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1.—Preliminary investigation of the palynology of the Upper Eocene Werillup Formation, Western Australia

by D. Hos¹

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ABSTRACT

A diverse Late Eocene plant microfossil assemblage was recovered from the Werillup Formation (Plantagenet Group) in Werillup No. 17 bore near Albany. The assemblage is composed predominantly of angiosperm pollen, with minor cryptogam and gymnosperm elements.

Common species are *Nothofagidites* spp. (mainly *brassi* group), *Proteacidites* spp., *Haloragacidites harrisi*, *Malvacipollis diversus*, *Myrtacidites* spp., *Tricolporites prolata*, *Cyatidites minor*, and podocarpaceous species.

Most species are long ranging, however, *Proteacidites concretus*, *Cupanieidites reticularis* and *Tripoporipollenites gemmatus* restrict the assemblage to the Eocene and four other species are restricted to the Early Tertiary. Dinoflagellates in the borehole confirm the Late Eocene age determined by invertebrate fossils elsewhere in the Formation.

The following species are recorded for the first time in Western Australia: *Proteacidites concretus* Harris, *P. granulatus* Cookson, *P. reticulatus* Cookson, *P. subscabratus* Couper, *Simpliceipollis scabratus* McIntyre, *Tricolporites microreticulatus* Harris, and *Tripoporipollenites gemmatus* Harris.

The assemblage from the borehole, especially *Beaupreaidites* spp., *Cupanieidites* spp., and *Myrtacidites mesonesus*, suggests a warm and humid climate which is consistent with other palaeoclimatic and palaeomagnetic evidence.

Introduction

A transgressive sequence of fine-grained marine and paralic sediments was deposited on the south coast of Western Australia during the Late Eocene. The sediments compose the Plantagenet Group and contain a diverse fauna and flora that has been confidently dated.

The Plantagenet Group was intersected by a bore Werillup No. 17, drilled by the Geological Survey of Western Australia near Albany, Western Australia, and the samples collected from the sequence were examined palynologically. The aim of this study was to describe and identify the species of spores and pollen in the samples and to determine the distributions and frequencies of each species.

The samples are from the lower part of the basal formation of the Plantagenet Group. They consist of silt, sand and mud, and most have an abundant microflora. The microfloral assemblage from the bore is here related to other microfloras from the Plantagenet Group and Lower Tertiary sediments elsewhere in Australia. The assemblage is also discussed in relation to the Late Eocene climate of the

south coast of Western Australia, the palaeogeography of the region, and the environment of deposition of the sediments.

Stratigraphy of the Plantagenet Group

The stratigraphy of the Plantagenet Group was revised by Cockbain (1968) and a review of the literature is given in his paper. The Group consists of two formations: the Pallinup Siltstone and the underlying Werillup Formation, from which the samples for this study were collected. The distribution of the Group is shown in Fig. 1.

The Werillup Formation is a sequence of dark-coloured paralic siltstone, sandstone, carbonaceous claystone and lignite that has a sporadic distribution in Precambrian basement lows. The transgressive sequence includes basal conglomerates and lignites in places, deltaic and lagoonal sediments and deeper-water siltstones and claystones. Similar lignites are also found at Nornalup, Denmark and Fitzgerald River. The sequence passes up into the Pallinup Siltstone or is unconformably overlain by Quaternary sands.

The bryozoal Nanarup Limestone Member of the Werillup Formation is of restricted lateral extent and highly fossiliferous. It only occurs at Nanarup (about 18 km ENE of Albany) and has been dated by Quilty (1969) as uppermost Eocene.

The Pallinup Siltstone consists of a light-coloured siltstone and spongolite and either conformably overlies the Werillup Formation or onlaps the Precambrian basement. It is up to 60 m thick and outcrops from Walpole to 160 km east of Esperance where it passes laterally into the Toolinna Limestone of the Eucla Basin. Where terrigenous material was negligible and conditions favoured sponges, the sediment became extremely rich in sponge spicules. Lithistid sponges in the sediments indicated the depth of deposition may have been from 20 m to 200 m (de Laubenfels 1953). The same depths when applied to spongolites of similar age and type now occurring 273 m above sea level at Norseman, indicate that the Pallinup Siltstone may have been deposited in depths up to 474 m (Clarke *et al.* 1948).

Palaeontology of the Plantagenet Group

The Werillup Formation has abundant invertebrate remains including gastropods, cephalopods, bivalves, echinoids, sponges, foraminifers and bryozoans. The foraminifers and echinoids have been used to date the sediments

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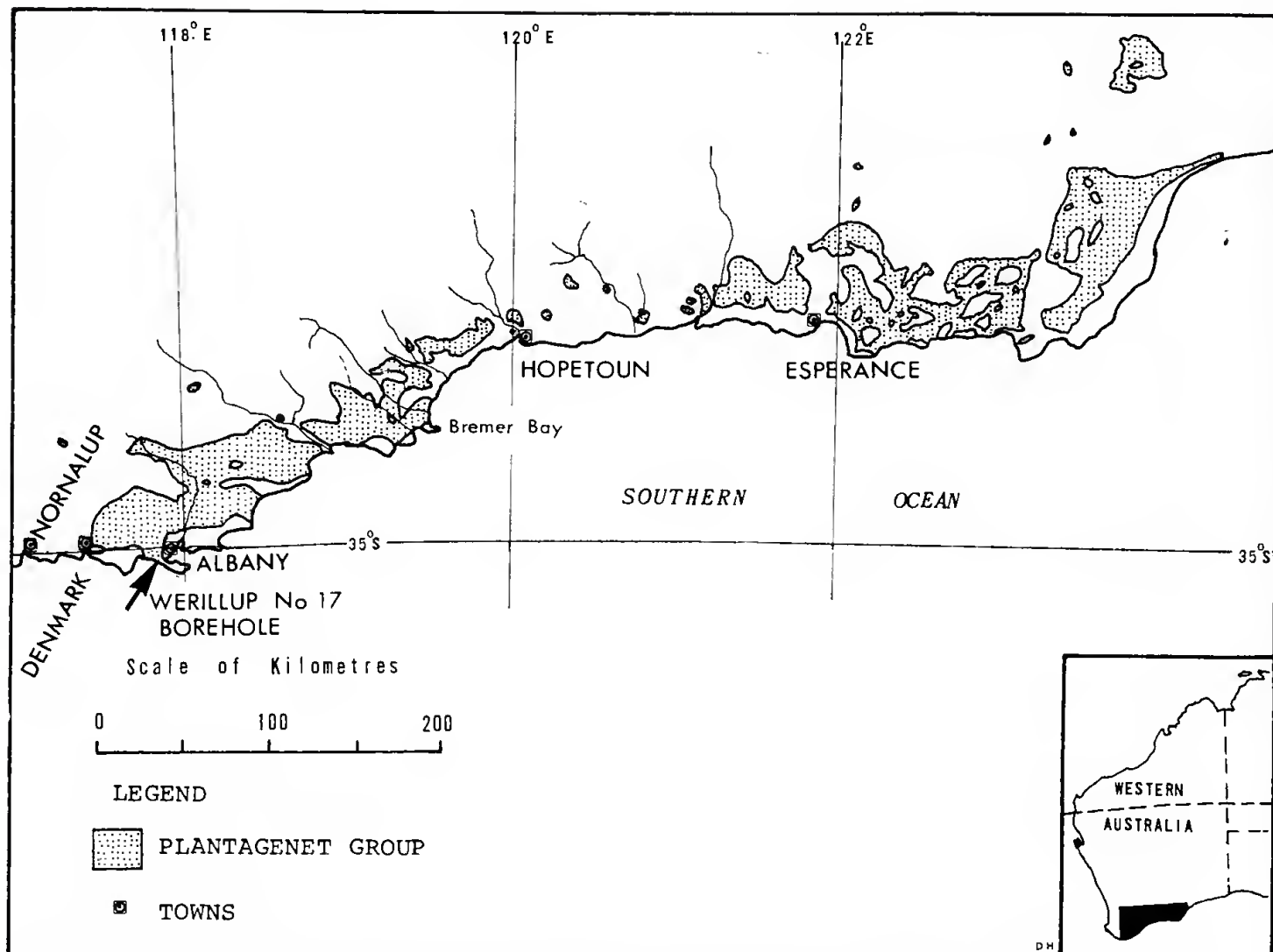


Figure 1.—Map showing location of Werillup No. 17 borehole and the distribution of the Plantagenet Group.

as Late Eocene (Quilty 1969); and *Asterocyclina* from the formation has been used as a warm-water indicator (Cockbain 1967). Cockbain (1969) recorded remains of dasycladacean algae in the Werillup Formation near Esperance which also indicated warm tropical waters.

The Kojonup Sandstone (Churchill *in* McWhae *et al.* 1958) was correlated with the Plantagenet Group and contains leaves and wood of *Nothofagus*, *Banksia* and *Araucaria*, a frond of *Gleichenia*, leaves of Moraceae, Proteaceae, a palm, and an unidentified monocotyledon.

The Pallinup Siltstone has a poorly preserved fauna of molluscs, sponges and bryozoans. Nautiloids and foraminifers are rare but both suggest a Late Eocene age (Cockbain 1968). Chapman & Crespin (1934) described leaf and wood impressions of *Agathis*, *Nothofagus* and *Bombax* from sediments considered to be part of the Pallinup Siltstone at Cape Riche (Cockbain 1968). Silicified coniferalean and proteaceous wood that is probably weathered from the Plantagenet Group is common along the south coast (Balme *in de* Jersey 1968).

Palynological work from the Lower Tertiary of Western Australia was reviewed by Balme

(*in de* Jersey 1968) and no further contributions have been published since then.

The earliest work on material from the Plantagenet Group is by Cookson (1953), who recorded *Phyllocladidites* (*Dacrydiumites*) *mawsonii* from the Group. Cookson & Pike (1953a, b, 1954a, b) recorded and described several new species from the same material. Cookson (1954b) listed all the species that had been recorded from the samples and she was able to relate the assemblage to 'Microflora C' from No. 1 Bore, Birregurra in Victoria (Cookson 1954a). The assemblage was also similar to Late Eocene microfloras from New Zealand (Couper 1953). Further records of species of *Nothofagidites* in the Plantagenet Group were given by Cookson (1954b). The assemblage reinforced plant macrofossil evidence of a pan-Australian Early Tertiary flora that had a tropical aspect (Burbidge 1960).

A Late Eocene microflora from sediments in bores and deep leads at Coolgardie was described by Balme & Churchill (1959), and on the basis of this microflora the sediments were correlated with the Plantagenet Group. The Coolgardie sediments were further examined by Churchill (1962, unpublished), who also de-

scribed the microfloras from lignites at Esperance and Norseman, and samples from Albany Bore No. 6 (near Lake Murrillup, north of the Stirling Ranges).

Upper Eocene plant microfossil assemblages from the Plantagenet Group in the Albany area were examined by Ingram (in Cockbain 1968) and similar microfloras have been found in other bores in the Albany area by the Geological Survey of Western Australia (unpublished reports).

Material

The material on which this study is based consists of 17 sludge samples from Werillup No. 17, a water bore which is located about 9.5 km west of Albany townsite at 35°02'05"S latitude and 117°48'20"E longitude (Fig. 1). The bore was drilled by the Geological Survey of Western Australia to a depth of 61.9 m. from an elevation of about 12 m above sea level. Werillup No. 17 is one of a series of bores that are named after a nearby trigonometrical station.

Werillup No 17 was drilled by a percussion rig in 1968 and sludge samples were generally collected at 3 m intervals. The lithology of the

bore and the location of the samples down the hole is shown in Fig. 2. The top 15 m of the hole consists of Quaternary quartz aeolianite and this has not been examined palynologically.

From 16.8 m to 49.4 m the strata consist of dark coloured silts and silty sands, and from 49.4 m to 61 m of kaolinitic clay. The bottom 0.9 m of the hole was logged as weathered granite and the bore ended in granite.

Ingram (1969, unpublished report) reported Gramineae and Compositae pollen in samples from 16.8 m to 18.9 m, but these may be modern contaminants. The white clay from 49.4 m to the bottom of the hole can be interpreted as weathered granite; however, as it contains a microflora that does not differ greatly from samples higher up the bore, it is considered to be a sediment. Thus, from 16.8 m to 61 m the sediments are interpreted as belonging to the Werillup Formation.

