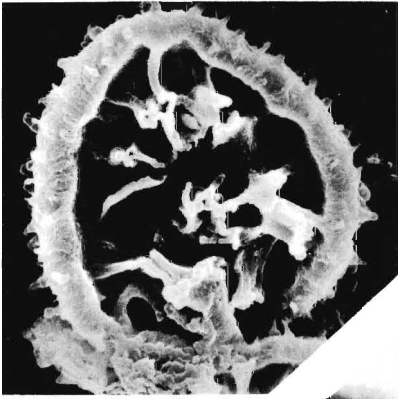
According to published records the oldest occurrence of pollen of the *Drosera* type appears to be that which Mildenhall (1980) reported from the Early Miocene of New Zealand, although this record is not substantiated by illustrations. In Europe, Krutzsch (1970) instituted the form genus

EXPLANATION OF PLATE 29

Fig. 1. *Drosera indica* L. SEM of a grain detached from the tetrad, showing the radial folds forming channels on the proximal exine, and a single (torn) central pore on the proximal face, $\times 1600$.

Figs. 2 and 3. Pollen of *D. petiolaris* R.Br., West Australian Herbarium no. 13676. Coll. A. S. George. SEMs showing proximal region between adjoining grains with rows of apertures representing the ends of channels formed by exine folds. 2, $\times 1480$; 3, $\times 3600$.

Figs. 4-8. Pollen of *Dionaea muscipula* Ell., Department of Botany, Berkeley, California. Coll. R. J. Smith. 4 and 5, light micrographs, $\times 500$. 4, single grain showing wall in optical section, with a thick nexine surmounted by a dense mat of grana and rare coni, $\times 500$. 5, same grain, showing it as part of tetrad, focus on apertures on proximal face. 6, SEM of a tetrad, showing apertures penetrating into main body of grain, $\times 540$. 7 and 8, remains of a tetrad showing three grains proximally united, without modification of the proximal exine into a folded zone. 7, $\times 540$; 8, detail of specimen in fig. 7, $\times 970$.



Droserapollis for tetrads of *Drosera* type which he described from the Miocene and Pliocene of central Europe. Oldest among these is *D. lusaticus* Krutzsch, the type species, which is found in the Middle Miocene of Germany; *D. pliocaenicus* Krutzsch and *D. buchenauensis* Krutzsch are Pliocene forms, reported from Germany and Czechoslovakia. While it is apparent that most species assigned to *Droserapollis* are comparable to pollen of *Drosera*, not all fossil records clearly reflect that genus: Huang's (1978) report of *Droserapollis gemmatus* from the Miocene of Taiwan was considered by Muller (1981) too poorly preserved to be admissible as *Drosera* type pollen.

It is apparent that pollen referable to *Droserapollis* is present in Australian Miocene sediments. Sluiter (1984) figured as 'Droseraceae', a species from the base of the Morwell IA Seam in the Latrobe Valley, Victoria. The morphology of the form is reminiscent of pollen of the extant *Drosera peltata* Thunb.; it occurs in an interval which is probably the Upper *Proteacidites tuberculatus* Zone of Stover and Partridge (1973), of Early Miocene age.

Other published records are less confidently linked with Droseraceae. Cookson (1947) described tetrads of spinose pollen grains from Kerguelen as *Droseridites spinosa*; they were from rich pollen suites in lignites interbedded with volcanics of probable Middle Miocene age. Cookson's illustrations show no germinal apertures, and the nature of the distal wall is uncertain. She was hesitant to assign these fossil forms to *Drosera*, and detailed re-examination of this material is still required before such an affinity can be established. The same applies to other records of tetrads of inaperturate spinose palynomorphs which have been assigned to *Droseridites*. Krutzsch (1970) summarized reports of the genus from European sediments ranging in age from probable Middle Eocene through to Miocene, but was unwilling to suggest an affinity for them. Some records may not even be pollen grains: Krutzsch noted that *D. spinulosus* Manum, from the early Tertiary of Spitzbergen (Manum 1962), is only dubiously referred to that genus as it may be a tetrad of perforate spores. Muller (1981) dismissed as representative of Droseraceae the briefly described species *D. parvus* from the Palaeocene of Assam (Sah and Dutta 1974).

Previous records of pollen bearing a morphological resemblance to that of extant *Dionaea* are confined to Krutzsch's (1970) record from the Middle Miocene of Germany. It was to accommodate this morphotype that Krutzsch erected the genus *Fischeripollis*. During the present study, it became apparent that pollen of the *Fischeripollis* type is well represented in Australian Tertiary deposits, in addition to the species formally described here. All other records are as yet unpublished. From the Palaeocene to Eocene Eyre Formation in the Frome embayment in South Australia, W. K. Harris provided specimens of a species clearly referable to *Fischeripollis*. From south-eastern Australia, A. D. Partridge provided specimens of one or more additional species from the Early Eocene to Pliocene of the Gippsland Basin, and the Eocene of the Otway Basin.

CONCLUSIONS

Evidence now available indicates a long history for Droseraceae in Australia, a history going back to perhaps before the Eocene. The fact that the pollen species *F. halensis*, described in this paper, differs from other, currently undescribed species from Eocene sediments in South Australia and Victoria, suggests that some differentiation of the group had already taken place by the Eocene. Further, the record now available suggests that the history of the group in Australia reflects not only *Drosera*, which is so abundantly represented on this continent today, but in the Eocene included members of the lineage represented by *Dionaea muscipula*, the Venus Fly Trap, which is now confined to the south-eastern United States. Unpublished records show that pollen of the *Drosera* type is present in Early Miocene sediments in Australia, and that the *Dionaea* type, as *Fischeripollis*, persisted until at least the Pliocene, indicating that the two lineages co-existed here during the later Tertiary. The Australian occurrences of *Fischeripollis*, recorded here, together with previously published records from Germany, suggest that members of the *Dionaea* lineage were once spread widely around the world. The fossil evidence is as yet too incomplete to attempt a reconstruction of phylogenetic history within Droseraceae, but the sketchy record available to date hints at the development of the

Aldrovanda and *Dionaea* lineages by at least the Eocene, and the subsequent differentiation of the *Drosera* complex, which has no unequivocal fossil record before the Early Miocene.

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