Palynological techniques

The technique used to macerate and concentrate the acid-insoluble microfossils was a modified hydrofluoric acid—Schultze's solution—alkali technique similar to that outlined in

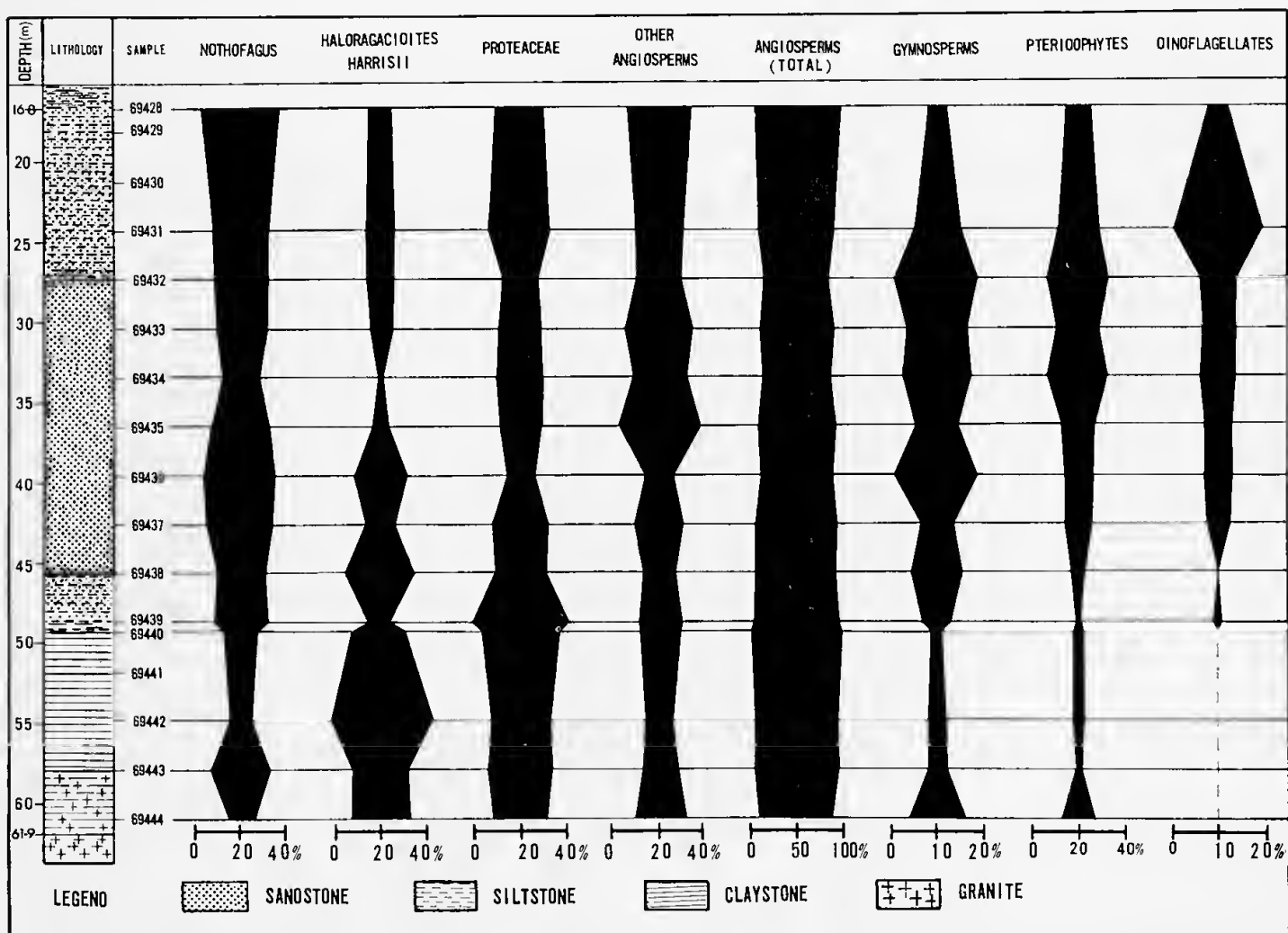


Figure 2.—Diagram showing sample depth and lithology in Werillup No. 17 borehole and the distribution of the pollen and spores of the major plant groups. The dinoflagellates are shown as a percentage of the total number of spores and pollen.

Balme & Hassell (1962). Further concentration was effected by heavy liquid separation in a zinc chloride solution of specific gravity 2.0.

Permanent strew mounts were prepared from each residue by smearing a drop of the residue on a cover slip with Clearcol (a mounting medium, H. W. Clark, Melrose, Mass., U.S.A.). The spores and pollen are able to settle in favourable orientations close to the coverslip while it is left to dry.

The cover slip was then fixed to a slide with a drop of Xam (G. T. Gurr Ltd, London). Single grain mounts of some of the species were prepared by placing the specimens in glycerine jelly under a cover slip sealed with beeswax.

The residues contained, with few exceptions, large numbers of spores, pollen and other acid-insoluble plant remains. Algal (dinoflagellate) cysts and reworked spores occurred in some samples.

Species counts were made for all except three samples which were practically barren of spores and pollen. Most samples required three or more slides to be counted to give a representative number of grains (usually about 100). The total pollen content was not determined as the samples are a sludge that may have resulted from the mixing of highly contrasting lithologies. Also, the samples may have been contaminated from higher up in the borehole (discussed below).

All samples, residues and slides used in this study are stored in collections of the Department of Geology, University of Western Australia, and all numbers given to slides and samples are from the general catalogue of the Department of Geology. The location coordinates cited in the text after the slide numbers for each specimen refer to the stage of Reichert microscope, No 256,251. A reference slide with a located point is included in the slide collection. The specimens were photographed using a Leitz Orthoplan microscope and a Leitz Orthophot camera body.

Composition and age of the microflora

Most of the spores and pollen found in the Werillup samples can be referred to previously described species and these are listed in Table 1. However, there are some species that do not appear to have been previously described or are slightly different from existing species, and these are listed in Table 2. Unfortunately, these species are too rare to determine the significance of the differences; or to warrant detailed description at present.

The microflora in Werillup No 17 was extracted from sediments that have been previously placed in the Upper Eocene Werillup Formation (Cockbain 1968). The sediments appear to be no younger than this, as the following species (see Table 1) are restricted

Table 1

List of previously described species found in Werillup No. 17 borehole. Ranges shown are those given in the literature for the species in southern Australia and New Zealand.

SPORE-POLLEN SPECIES (ALPHABETICAL LISTING)	FIGURES	LATE CRETACEOUS	PALEOCENE	EOCENE	OLIGOCENE	MIOCENE	PLIOCENE	QUATERNARY	SPORE-POLLEN SPECIES (STRATIGRAPHICAL LISTING)
26. <i>Banckseidites minimus</i>	27	1							<i>C. clavus</i>
36. <i>Beaupreaidites elegansiformis</i>	3	2							<i>Cycadopites</i> sp.
12. <i>Cicatricosisporites pseudotripartitus</i>	12	3							<i>L. ovatus</i>
1. <i>Cingutritiles clavus</i>	4	4							<i>L. austroclavatidites</i>
27. <i>Cupaniidites orthoichus</i>	28	5							<i>M. antarcticus</i>
40. <i>C. reticularis</i>	17	6							<i>P. ellipticus</i>
9. <i>Cyathidites minor</i>	13	7							<i>P. microreticuloidatus</i>
2. <i>Cycadopites</i> sp.	5	8							<i>P. mawsonii</i>
22. <i>Dacrycarpites australiensis</i>	29	9							<i>C. minor</i>
21. <i>Dacrydiumites florinii</i>	30	10							<i>L. variegatus</i>
14. <i>Dilwinites granulatus</i>	31	11							<i>P. parvus</i>
24. <i>D. tuberculatus</i>	32	12							<i>C. pseudotripartitus</i>
19. <i>Haloragacidites harrisii</i>	33&34	13							<i>N. (brassi group)</i>
3. <i>Laevigatosporites ovatus</i>	6	14							<i>D. granulatus</i>
10. <i>Liliacidites variegatus</i>	7	15							<i>P. granulatus</i>
4. <i>Lycopodiumsporites austroclavatidites</i>	8	16							<i>P. annularis</i>
23. <i>Malvacipollis diversus</i>	35	17							<i>P. adenanthoides</i>
5. <i>Microcachryidites antarcticus</i>	14	18							<i>P. incurvatus</i>
20. <i>Myrtacidites eucalyptoides</i>	36	19							<i>H. harrisii</i>
32. <i>M. mesonesus</i>	37	20							<i>M. eucalyptoides</i>
33. <i>M. parvus</i>	38	21							<i>D. florinii</i>
13. <i>Nothofagidites</i> sp.(brassi group)	9	22							<i>D. australiensis</i>
34. <i>N. sp. (fusca group)</i>	18	23							<i>M. diversus</i>
8. <i>Phyllocladidites mawsonii</i>	10	24							<i>D. tuberculatus</i>
6. <i>Podocarpidites ellipticus</i>	15	25							<i>T. psilatus</i>
7. <i>P. microreticuloidatus</i>	16	26							<i>B. minimus</i>
35. <i>Polycopites esobalteus</i>	39	27							<i>C. orthoichus</i>
17. <i>Proteacidites adenanthoides</i>	40	28							<i>P. pachypolus</i>
16. <i>P. annularis</i>	41	29							<i>T. microreticulatus</i>
38. <i>P. concretus</i>	19	30							<i>P. subscabratus</i>
15. <i>P. granulatus</i>	20	31							<i>T. prolata</i>
18. <i>P. incurvatus</i>	42	32							<i>M. mesonesus</i>
28. <i>P. pachypolus</i>	21	33							<i>M. parvus</i>
11. <i>P. parvus</i>	11	34							<i>N. (fusca group)</i>
39. <i>P. reticulatus</i>	43	35							<i>P. esobalteus</i>
30. <i>P. subscabratus</i>	22	36							<i>B. elegansiformis</i>
37. <i>Simplicipollis scabratus</i>	23	37							<i>S. scabratus</i>
29. <i>Tricolporites microreticulatus</i>	24	38							<i>P. concretus</i>
31. <i>T. prolata</i>	25	39							<i>P. reticulatus</i>
25. <i>'Triorites' psilatus</i>	44	40							<i>C. reticularis</i>
41. <i>Triporopollenites gemmatus</i>	26	41							<i>T. gemmatus</i>

Table 2

List of species found in Werillup No. 17 borehole that do not appear to have been previously described, or which could not be assigned with confidence to existing species due to their very rare occurrence.

<i>Bombacacidites</i> sp., fig. 45, rare
<i>Ceratospores</i> sp. cf. <i>C. equalis</i> Cookson & Dettmann, fig. 46, rare
<i>Clavatipollenites</i> sp. cf. <i>C. ascarinoides</i> McIntyre, fig. 47, rare
<i>Liliacidites</i> sp. cf. <i>L. aviemorensis</i> McIntyre, fig. 48, rare
<i>Liliacidites</i> sp., fig. 49, common
<i>Monosulcites</i> spp., figs 50 and 51, rare
<i>Polypodioidites</i> sp., fig. 52, rare
<i>Polyporina</i> sp., fig. 53, common
<i>Proteacidites</i> sp. cf. <i>P. annularis</i> Cookson, fig. 54, common
<i>Proteacidites</i> sp. cf. <i>P. crassus</i> Cookson, fig. 55, rare
<i>Proteacidites</i> sp. cf. <i>P. minimus</i> Couper, fig. 56, rare
<i>Proteacidites</i> sp. cf. <i>P. parvus</i> Cookson, fig. 57, rare
<i>Proteacidites</i> sp. 1, fig. 58, common
<i>Proteacidites</i> sp. 2, fig. 59, rare
<i>Proteacidites</i> sp. 3, fig. 60, rare
<i>Proteacidites</i> spp., figs 61 to 68, abundant
<i>Retitricolporites</i> sp., fig. 69, rare
<i>Tricolpites</i> sp. cf. <i>T. aspermarginis</i> McIntyre, fig. 70, rare
<i>Tricolpites</i> sp. cf. <i>T. lilliei</i> Couper, fig. 71, rare
<i>Tricolpites</i> sp. cf. <i>T. matauraensis</i> Couper, fig. 72, rare
<i>Tricolpites</i> sp. cf. <i>T. pachyexinous</i> Couper, fig. 73, rare
<i>Tricolpites</i> sp., fig. 74, rare
<i>Tricolporites</i> spp., figs 75 and 76, rare
' <i>Triorites</i> ' sp. cf. <i>T. minisculis</i> McIntyre, fig. 77, common
' <i>Triorites</i> ' sp. cf. <i>T. minor</i> Couper, fig. 78, rare
' <i>Triorites</i> ' sp. cf. <i>T. orbiculatus</i> McIntyre, fig. 79, rare
' <i>Triorites</i> ' spp., figs 80 and 81, rare

to the Eocene: *Proteacidites concretus*, *P. reticulatus*, *Cupanieidites reticularis* (described from two localities in Victoria) and *Triporopollenites gemmatus*. Also, the Nanarup Limestone Member, which is stratigraphically higher than the Werillup No 17 sequence is no younger than uppermost Eocene (Quilty 1969).

The age of the base of the Werillup Formation has not been determined precisely and whether it extends into Middle Eocene cannot be resolved satisfactorily with the present data. The species identified as *Proteacidites incurvatus* and "*Triorites*" *psilatus* require further study before their chronostratigraphic significance can be fully assessed. *Triporopollenites gemmatus* is the only species useful in placing a lower limit on the age of the microflora as it is known only from Middle and middle-Upper Eocene strata in South Australia and the Great Artesian Basin (Harris 1972). Some of the dinoflagellates in the samples, e.g. species of *Wetzeliella* (figure 82) and *Cordosphaeridium* (figure 83), support the assignment of the sediments to the Upper Eocene (Dr. B. E. Balme 1972, personal communication).

Several specimens of reworked spores were encountered in the uppermost samples (figures 84, 85 and 86) and they have been identified by Dr. B. E. Balme as characteristic Lower Cretaceous forms. Lower Cretaceous sediments are found in the Eucla Basin (Ingram 1968) and in the southern Perth Basin (Lowry 1965). However these are too far away to be considered as possible sources.

There may have been pockets of Lower Cretaceous sediments nearby that were eroded during the transgression and have since been covered up or completely removed.

Comparison of the microflora with other assemblages

The microfloral assemblage from Werillup No 17 is similar to Late Eocene microfloras previously described from southern Australia and New Zealand. Differences between the Werillup microflora and other assemblages from sediments correlated with the Plantagenet Group by Cookson (1954b), Balme & Churchill (1959) and Churchill (1962, unpublished) have no stratigraphical significance as the species are long ranging. They may have a phytogeographical significance, but there are insufficient data on which to base evaluations.

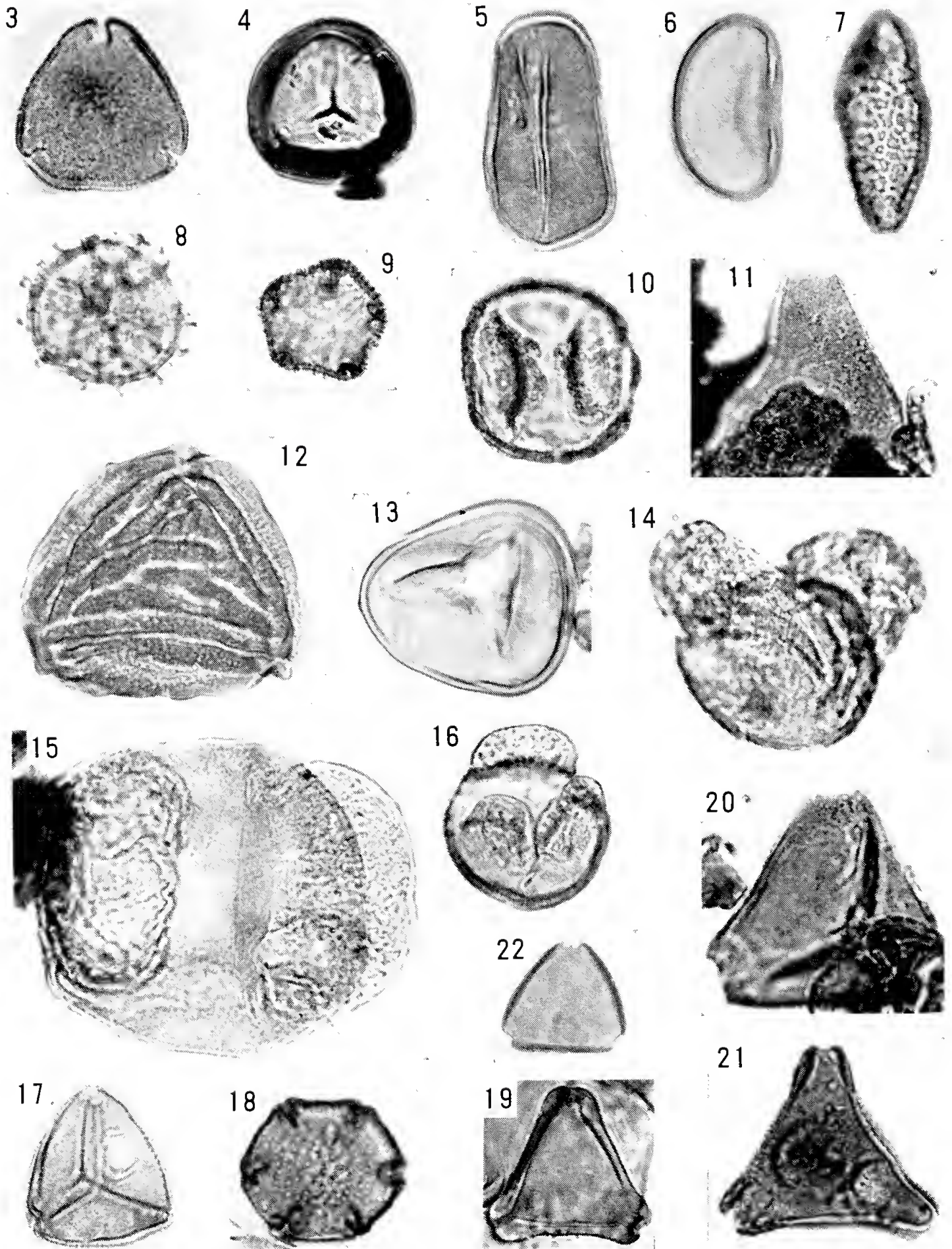
Cookson (1954b) correlated the microflora from the Plantagenet Group with Microflora C from Victoria, mainly on the basis of *Proteacidites pachypolus*, which is now known to be long-ranging. Harris (1971) related Microflora C to the *Triorites magnificus* Zonule of the Otway Basin (Middle to Late Eocene). There are only 5 species from the Werillup microflora that are common with the *T. magnificus* Zonule, but they are of limited stratigraphical value as they also occur in the uppermost Palaeocene *Cupanieidites orthoteichus* Zonule.

Correlations with the other palynological zonules of Harris (1971) are also not possible. The Upper Eocene "*Aglaoreida barungensis*" (Harris, unpublished) Zonule could not be recognized as it does not have any characteristic species that are present in the Werillup borehole. The Werillup microflora contains at least 14 species that are present in the informal Oligocene *Verrucatosporites* Zonule in the Otway Basin.

Most of the species in the microflora are found in the Early Tertiary Unit 1 set up by Hekel (1972) and in the Late Eocene microfloras of New Zealand (Couper 1960, Wilson 1968). However, the species only allow a broad correlation. McQueen *et al.* (1968) note that from the Kaiatan to Runangan there is an abrupt change from the *Nothofagus fusca* group to a dominance of the *Nothofagus brassi* group. The latter group is similarly dominant in the Werillup microflora and it is the same age as part of the Runangan Stage of New Zealand. The apparent uniformity of the microfloras throughout southern Australia and New Zealand during the Late Eocene suggests that the climate over the region was very uniform.

Palaeoecology of the microflora

The palaeoecological interpretation of a microflora depends on the reliability with which the spores and pollen can be related to modern plants. Such determinations become less reliable as older spores and pollen are examined and are usually not attempted with pre-Tertiary fossils. However, many of the species in the Werillup microflora have been related fairly



confidently to living genera and families. Most workers accept that the ecological tolerances of the plants that are represented in Early Tertiary microfloras have not altered during the Cainozoic (Burbidge 1960). The microflora as a whole will be discussed first, and then the variations within the microflora.

The palaeoecology of the assemblage

The general microfloral assemblage in the samples does not differ greatly from other assemblages described in the Plantagenet Group, and the additional species encountered do not alter the palaeoecological conclusions of previous authors. Three floristic elements have been recognized in the Lower Tertiary floras of southern Australia (Burbidge 1960). They have been called the 'Antarctic', 'Tropical' and 'Australian' elements, and the spores and pollen that belong to these groups will now be discussed.

The 'Antarctic' elements in the microflora are species of *Nothofagidites* and Podocarpaceae whose major development has been in the southern hemisphere and appear to have migrated to Australia and New Zealand from Antarctica. *Nothofagidites* is the most commonly represented pollen in the assemblage (though pollen from other plant groups is more abundant in several samples) and it is predominantly of the type that has been closely related to the pollen of species of the *Nothofagus brassi* group (Cookson & Pike 1955).

The *Nothofagus brassi* group at present grows in areas of moderate to high rainfall in New Caledonia (above 600-900 m) and in New Guinea (above 2400 m). It indicates a climate of constant humidity and one warmer than that occupied by the *N. fusca* group (McQueen *et al.* 1968). Pollen from the *brassi* group is recorded from Eocene to Pliocene in New Zealand and is abundant in Queensland from Eocene to Miocene. The *N. brassi* group is an evergreen forest dominant that requires dense forest for regeneration. It is a very heavy pollen producer and is probably over-represented in the pollen spectrum (Cranwell 1964).

Gymnosperms were probably not an important part of the vegetation as they make up only 9% of the microflora. They are mainly podocarps with extant genera now living in a wide range of climates. High proportions of *Podocarpus* pollen in a Quaternary core off Argentina was used as an indicator of cooler climates when compared with the proportions of pollen from

Nothofagus, Cupressaceae and *Weinmania* (Groot & Groot 1966).

Dilwynites has a down-hole distribution similar to the conifers and has been compared to several living conifers (for example *Callitris*), however, Harris (1965) considers an angiospermous affinity for the pollen more likely. *Dacrycarpites australiensis* was compared to the pollen of *Podocarpus* section *Dacrycarpus* which has its major development in New Guinea (Cookson and Pike 1953a). *Microcachrydites antarcticus* and *Phyllocladidites mawsonii* are common compared with the other podocarps in the assemblage, and have been related to two living podocarps, *Microcachrys tetragona* and *Dacrydium franklinii* respectively, both of which are restricted to Tasmania (Cookson 1947). These podocarps flourish under cool temperate conditions with a moderate rainfall.

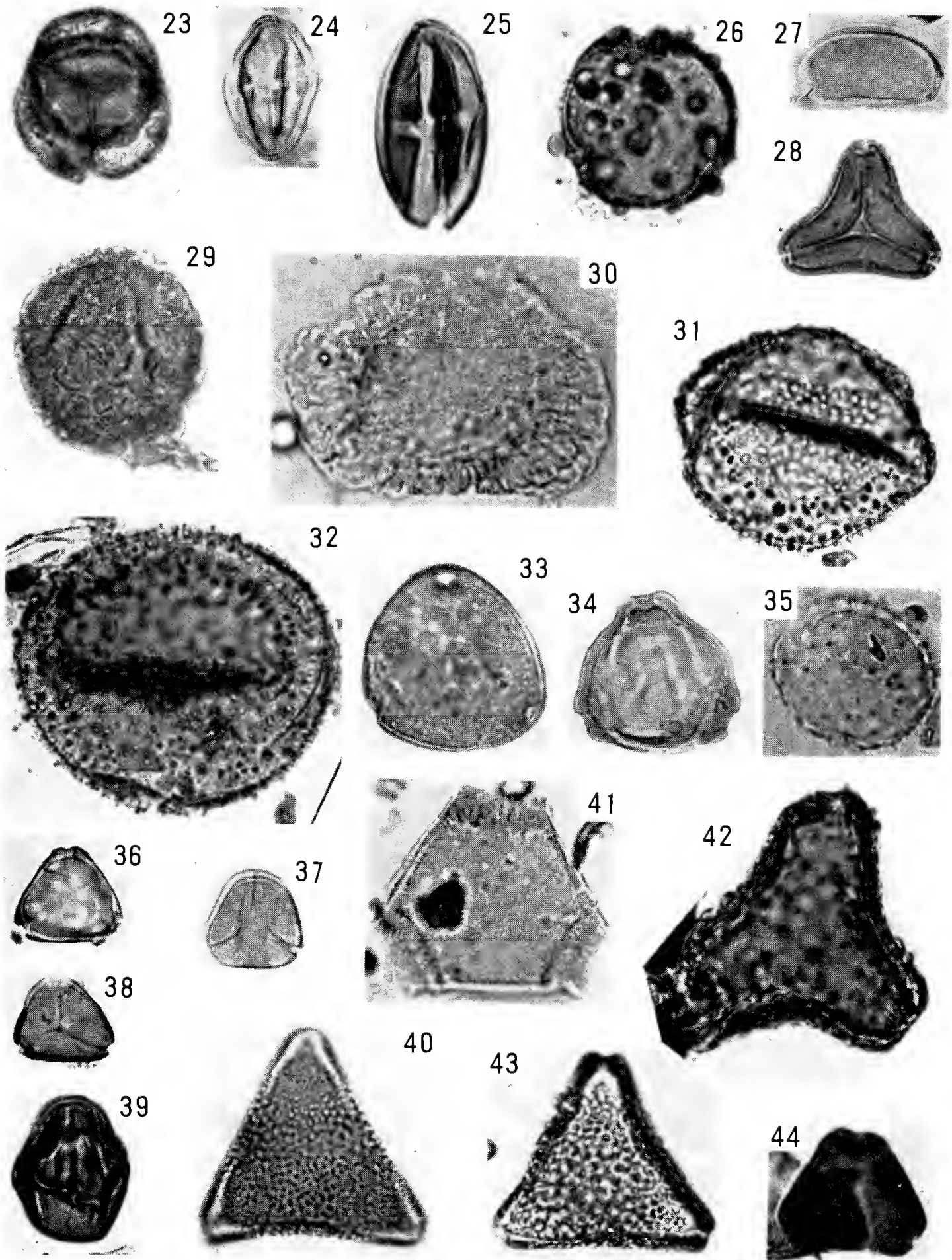
Podocarpidites represents pollen with general podocarpaceous affinities, and which may now be found in plants living in both tropical and temperate conditions. A similar distribution is found for a number of species of *Dacrydium*, which have the same pollen as *Dacrydiumites florinii* (Cookson and Pike 1953b).

Thus the mesophytic 'Antarctic' species of *Nothofagus* and the podocarps, which are now restricted to cool temperate and tropical submontaine regions, indicate a rainforest vegetation. The moss *Sphagnum* is represented in the assemblage by *Cingutriteles clavus* (Dettmann 1963) and indicates swampy conditions. Lycopods are represented by *Lycopodiumsporites*, and *Selaginella* by *Ceratospores* (Dettmann 1963).

Pteridophytes make up a small proportion of the assemblage and several families are present, including tree ferns. *Cyathidites minor* has been related to ferns such as Cyatheaceae and Dicksoniaceae, and *Cicatricosisporites* resembles some modern spores of *Anemia* in the family Schizeaceae (Dettmann 1963). *Laevigatosporites* and *Polypodiidites* have been compared to spores from Polypodiaceae. The pteridophytes have a broad distribution in high rainfall areas of the tropical and temperate regions and their presence in the microflora indicates conditions wetter than at present.

The "Tropical" elements in the microflora from Werillup No. 17 are species that have been related to families now distributed mainly in the tropical and subtropical regions of Australia and the Indo-Pacific. The species are *Beaupreaidites elegansiformis*, *Bombacacidites* sp., *Cupanieidites* sp., *Malvacipollis diversus* and

Figures 3 to 22.—All figures at x1000 unless otherwise stated. 3.—*Beaupreaidites elegansiformis* Cookson. Slide 69428b, 132.9 x 42.5. 4.—*Cingutriteles clavus* (Balme) Dettmann. Slide 69445. *Cycadopites* sp. Slide 69428a, 129.0 x 47.5. 6.—*Laevigatosporites ovatus* Wilson and Webster. Slide 69444a, 115.7 x 24.9. 7.—*Liliacidites variegatus* Couper. Slide 69451. 8.—*Lycopodiumsporites austroclavatidites* (Cookson) Potonié. Slide 69428b, 120.2 x 32.2. 9.—*Nothofagidites* sp. (*Nothofagus brassi* group). Slide 69486. 10.—*Phyllocladidites mawsonii* Cookson. Slide 69450. 11.—*Proteacidites parvus* Cookson. Slide 69431a. 125.9 x 43.7. 12.—*Cicatricosisporites pseudotripertitus* (Bolikhovtina) Dettmann. Slide 69428b, 123.2 x 32.2. 13.—*Cyathidites minor* Couper. Slide 69428b, 123.9 x 35.0. 14.—*Microcachrydites antarcticus* Cookson. Slide 69428b, 128.9 x 28.8. 15.—*Podocarpidites ellipticus* Cookson. Slide 69428b, 133.8 x 45.6. 16.—*Podocarpidites microreticuloidatus* Cookson. Slide 69428a, 113.1 x 37.4. 17.—*Cupanieidites reticularis* Cookson and Pike. Slide 69428b, 125.2 x 35.7. 18.—*Nothofagidites* sp. (*Nothofagus fusca* group). Slide 69438b, 131.4 x 39.5. 19.—*Proteacidites concretus* Harris. Slide 69428b, 136.3 x 25.8. 20.—*Proteacidites granulatus* Cookson. Slide 69428b, 132.7 x 25.8. 21.—*Proteacidites pachypolus* Cookson and Pike. Slide 69428b, 134.2 x 35.4. 22.—*Proteacidites subscabratus* Couper. Slide 69428b, 135.6 x 38.5.



Myrtacidites mesonesus. Additional "Tropical" species previously described from the Plantagenet Group but not found in the present study are *Anacolosidites* sp., "*Palmidites*" sp. and "*Santalumidites Cainozoicus*".

Beaupreaidites has been related to the pollen of *Beauprea* (Proteaceae) which occurs in New Caledonia and New Guinea (Cookson 1950). The determination of *Bombacacidites* sp. is not reliable, however, the pollen is common in the Eocene of New Zealand (Couper 1960). Leaves of *Bombax* (kapok tree) are recorded from the Plantagenet Group at Cape Riche (Chapman and Cressin 1934), thus there is evidence that the tropical species was present on the south coast of Western Australia during the Eocene.

The two species of *Cupanieidites* in the Werillup microflora have been compared to the pollen from Sapindaceae tribe Cupanieae, which is a component of tropical and south-eastern Australian rainforests (Cookson and Pike 1954b). The family Malvaceae has its major distribution in the tropics at present, and is represented in the microflora by *Malvacipollis diversus*. *Myrtacidites mesonesus* has been related to a species of *Whiteodendron* now living in Indonesia (McWhae 1957).

Anacolosidites is from the family Olacaceae in which the genera are now restricted to the tropics. It was pan-tropical from Palaeocene to Eocene, and was common in Borneo and Queensland throughout the Tertiary (Germeraad *et al.* 1968, Hekel 1972). "*Santalumidites Cainozoicus*" is considered (in part) a synonym of *Florschuetzia levipoli* (Germeraad *et al.* 1968). This species is similar to the pollen of *Sonneratia caseolaris*, a mangrove at present growing in estuaries along the Indo-Malesian coasts. The form genus '*Palmidites*' is of uncertain reliability, however, palm pollen is recorded from the Upper Eocene of New Zealand, and supports the evidence for warmth (McQueen *et al.* 1968).

The above 'Tropical' species indicate that the Late Eocene climate on the south coast was sub-tropical or warmer. These 'Tropical' species are also represented elsewhere in the Late Eocene of southern Australia, and in New Zealand (Harris 1971, Couper 1960), and suggest that the Australasian region was characterised by a warm and humid climate during this period.

The 'Australian' elements in the microflora are species such as *Myrtacidites eucalyptoides*, *Haloragacidites harrisii*, *Banksiaeaidites* and *Proteacidites*. *Banksiaeaidites* is similar to the

pollen found in *Banksia* and *Dryandra* (Cookson 1950). *Proteacidites adenanthoides* has been compared to the pollen of *Adenanthos* and *P. annularis* has been related to the pollen of *Xylomelum occidentale*, a tree occurring in the Jarrah forest of the south-west of Western Australia (Cookson 1950).

Other species of *Proteacidites* found in the Plantagenet Group by previous workers include *P. rectomarginis*, which has a possible affinity to *Petrophile*, and *Proteacidites symphyonemoides*, related to *Symphyonema* (Cookson 1950).

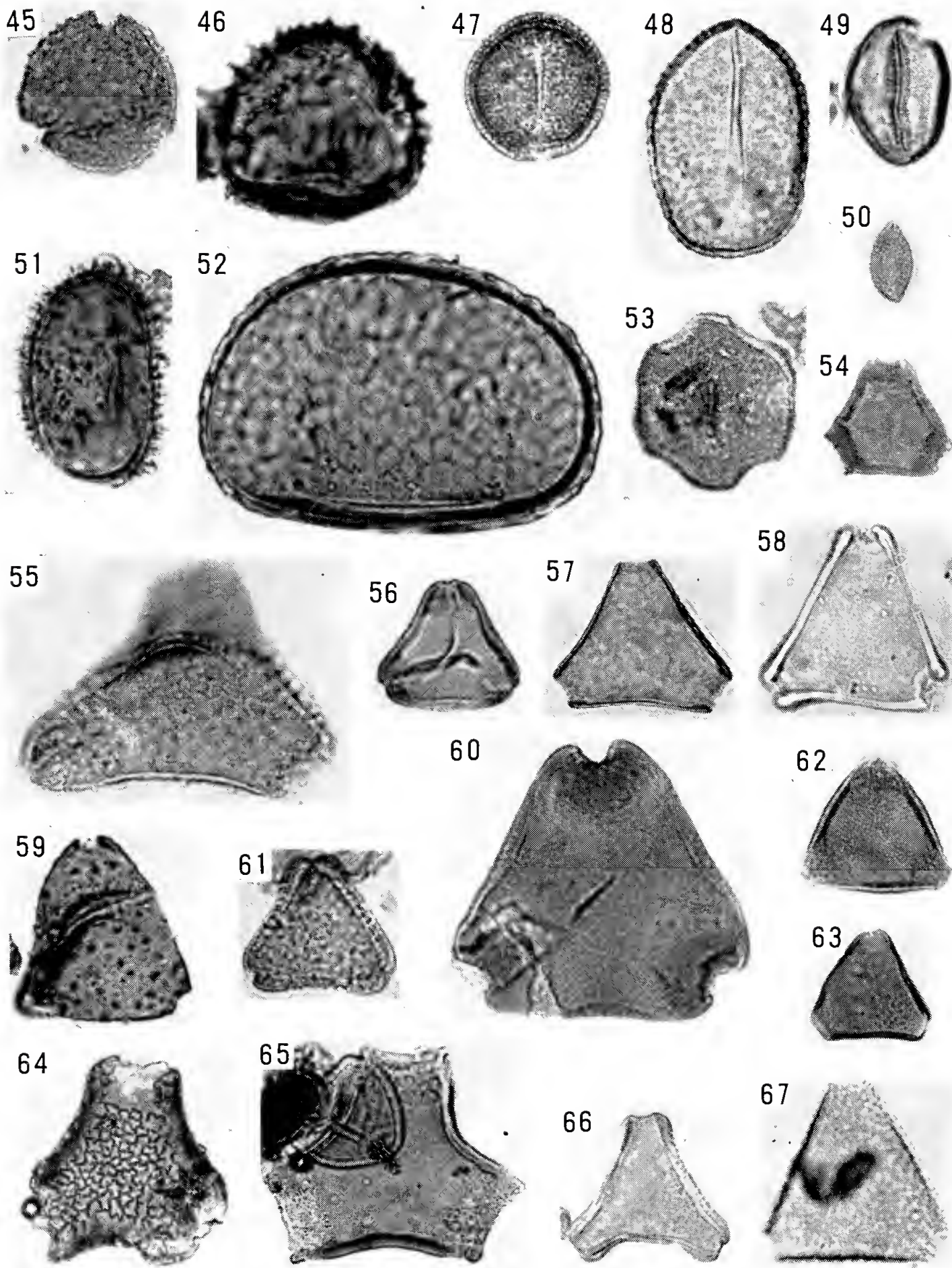
The family Proteaceae diversified in the Late Cretaceous and possibly originated in the rain-forest environment of south-eastern Australia and South-West Pacific (Muller 1970). The Werillup microflora includes over 30 proteaceous species and these compose up to 24% of the total microflora. Proteaceous pollen is the most abundant pollen type in several samples, and it is more abundant towards the bottom of the borehole. The wide diversity and abundance of proteaceous pollen suggest that Proteaceae were a major constituent of the vegetation and that the climate was warmer than cool temperate.

The form species *Haloragacidites harrisii* principally represents pollen from *Casuarina*, though other plants with similar pollen were probably present in the vegetation. The form species composes up to 16% of the total microflora and it is considerably more abundant in some samples. The less markedly aspidate pollen grains placed in the form species have been related to pollen from Haloragaceae and genera such as *Geniostoma* and *Canacomyrca*. These are now living mainly in the tropics (Mildenhall & Harris 1971).

The broad palaeovegetative pattern gained from the spores and pollen is that of a tropical to subtropical rainforest (closed-forest). The predominance of tree pollen relative to the proportion of non-tree pollen is indicative of a rainforest (Churchill 1962, unpublished). The subtropical vegetation suggests a climate considerably warmer and more humid than the present climate along the south coast of Western Australia, which is mild, cool temperate, with a warm to hot dry summer.

The southern beeches (*Nothofagus*) appear to have been forest dominants, with Proteaceae and *Casuarina* as subdominants. Other elements of the forest were podocarpaceous conifers, pteridophytes and the 'Tropical' species.

Figures 23 to 44.—All figures at x1000 unless otherwise stated. 23.—*Simplicepollis scabratus* McIntyre. Slide 69473. 24.—*Tricolporites microreticulatus* Harris. Slide 69439a, 123.1 x 31.2. 25.—*Tricolporites prolata* Cookson. Slide 69428b, 132 x 40.7. 26.—*Tripoporollenites gemmatus* Harris. Slide 69428d, 119.0 x 44.1 (single grain). 27.—*Banksiaeaidites minimus* Cookson. Slide 69439a, 127.0 x 26.4. 28.—*Cupanieidites orthoteichus* Cookson and Pike. Slide 69428a, 121.7 x 50.7. 29.—*Dacrycarpites australiensis* Cookson and Pike. Slide 69428b, 125.8 x 30.2. 30.—*Dacrydiumites florinii* Cookson and Pike. Slide 69449. 31.—*Dilwynites granulatus* Harris. Slide 69447. 32.—*Dilwynites tuberculatus* Harris. Slide 69448. 33, 34.—*Haloragacidites harrisii* (Couper) Harris. Fig. 33, slide 69453. Fig. 34, slide 69428a, 129.8 x 27.2. 35.—*Malvacipollis diversus* Harris. Slide 69439a, 123.7 x 48.1. 36.—*Myrtacidites eucalyptoides* Cookson and Pike. Slide 69471. 37.—*Myrtacidites mesonesus* Cookson and Pike. Slide 69428b, 121.5 x 49.3. 38.—*Myrtacidites parvus* Cookson and Pike. Slide 69472. 39.—*Polycopites esobalteus* McIntyre. Slide 69428b, 132.7 x 32.8. 40.—*Proteacidites adenanthoides* Cookson. Slide 69444a, 115.7 x 24.9. 41.—*Proteacidites annularis* Cookson. Slide 69439a, 133.5 x 39.3. 42.—*Proteacidites incurvatus* Cookson. Slide 69431b, 121.3 x 29.5. 43.—*Proteacidites reticulatus* Cookson. Slide 69457. 44.—"*Triorites*" *psilatus* Harris. Slide 69428a, 121.8 x 45.5.



The diverse 'Australian' element, especially the Proteaceae, is now characteristic of a climate with a marked dry season. It is difficult to explain the presence of this element in a vegetation growing in humid conditions and that includes *Nothofagus*, which cannot withstand long periods of dry conditions.

A Middle Eocene flora from Maslin Bay, South Australia includes *Araucaria*, *Casuarina* and Proteaceae, and a leaf macroflora which has a broad similarity to some leaf litters from present day Queensland wet forests (Lange 1970). Thus, it is possible that the Early Tertiary rain-forest vegetation on the south coast included a high proportion of Proteaceae. An alternative interpretation is that the "Australian" element represents species from a flora further inland in a drier and more seasonal climate.

Analysis of down-hole variations in the microflora

Palaeoecological interpretations from palynological data are subject to many reservations, and when based on the results from one bore-hole, must be regarded with even more caution. The importance of the relative pollen production of the plants and the hydrodynamic properties of the grains have been stressed; yet there is very little quantitative information on these parameters (Davis 1963, Brush & Brush 1972). Additional cause for concern is the possibility of sampling errors during drilling.

Differential effects resulting from processing techniques were probably minimal, as were errors due to counting techniques and identifying the species. Most of the spores and pollen in the samples were well-preserved and contamination with modern pollen was negligible.

The number of counts per sample though not ideal was probably representative. The total number of spores and pollen in each sample was selected as the pollen sum. This is probably not justified ecologically, and it can be seen that the angiosperms are over-represented (Fig. 2). Thus, changes in the frequencies of the pteridophytes or gymnosperms will be masked to some extent. However, the total pollen sum is the most commonly used, and the easiest to interpret.

The down-hole distribution of the major plant groups is shown in Fig. 2. There appear to be several horizons with simultaneous changes in the groups. However, three of these horizons represented by samples 69443, 69439 and 69432 coincided with lithological changes, and this is almost certainly significant. Brush & Brush

(1972) found that pollen frequencies were dependent on distance from source and lithology. However, Cross & Shaeffer (1965) concluded that pollen frequencies in surface sediments of the Gulf of California were independent of sediment types, except where these were coarse.

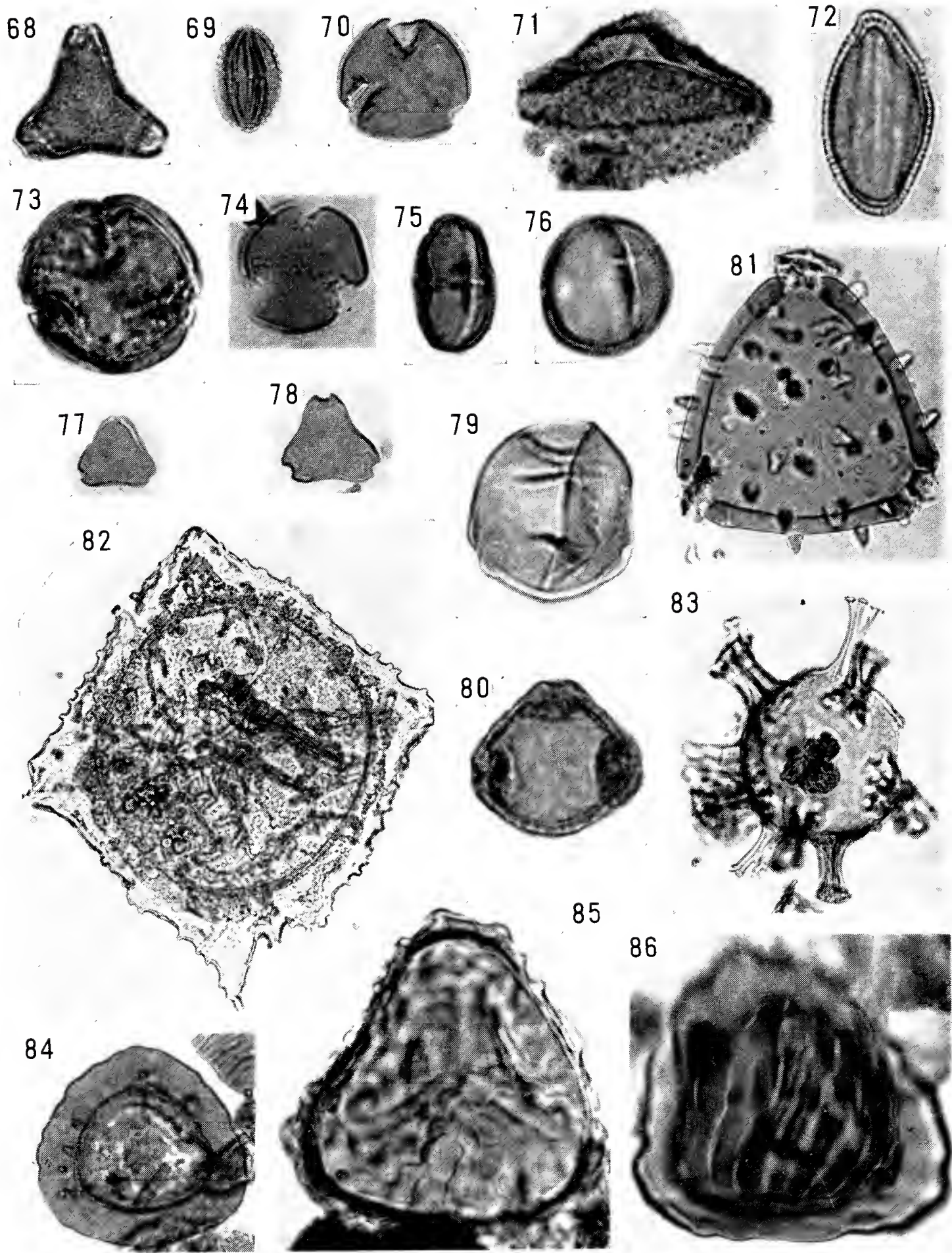
Contamination during sampling is unpredictable but could be expected to occur, as the samples are a sludge from poorly consolidated sediments. It was indicated above that samples 69443 and 69444 were logged as weathered granite. However, they appear to contain a microflora similar to the samples stratigraphically higher, and this may be the result of contamination due to caving higher up. It is not possible to determine from the lithology of the samples whether they are detrital or the result of *in situ* weathering of the underlying granite and it was accepted that the pollen frequencies obtained from the samples were reliable. However, down-hole contamination may have occurred continuously during drilling and cannot be neglected. It may be the reason for the general uniformity of the frequencies down the hole and thus any interpretation of the pollen diagram must be regarded with caution.

The sediments from the bore can be interpreted as a standard transgressive sequence of paralic sediments grading into deeper-water facies. At Sample 69438, there is a change from clays and silts to a sand that becomes progressively finer upwards, until it is a clayey silt at the top. This suggests an increasingly deeper-water environment and the presence of dinoflagellates (Fig. 2) indicates that the upper sediments are marine.

If the sediments were being deposited in water that was becoming deeper with time, a change in the frequencies of the spores and pollen could be expected with increasing distance from the shoreline. Such a trend could not be differentiated from changes in the contributing vegetation resulting from changes in the climate. Local topography may also have influenced spore and pollen frequencies. There are nearby hills up to 150-180 m high that were probably vegetated during early stages of the transgression. These may have contributed spores and pollen to the sediments. Little can be said of Early Tertiary relief elsewhere on the south coast, but it was probably not high enough to affect vegetational patterns in any pronounced way.

The problems of contamination, increasing distance from the shoreline and changes in

Figures 45 to 67.—All figures at x1000 unless otherwise stated. 45.—*Bombacacidites* sp. Slide 69428b, 126.5 x 40.0. 46.—*Ceratosporites* sp. cf. *C. equalis* Cookson and Dettmann. Slide 69431a, 123.3 x 47.2. 47.—*Clavatiipollenites* sp. cf. *C. ascarinoides* McIntyre. Slide 69467. 48.—*Liliacidites* sp. cf. *L. aviemorensis* McIntyre. Slide 69428a, 125.2 x 39.2. 49.—*Liliacidites* sp. Slide 69428b, 124.8 x 28.2. 50, 51.—*Monosulcites* spp. Fig. 50, slide 69428b, 132.8 x 34.9. Fig. 51, slide 69428a, 135.0 x 34.6. 52.—*Polyodiidites* sp. Slide 69442a, 132.0 x 39.5. 53.—*Polyporina* sp. Slide 69428b, 130.7 x 35.9. 54.—*Proteacidites* sp. cf. *P. annularis* Cookson. Slide 69454. 55.—*Proteacidites* sp. cf. *P. crassus* Cookson. Slide 69444a, 118.3 x 27.4. 56.—*Proteacidites* sp. cf. *P. minimus* Couper. Slide 69428b, 132.8 x 29.2. 57.—*Proteacidites* sp. cf. *P. parvus* Cookson. Slide 69432a, 125.7 x 34.7. 58.—*Proteacidites* sp. 1. Slide 69458. 59.—*Proteacidites* sp. 2. Slide 69428a, 127.9 x 44.3. 60.—*Proteacidites* sp. 3. Slide 69428b, 134.2 x 41.7. 61 to 67.—*Proteacidites* spp. Fig. 61, slide 69428a, 127.0 x 26.5. Fig. 62, slide 69543a, 128.4 x 39.1. Fig. 63, slide 69459. Fig. 64, slide 69460, x 540. Fig. 65, slide 69456, x 540. Fig. 66, slide 69428a, 121.1 x 25.7. Fig. 67, slide 69465.



lithology make detailed inferences concerning changes in the vegetation with time impossible. However, several broad trends in Fig. 2 may be significant.

The proportions of pteridophytes, gymnosperms and *Nothofagus* are slightly greater in the marine section above sample No. 69440 and this may reflect either cooler conditions or increased humidity. The marine section, as noted above, appears to have been deposited in deeper water, which implies that a greater area of the southern shield was covered by the shallow sea. Topographical highs, however, would remain as islands and form an archipelago with a much higher humidity and rainfall. If part of the contributing vegetation was growing on the islands and low-lying areas near the shallow sea, it may explain the trend shown by the spores and pollen. A general reduction in the temperature of southern Australia began at the end of the Eocene (Dorman 1968), but whether this is also reflected in the samples cannot be stated.

The palaeolatitude of the south coast of Western Australia during the Late Eocene was higher than 41°S and possibly as high as 60°S (Le Pichon & Heirtzler 1968, Wellman *et al.* 1969). That the subtropical vegetation represented by the Werillup microflora was able to flourish on the south coast at such a high latitude indicates that the climate during the Late Eocene was considerably warmer than at present.

Tropical dasycladacean algae and the warm-water foraminifer *Asterocyclina* present in the Plantagenet Group (Cockbain, 1967, 1969) indicate that the Southern Ocean was warmer during the Late Eocene. This is supported by oxygen isotope data from south-eastern Australia and New Zealand (Dorman 1968, Devereux 1967).

The warmer temperatures agree with worldwide palaeoclimatic data from the Eocene reviewed by Frakes & Kemp (1972). They used oxygen isotope palaeotemperatures that had been determined from the Middle Eocene of New Zealand to infer that even at a latitude of 60°S the temperature of ocean surface water probably exceeded 15°C.

The warmer oceans would have a high evaporation rate, producing high humidity and rainfall on the south coast of Western Australia. The warm, shallow transgressive sea would also have modified the coastal region, reducing the influence of cooler winter temperatures. An inland vegetation in a drier and more seasonal climate is also possible.

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Figures 68 to 86.—All figures at x1000 unless otherwise stated. 68.—*Proteacidites* sp. Slide 69462. 69.—*Retitricolporites* sp. Slide 69428a, 128.0 x 25.0. 70.—*Tricolpites* sp. cf. *T. aspermarginis* McIntyre. Slide 69428b, 122.4 x 38.2. 71.—*Tricolpites* sp. cf. *T. lilliei* Couper. Slide 69428b, 134.1 x 47.5. 72.—*Tricolpites* sp. cf. *T. matauraensis* Couper. Slide 69474. 73.—*Tricolpites* sp. cf. *T. pachyexinous* Couper. Slide 96444a, 137.3 x 36.1. 74.—*Tricolpites* sp. Slide 69428b, 130.5 x 42.4. 75, 76.—*Tricolporites* spp. Fig. 75, slide 69475. Fig. 76, slide 69476. 77.—*Triorites* sp. cf. *T. minisculis* McIntyre. Slide 69428b, 134.7 x 20.2. 78.—*Triorites* sp. cf. *T. minor* Couper. Slide 69428a, 126.0 x 49.6. 79.—*Triorites* sp. cf. *T. orbiculatus* McIntyre. Slide 69428b, 131.5 x 30.4. 80, 81.—*Triorites* sp. Fig. 80, slide 69479. Fig. 81, slide 69451, x 540. 82.—*Wetzeliella* sp. Slide 69488, x 540. 83.—*Cordosphaeridium* sp. Slide 69428c, 130.9 x 45.8, x 540. 84.—*Cingulatisporites saevus* Balme. Slide 69428a, 135.3 x 43.7. 86.—*Contignisporites glebulentus* Dettmann. Aptian to Albian. Slide 69428c, 135.3 x 30.0. 85.—*Klukisporites* sp. cf. *K. pseudoreticulatus* Couper. Late Jurassic to Early Cretaceous. Slide 69428a, 125.7 x 30.0

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2.—Local taxonomy and terminology for some terrestrial arthropods in five different ethnic groups of Papua New Guinea and Central Australia

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Abstract

Lists of local names of spiders and insects in five different ethnic groups of Papua New Guinea and Central Australia are presented. Additional information is given on the use of particular species. It is suggested that in the nomenclature of indigenous peoples a species is likely to get an individual name to contrast it with the more general term or to distinguish it from the term of a related "type-specimen", if it is harmful, edible, or in any other way outstanding.

Introduction

Our knowledge of the names of insects and spiders in certain non-European languages is poor. Three main reasons are thought to be responsible for this:

Firstly, insects and spiders cannot normally be identified by the field anthropologist or linguist because he has not had the training to distinguish between major arthropod taxa. Also a lack of books for the field identification of spiders and insects is more apparent than for other groups such as birds and mammals.

Secondly, insects and spiders are usually small, and in spite of their great abundance are more easily overlooked than birds, reptiles and mammals.

Thirdly, insects and spiders rarely play as important a role as, for example, larger game animals or venomous species.

The aims of this paper are therefore to place on record some of the names used for terrestrial arthropods by certain peoples, and to stimulate more systematic research along these lines. As a biologist I have had the opportunity on three recent field trips to make "on-the-spot" identifications of insects and spiders, sometimes at the generic, but more often at the family or higher taxon level. These were either collected by myself or local helpers, and shown to some knowledgeable locals. For greater details see "Material and Methods".

Of the three ethnic groups studied in Papua/New Guinea (Kiriwina, Chuave and Onabasulu) no previously published lists of names of insects and spiders appear to exist. However, thanks to the efforts of Mr. R. C. Thurman,² who compiled a similar list to that reported for Chuave

below, we can at least compare our Chuave terms with those of the neighbouring "Kinuku" dialect (Thurman 1973 in litt.).

A few names of arthropods have been collected from the Pintupi tribe of Central Australia by Hansen (1974). The Walbiri were the subject of Meggitt's book "Desert People" (1956) in which he gives a list of 28 terms for insects and spiders. This list has been compared with, and supplements, our collection.

Edible insects of the three ethnic groups studied in Papua/New Guinea have been the subject of an earlier paper by Meyer-Rochow (1973a) and the insect food of Australian Aborigines has been reviewed in some detail by Reim (1962), and briefly summarized by Meyer-Rochow (1973b). Since edible insects of Australian Aborigines and New Guineans have been dealt with in separate publications, in the compilations below no further details other than whether a species is consumed by the natives or not will be given.

Almost certainly the lists given in this paper are incomplete. Firstly, most species of insects and spiders are seasonally abundant whether tropical or not, and so a considerable number of species might not have been present during the time of our field work. Secondly, by manually collecting species of various habitats over a period of two weeks some forms will have been overlooked. Undetected and uncollected they will therefore have not been mentioned by the people questioned. Thirdly, particular species may not have been mentioned or collected because of taboos associated with them.

In a first attempt, however, to record names of insects and spiders in these languages (some of which may in fact be regarded as dying out), the manual collecting procedure can even be considered advantageous, since the common and more abundant arthropods would be found rather than a multitude of rare forms that might not even have names at all.

Materials and methods

Communication difficulties, where they arose, were usually overcome with the aid of an interpreter or by the use of signs. In cases where natives were asked to collect insects, they would normally return with large numbers of individuals belonging to one or two most common species. Furthermore they would catch those forms which were large and easy to catch. To avoid this unwanted "selection", in most cases I collected the material myself, taking care

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that I would get as many representatives of taxonomically-different groups, i.e. orders and families, as possible.

The animals were then shown to local persons regarded as knowledgeable by their companions. In the case of the Kiriwinians this was a group of five elderly men; in the Chuave it was a young man who had experienced some degree of Mission education, with the Onabasulu there were three young men in turn; in the central Australian Walbiri it was one old and one young man; in the Pintupi it was well-known 'Nose-peg', a very clever old man who has led governmental patrol-expeditions into the Gibson Desert during which previously-uncontacted Pintupi nomads were found (Lockwood 1964). While in more systematic work a larger number of persons should be consulted, the time available did not permit a more extensive survey.

Occasionally the locals were shown drawings of insects in the book 'The Insects of Australia' (CSIRO 1970), but in agreement with Waldron and Gallimore (1973) we found that these untrained people had great difficulty in recognizing line-drawings of insects—even an insect as common as the fly was not identified. The problem of picture recognition is thought to be attributed mainly to three factors: a) book figures of insects and spiders are not usually drawn to natural size, b) most of the line-drawings lack colouration and c) all figures including colour photographs are two-dimensional representations.

The replies of the Walbiri and Pintupi informants were recorded on tape, and the cassettes are now kept at the Department of Linguistics, Australian National University, Canberra. In the case of the three peoples of Papua and New Guinea the answers were written down phonetically and later transcribed phonemically with the assistance of Rev. R. Lawton¹ (Kiriwina), Mr. R. C. Thurman² (Chuave) and Dr. C. L. Voorhoeve³ (Onabasulu). The transcription used for the Walbiri material was that of Meggitt (1956), while Pintupi material, following advice by Dr D. Laycock³, was written down as the author heard it, and compared with a list which was kindly made available to the author by Mr. K. Hansen.⁴

Some of the insects and spiders were identified on the spot, others were preserved in 50% ethanol or air-dried, and taken to the Australian National University for examination. Identification to the family level, and sometimes to generic or specific grades, was normally possible.

Results

A. Kiriwina

The Kiriwinians are an anthropologically well-studied Melanesian people inhabiting the Trobriand Islands. They have been in continu-

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² See page 15.

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⁴ K. Hansen, Yayayi Outstation, Papunya Settlement via Alice Springs, N.T.

ous contact with Europeans (missionaries, explorers, anthropologists, Australian instructors and more recently tourists) for about 90 years. Through translations of their myths and sagas, primarily by Malinowski (1929), we know quite a lot of their vocabulary. These first compilations, which omit most insect names, will soon be updated by an English-Kiriwina dictionary by Lawton¹ and Leach (in preparation).

The names of insects and spiders reported below were collected during a stay of two weeks in May/June on the island of Kiriwina (Table 1).



Figure 1.—According to Malinowski (1929) "delousing" is the only physical contact during the day permitted between opposite sexes in Kiriwina people.

B. Chuave

The Chuave are part of the Chimbu people who live in the central Highlands of New Guinea. They were only contacted regularly from the 30s on of this century. They make considerable use of insects as human food, a habit which may be related to the high population density in the area of approximately 250/km² and the lack of larger game animals (Meyer-Rochow 1973a). Collecting of insects was carried out during June (Table 2).

Table 1
Names for arthropods in Kiriwina

English name	Scientific name	Kiriwina	Remarks
Damselflies and dragonflies	Odonata: Libellulidae, Corduliidae, Coenagrionoidea	pilibuwa	
Cockroaches	Blattodea (taxonomy of New Guinea forms inadequately worked out)	kaikorosi liwoliusa bukibwaki	big forms small forms black, stinking forms
Termites	Isoptera	uku uku kukuwa, pwakakia	species distinguished by nest or mound
Praying mantis	Mantodea: <i>Tenodera</i> sp., <i>Hierodula sternosticta</i>	tataya	eaten
Earwigs	Dermaptera: <i>Acanthocordax</i> sp.	no name	known
Cave cricket	Gryllaeridoidea: <i>Tachycines</i> sp.	bubunaweta	
Longhorned grasshoppers	Tettigonidae: <i>Caedicia</i> sp., <i>Valanga</i> sp.	dila pwewesa	chirps, not eaten does not chirp, eaten
Shorthorned grasshoppers and locusts	Caelifera: Acrididae	nipawa gagata	big forms, some eaten small forms, some eaten
Crickets	Grylloidea <i>Teleogryllus commodus</i> <i>Metioche</i> sp.	sigwa sigwapolu kinancita	some bush-crickets eaten form with vestigial wings
Various small green hoppers	Orthoptera	kilili	all edible "hoppers"
Mole cricket	<i>Gryllotalpa</i> sp.	si kaitukwa bogau	"The evil spirit's walking stick" (local information)
Stick insects	Phasmatodea: <i>Eurycantha horrida</i> Phasmatinae	kidoka kwapu	eaten some eaten
Lice	Phthiraptera: <i>Pediculus humanus</i>	kutu	eaten (Fig. 1)
Bed bug	<i>Cimex lectularius</i>	ginigeni	
Leaf bugs	<i>Mictis</i> sp.	pwadu kula	eaten
Water strider	Gerridae: <i>Halobates</i> sp.	no name	well known
Cicadas	Cicadidae: <i>Diceropyga</i> sp., <i>Baeturia</i> sp.	siekwapa padidi	female forms male forms
Ant lion	Neuroptera: <i>Myrmeleon</i> sp.	ginuvavalia	
Beetles: cockchafer, dung beetles, Christmas beetle	Coleoptera: Scarabaeidae	kim	general term for 'typical' beetle, some eaten as grubs
Longicorn beetle	Cerambycidae	dila	like longhorned grasshopper
Ladybird	Coccinellidae	no name	known
Weevils	Curculionidae	no name	known

English name	Scientific name	Kiriwina	Remarks
Click beetles	Elateridae	tama	cause of amusement
Jewel beetles	Buprestidae	papaku	
Firefly	Lampyridae	kwanekwane	shine brightest after thunderstorm (local information)
Fleas	Siphonaptera: <i>Pulex irritans</i>	kutu	like lice
Flies and Mosquitoes	Diptera	nigunagu	general term
Mosquito	Culicidae	nim	
Robber flies	Asilidae	dukupipila	
House flies	Muscidae and other families	mdowali, mdukovivia	
Flesh flies	Calliphoridae	nituma	come to corpse (local information)
Butterflies and moths	Lepidoptera: e.g. <i>Coscinocera hercules</i> , <i>Indula arsinoe</i> and approx. 25 more spp.	beba	general term
Female birdwing	<i>Ornithoptera goliath</i>	bebakoya	
Male birdwing	<i>Ornithoptera goliath</i>	bebaim	tied to arm alive, used as decoration and toy (personal observation)
Hawk moth	Sphingidae	polaulau	injures eyes of people coming to light at night (local information)
Caterpillar	Lepidopteran larva	motatana	
Chrysalis	Lepidopteran pupa	poula beba	egg of butterfly (local information)
Weaver ant	<i>Oecophylla smaragdina</i>	siboyeki	caten
Winged ants	males and queens	seva	
Large black ant	<i>Camponotus</i> sp.	kaibibasia	
Small black ant	?	kasususila	
Wasps	<i>Polistes</i> ? sp. Sphecoidea?	kapiwa tobuynsapi tobuyuyivi	builds small nest in trees; builds large nest in trees; lives in the ground
Spiders and kiu—Arachnida			
Scorpions	Scorpiones	kudukika	causes pain (local information)
Whip scorpions	Amblypygi	si kankwa bogan	
Harvestmen	Opiliones	no name	if around, water is poisonous (local information)
Orb web spiders	Araneidae: e.g. <i>Nephila</i> sp.	kapari	
Jumping spider	Salticidae	kapari	
Crab spider	Thomisidae	kapari	
Sheet—or tangled web spiders	various families	pwada kola	
red mite	Acari: <i>Thrombidium</i> sp.	uweilato	

English name	Scientific name	Kiriwina	Remarks
Other terrestrial arthropods			
Millipede	Diplopoda	mtakwaibwagina	general term
big form	<i>Orthomorpha</i> sp.	monita	both considered dangerous by locals
small form	<i>Trigoniulus</i> ? sp.	monitakai	
Black centipede	Lithobiidae	waikapula	
Red scolopender	Scolopendridae	wai or wayi	
Earth runner	<i>Geophilus</i> ? sp.	msubili	
?	<i>Scutigera</i> ? sp.	no name	known



Figure 2.—Many individuals of the Tenebrionid beetle *Lomapteria yorkiana*, made into a decorative band, are used by New Guinea Highlanders from the Wahgi Valley during a pig-exchange ceremony.

C. Onabasulu

Until recently the Onabasulu, inhabiting the area north of Mt. Bosavi in the Southern Highlands, were cannibals. The first census of the people was made in 1966, resulting in a figure of about 200 individuals and a very low population density of 12/km² (Ernst¹, personal communication). Since then contacts to our kind of civilization have been restricted to occasional

¹ T. Ernst, Department of Anthropology, Flinders University, Adelaide, South Australia.

bush patrols by an Australian officer, a stay of one and a half years by the American anthropologist T. Ernst, a two-week visit in July 1972 by Ernst and myself, and to the influence of the Mt. Bosavi missionary. The latter, however, lies in the territory of the Kaluli, some 30 km away. Results are given in Table 3.

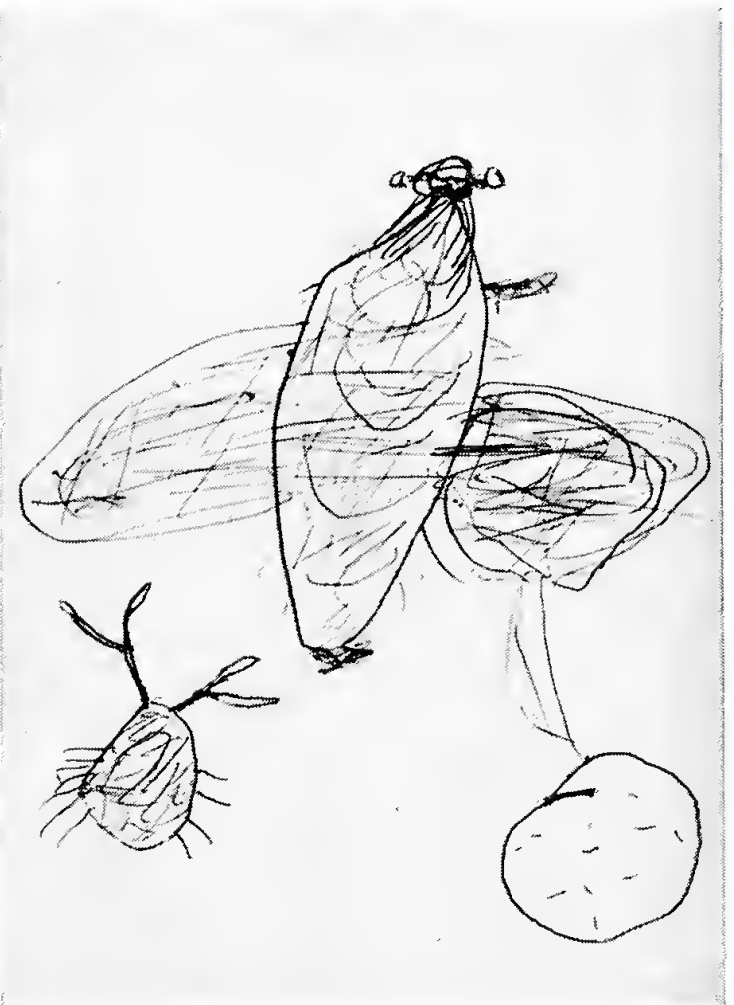


Figure 3.—This ballpoint-drawing of a butterfly and its pupa was prepared by an approximately 25 year old Onabasulu man, whose experience of using pencil and paper was virtually nil. More drawings of this and other artists (Onabasulu cannibals) have been published in Meyer-Rochow (1973 a,c).

Table 2
Names for arthropods in Chuave

Insects—Hexapoda				
English name	Scientific name	Chuave	Kinuku dialect ¹ (from Thurman)	Remarks
Damselflies and dragonflies	Odonata: Anisoptera, Zygoptera	mégawa bógawa	moiyokora (mepo gapo = dog)	
Cockroaches	Blattodea	gunago		
Termites	Isoptera	gomuna	homina	
Praying mantis	Mantodea: <i>Hierodula sternosticta</i>	keikabu	kei kapu	eaten
Earwigs	Dermaptera: <i>Chelisoches morio</i>	kopa kabu	kopa kapu	
Tree- and cave crickets	Rhaphidiphoridae: <i>Tachycines</i> sp.	mógulum pediporu	mongurom fekiporu	means a bent back (local information)
Longhorned grasshoppers	Tettigonidae	weriwawa	sirikine	eaten
Shorthorned grasshoppers and locusts	Acrididae, e.g. <i>Valanga</i> sp.	giba	siname	eaten
Crickets	Grylloidea: <i>Teleogryllus commodus</i>	keko	ekera	eaten
Mole cricket	<i>Gryllotalpa</i> sp.	wiwi	kuoko	eaten
Stick insect	Phasmatodea: <i>Eurycantha horrida</i>	kumatóru komatóru	?	
Bugs, leaf bugs	Hemiptera: <i>Mictis</i> sp.	ga(d)raniba	garan ipa	eaten, spray poison in human eyes (local information)
Lice	Phthiraptera	numan	numan	
Water strider	Gerridae	nurisinesine	?	
Cicadas	Cicadidae	giuro	giuro	eaten
Beetles Ground beetles	Coleoptera: Carabidae	ganefarma	?	(Fig. 2)
Sugar beetle	Passalidae	gomuna	gomina	like termites, live in rotten wood, eaten as grub
Rhinoceros beetle	Scarabaeidae: <i>Xylotrupes gideon</i> <i>Oryctes</i> sp.	wawe	wawe gomina	grub eaten
Stag beetles	Lucanidae	gomuna	gomina	grub probably eaten
Longhorn beetles	Cerambycidae	emeiba	emei ipa	eaten
Weevils	Cureulionidae	emeiba	emei ipa	eaten
Firefly	Lampyridae	derégure	dere gouro	means "to light and finish" (Thurman, in litt.)
Wood-boring grubs	mostly coleopteran larvae	omun	omon	some eaten

¹ Thurman (1973) obtained a Kinuku-dialect list by reading out those terms which I had previously recorded and written down from a Chuave informant. That the people he consulted in fact understood almost all the terms which he as a European read to them, proves the validity of the original Chuave list.

English name	Scientific name	Chuave	Kinuku dialect	Remarks
Fleas	Siphonaptera: <i>Pulex irritans</i>	toridi	toreri	
Crane flies and mosquitoes	Tipulidae and Culicomorpha	kunkabu	denkapu	
Small flies	Diptera	oremei	oremei	
Big flies	Diptera	oremei garomabu	oremei garumapu	
Butterflies and moths	Lepidoptera	kono kono	topa topa	general term
Chrysalis	pupa	kono nu	topa topa murom	means "egg of butterfly" (local information)
Caterpillars	Lepidopteran larvae	monsúmuna	?	social caterpillars in a sort of nest. Eaten
Taro-leaf Caterpillar	?	kímina mégoma	kimina mekoma	big eaterpillar
Green/yellow/white caterpillar	?	kímina kánkabu	kankapu gima gima	small eaterpillar (local description)
Insect (butterfly?) eggs		duam	?	
Ulysses butterfly	<i>Papilio ulysses</i>	omula gáulum	omura topa topa	
Ants	Formicoidea	sin	sin	some eaten
Ant eggs	ant pupae	sin morena	sin morena	some eaten
Tree wasp	<i>Polistes?</i> sp.	oremei gar(u)mábu	oremei garimapo	
Honey bee	Apidae	dum	ipa dum	
Bumble bee	Bombinae	oremei mam	den mam	mam means mother (local information)
Spiders and kin—Arachnida				
Scorpion and whip scorpions	Scorpiones, Uropygi	wiwi	ekera	like mole cricket
Harvestmen, Huntsman- and crab spiders	Opiliones, Isopodidae, Thomisidae	maimadonamu	maima donamu	
Wolf spiders	Lycosidae	gourake	gourake	
Sheet or tangled web spiders	Various different families	gimabu	gimapo	
Orb web spiders	Araneidae, e.g. <i>Nephila</i> sp.	gimgam	?	
Stick spiders	e.g. Tenthredinidae	emeiba	emei ipa	
Jumping spiders	Salticidae	torídi	toreri	
Other terrestrial arthropods				
Walking worm	Peripatidae	onoba múgan	onopa mukan	identified from book, eaten (local information)
Millipede	Diplopoda	onoba múgan	onopa mukan	
Centipede	Chilopoda	gainobari	gainopari	

Table 3

Names for arthropods in Onobasulu

Insects—Hexapoda

English name	Scientific name	Onobasulu	Remarks
Silverfish	Lepismatidae	hahuago	
Damselflies and dragonflies	Odonata: Anisoptera Zygoptera	wodien	larva considered small crayfish, eaten
Cockroaches, field cockroach, house cockroach	Blattodea	afia dofene horole	
Praying mantis	Mantodea: <i>Hierodula sternosticta</i>	hayabelu	
Egg case of mantis	Ootheca	isyo	
Earwigs	Dermaptera	maidagana	like scorpion
Cave- and tree- crickets	Rhaphidiphoridae: <i>Tachycines</i> sp.	gawobodo	
Longhorned grasshoppers	Tettigonidae: <i>Valanga</i> sp.	sak(g)é	eaten
Shorthorned grass- hoppers and locusts	Acerididae	maifo	
Crickets	Grylloidea: <i>Teleogryllus</i> <i>commodus</i> <i>Metioche</i> sp.	gúfu shuni	
Mole cricket	<i>Gryllotalpa</i> sp.	gúfu	like 'house cricket'
Stick insects	Phasmatodea	fifurebio	
Leaf bugs	Hemiptera: Coreidae, <i>Mictis</i> sp.	gáyamu	
Mud bugs	Ochteridae	gofupa	
Leaf hoppers	Cercopoidea, Cyeadelloidea	hakiago	
Water strider	Gerridae	sasyon	like some water spiders
Cicadas	Cicadidae	a(r)len, ayauwe	two different forms
Ant lion	Neuroptera: larval <i>Myrmeleon</i> sp.	totoróni	compare with Chuave term "toridi"
Beetles	Coleoptera	segema	general name for 'typical' beetle
Ground beetles	Carabidae	kofaba	
Cockchafers, dung and Xmas beetles	Scarabaeidae	u(k)gabili	
Longicorn beetles	Cerambycidae	gitawo	
Click beetles	Elateridae	udgunu	cause for amusement
Firefly	Lampyridae	samin	
Sago palm beetle	Cureulionidae: <i>Rhynchophorus bilineatus</i>	yagi	eaten

English name	Scientific name	Onabasulu	Remarks
'Musical' weevil	<i>Rhynchophorus ferrugineus</i>	húgu	eaten (Fig. 4)
Hardwood borers	larval beetles of various families	waba	grubs are classified according to host tree
Fleas	Siphonaptera: <i>Pulex</i> sp.	kulubeno	
Mosquitoes	Nematoeera	ẽn(r)o	
Crane flies	Tipulidae	godien	may be same name as dragon/damselfly
Flies	Brachycera, various families	fofan(e)	
Butterflies and moths	Lepidoptera	áulaba	general term (Fig. 3)
Ulysses butterfly	<i>Papilio ulysses</i>	hagág(k)u	
Chrysalis and caterpillar	Pupae and larvae	kẽgab(i)	some eaten
Medium size flying insects	Various orders	búnye	general term
Sawflies	Symphyta	kiwon	
Honey bee	Apidae	norunai, yátu	unidentified form
Wasp	<i>Polistes?</i> sp.	weni	also used as a "given name" by locals
Various ants	Formicoidea	wamurúgu, wariososapule humaiye	collected ant material was lost
Weaver ant	<i>Oecophylla? smaragdina</i>	yési	eaten
Bull ant	Myrmeciinae	ebene giligelelo	known to sting painfully
Spiders and kin—Arachnida			
Scorpion, whip-scorpions	Scorpiones, Uropygi	maidagana	handled with care
Harvestman	Opiliones	áube	
Orb web spiders	Araneidae <i>Gasteracantha</i> sp.	samóro sáubwa	
Wolf spiders	Lycosidae	hada	
Water spiders	Agelenidae, Pisauridae?	sasyou	like water strider
Jumping spider, Huntsman spiders	Salticidae Isopodidae	sáubwa	
Stick spiders	e.g. Tetragnathidae	saro	
Others			
Centipede	Chilopoda	sasákenu	
Earthworm	Lumbricidae	tabaya	every animal living in the earth causes fright
Leeches	Hirudinidae	hibi	



Figure 4.—Onabasulu man using the buzzing weevil *Rhynchophorus ferrugineus* as a "musical instrument", and his mouth cavity as a resonance chamber.

D. Walbiri

The Australian Aboriginal people of the Walbiri tribe, who led the semi-traditional life of a hunter-gatherer society in the country north of the Gibson Desert, were known to early settlers and prospectors around the turn of the century. However, contacts were largely



Figure 5.—Walbiri people, delousing each other in front of their huts.

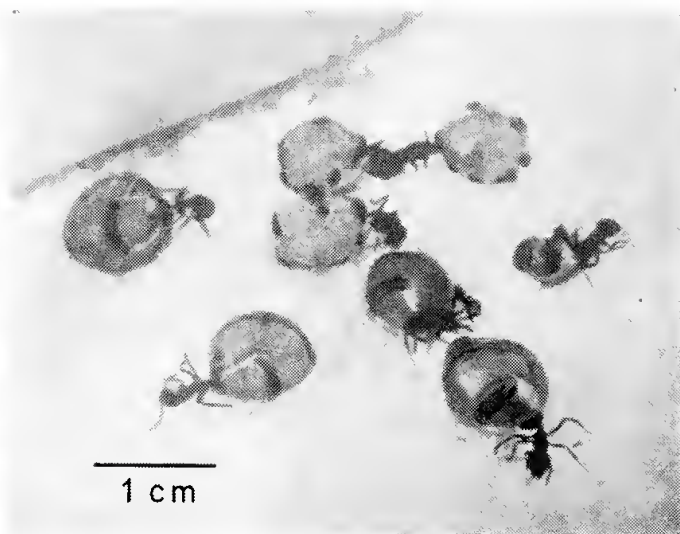


Figure 6.—Walbiri and Pintupi people praise honey-pot ants as delicacies.

limited to visits to pastoral stations until the end of World War II, when Yuendumu, the chief settlement in their reservation, was founded. An account of their traditional way of life as well as lists of plant and animal names is given by Meggitt (1962). Our investigations were carried out during July (Table 4).

E. Pintupi

The Pintupi were one of the last groups of Australian Aborigines contacted by Europeans and it is claimed that the last Pintupi to have given up their semi-nomadic life in the Gibson Desert did so only 5 or 6 years ago (Gould 1970; Hummerston and Dann 1971). Our investigations were carried out during August (Table 5).

Discussion

Papua and New Guinea

The three languages Kiriwina, Chuave and Onabasulu have no common terms for insects and spiders. There is no doubt that the three languages are distinct from each other—two (Chuave and Onabasulu) belonging to only very remotely related linguistic families (Wurm, personal communication), and one (Kiriwina) being completely unrelated. Therefore the phonetic similarity between the Onabasulu "feleli" for edible sago palm grub and the Kiriwinian "kilili" for edible grasshoppers and crickets is almost certainly coincidence.

Walbiri and Pintupi

Walbiri and Pintupi are considered different but closely related languages, and not just dialects. According to Wurm (1971) Pintupi and Walbiri together with Loritja and Pitjantjarra belong to the South-West group of the Pama Nyungan Phylic language family. These linguistic findings are in agreement with genetical analyses based on blood group studies, serological and enzymatical investigations in various Aboriginal tribes of Central Australia

Table 4
Names for arthropods in Walbiri

Insecta—Hexapoda

English name	Scientific name	Walbiri	Meggitt 1962	Remarks
Damselflies and dragonflies	Odonata: Anisoptera, Zygoptera	minduwárara		
Cockroaches	Blattodea	mingindjiri		small forms are considered babies of large species
Mayflies	Ephemeroptera: Leptophlebiidae	(j)imangi		
Termites	Isoptera	máloru		
White ant winged form	<i>Eutermes</i> sp.? <i>Eutermes</i> sp.?		jarinju bandjidi	
Praying mantis	<i>Orthodera</i> sp. (adult) (juvenile)	ieldjildju ninga	julduldju	
Earwigs	Dermaptera	tildigá		
Crickets	<i>Teleogryllus commodus</i>	djábalari djabalari		rarely eaten
Mole cricket	<i>Gryllotalpa</i> sp.		lirinba	
Bush cricket	<i>Oecanthus</i> sp.	tindilga		
Grasshoppers, locusts	Aeridoidea	tindilga	djindilga	occasionally eaten
Stick insects	Phasmatidac <i>Extatosoma</i> sp.	ninga ieldjildju	njinga	
Leaf bugs and other bugs	Hemiptera, e.g. <i>Mictis</i> sp.	brilji brilji		considered a young beetle
Cicadas	Cicadidae		lirinba	occasionally eaten
White aphid	Aphididae	múlulu		
Scale insect	Coccoidea	mandá		some forms eaten
Manna	Psyllid lerp		jiljalbu	eaten
Plant gall	Various families, if not orders	pilburi		some occasionally eaten
Lace wings	Neuroptera: Berothidae	(j)imangi		like other insects that come to light at night
Beetles	Coleoptera, e.g. <i>Blockburnium truncatum</i>	brilji brilji	birailji- birailji	general term
Bark beetle	<i>Sclerorhinus convexus</i>	mándala- ilbrum		
Ladybird, leaf beetles	Coccinellidae, Chrysomelidac	brilji brilji		at first "idilba" given for ladybird but then changed
Water beetles	<i>Eretes sticticus</i>	tjiri		
Large ground beetle	<i>Calsoma schaperi</i>	péndegana		
Scarab beetle	<i>Euryscaphus</i> sp.	ni(e)di ni(e)di		eaten

English name	Scientific name	Walbiri	Meggitt 1962	Remarks
Longicorn grub	Larval Cerambycidae		mijamija	eaten
Weevils, lice	Curculionidae, Phthiraptera		lođu	occasionally eaten (Fig. 5)
Mosquitoes	Nematocera	kjuinjuini	giwinjiwinji	
Flies	Brachycera	ji(u)máangi	jimangi	
March flies	Tabanidae		judulu	
Butterflies and moths	Lepidoptera	binda binda	binda binda	general term
Caterpillar	Larval Lepidoptera	waiburi, wai(o)upi	ladjul	some eaten
Witchetty grub	Cossidae larvae?	málguri	ngalgari	eaten, lives in roots of <i>Acacia kempeana</i> . Collected by girls (pers. obs.).
Caddis caterpillar	Psychidae	álargu		
Ants	Formicoidea, e.g. <i>Bothroponera</i> sp. <i>Polyrhachis</i> sp.	bíngi	bingi	
Honeypot ant	<i>Camponotus inflatus</i>	ing(ü)rani		eaten. Collected by girls under Mulga scrub (pers. obs.)
Honey ant	<i>Melophorus</i> spp.		jirambi, jagula	eaten
Small black ant	<i>Melophorus</i> sp.	nama		
Small shiny ant	<i>Camponotus</i> sp.	gádili gadili		
Winged ants	Males and queens	á(r)ldjimba		
Bull ant	Myrmeciinae	kalda kalda	gadili gadili	
Native honey bee	<i>Trigona</i> sp.	djolala		eaten, collected by men, who smell and listen at possible "honey trees". Examine webs of spiders to find traces of bees (pers. obs.)
Wild bee	<i>Trigona</i> sp.		mnagi	
Wasps hornet	<i>Polistes</i> sp.	kalda kalda	mururururu	like bull ant
Spiders and kin—Arachnida				
Scorpion	Scorpiones	ganda ganda	garangara	
Most spiders	Araneae, various families	(e)inargi	jinargi	including red back spiders
Trapdoor spider	<i>Arbanitis</i> sp.	mambúr(u)mba	mamburunba	
Social spider	<i>Phryganoporus</i> = (<i>Ixeuticus</i>) sp.	málguridjin- bílba		
Other terrestrial arthropods				
Centipedes	Chilopoda	jukungáli	jirindji	
Wood lice	Armadillidiidae	iodínba		

Names for arthropods in Pintupi

Insecta—Hexapoda

English name	Scientific name	Pintupi	Pintupi	Remarks
		(from tape material)	(from Hansen, 1974)	
Damselflies and dragonflies	Odonata: Anisoptera, Zygoptera	wírukuriburi	?	
Cockroaches	Blattodea: <i>Polyzosteria viridissima</i> , <i>Calolampra</i> sp.	kúmpukari nálbidjara	kumputjitjipa ?	recognized from colour plate
Termites	Isoptera	lóngurlma	lungkunpa	eaten
Praying mantis	Mantodea: <i>Orthodera</i> sp.	múndikuero-(pu)	?	considered poisonous
Grasshoppers and locusts	Acridoidea	djíndilga	tjintilyka	occasionally eaten
Cricket?	Grylloidea?	kuć(r)dji kue(r)dji	?	
Bush ericket	<i>Oecanthus</i> sp.	dérkowara	?	
Brown bug	Pentatomidae	énargi	?	
Leaf hopper	Cicadelloidea	júgri jugri	?	some eaten
Stink bug	<i>Mictis</i> sp.	p(l)índilga	?	
Stick bug	<i>Leptocorisa?</i> sp.	wáldoru	?	
Typical leaf bug	Hemiptera: various families, e.g. Lygaeidae, Reduviidae, Pentatomidae	pátana	?	some eaten
Cicada	Cicadidae		tjirrirri	
Stick insect	Phasmatodea	múndikueropu	?	
Lice	Phthiraptera		pilu	
Lacewings and other nocturnal insects	Neuroptera, also Ephemeroptera, Plecoptera, some Hymenoptera	ki(u)wini	?	general term for insects that come to the light at night
Big Lacewings	Neuroptera	wírukuriburi	?	some myths attached to species
Beetles	Coleoptera: Staphylinidae, Scarabaeidae, Tenebrionidae, etc.	nídi nídi	nirrinirri	general term, some adults and some grubs regularly eaten, some species only to be called by particular people (local information)
Ground beetles, large water beetle	Carabidae: <i>Calosoma schaperi</i>	pétidjalili	?	
Water beetle	<i>Eretes sticticus</i>	náng(m)i	?	

English name	Scientific name	Pintupi (from tape material)	Pintupi (from Hansen, 1974)	Remarks
Desert beetle	<i>Sarogus clathratus</i>	nárabai	muputati	
Bark beetle	<i>Sclerorhinus convexus</i>	níripur(l)ka	?	walks and drops dead (local information)
Weevil	<i>Eurhamphus?</i> sp.	búru buru	?	
Ladybird	Coccinellidae	kádilka	katilyka	
Flea	Siphonaptera	kítu	tjitu	presumably eaten
Flies	Diptera	moong	muungu	
Mosquito	Nematocera	ki(u)wini	kiwinyi	
Butterflies and moths	Lepidoptera	bínd(t)a bind(t)a	pintapinta	general term
Caterpillar	Larval Lepidoptera	enomara	yanumarra	
Moth	Lymantridae	máku	nyalpitjarra	like witchetty grub (compare "Remarks" for Walbiri term)
Moth eggs	Lymantridae	mál(b)puru	?	
Witchetty grub	Stem-boring moth larvae	máku	maku	
Bull ant	Myrmeciinae	káldoga	kaltuka	stings painfully
Small black ant	<i>Melophorus</i> sp.	wálga walga	minga	
Large black ant	<i>Camponotus nigriceps</i>	kátapulka	minga	
Winged ants	males and queens	klotap(u)	mukura	
Honey-pot ant	<i>Camponotus inflatus</i>	ngári	ngari	eaten (compare "Remarks" for Walbiri term and Fig. 6)
Native honeybee	<i>Trigona</i> sp.	djórata	tjurratja = delicacy	
Wasp	Sphecidae	mópotari	yiliyilpa	
Others				
Scorpion	Scorpiones	káuparka	kanparrka	
Spider	Various families of Araneae	wálga	wanka	including red-back spider "little bit poisonous" (local information)
Wood louse	Armadillidiidae	kinara(u)	?	

(Kirk, Sanghri and Balakrishnan 1972). There are some terms in our material that are common to both languages. The shared vocabulary either has the same meaning in both ethnic groups e.g. "ni(e)di ni(e)di" for scarabaeid beetle (including Australian Christmas beetle, cockchafer, dung beetles, etc.), or the same term describes different species in the two languages, e.g. "enargi", which in Walbiri means web-spider but in Pintupi depicts a little brown pentatomid bug. The phenomenon that

the same word is used for different things in different but related languages is not extraordinary; for instance, "shellfish" in English means a crustacean or a mollusc, while in German the homophonous term describes a cod-fish.

In other cases two words for the same animal differ only slightly, e.g. "kalda kalda" for bull ant in Walbiri and "kaldoga" in Pintupi; or "djolala" for stingless native honey-bee in Walbiri and "djorata" in Pintupi.

By comparing some of the more similar words in Walbiri and Pintupi—e.g. “ingurani” for honeypot ant in Walbiri and “ngari” in Pintupi; or “kalda kalda” for bull ant in Walbiri and “kaldoga” in Pintupi—a tendency to shorten the Walbiri term appears to exist in the Pintupi language. Also, while in Walbiri at least a few terms have no stress on the first syllable—e.g. “mingindjiri” (cockroach) or “manda” (scale insect)—the accentuation of Pintupi words was found to lie exclusively on the first syllable, even if the words were long, e.g. “wirukuriburi” (dragonflies) or “kátapulka” (large black ant). However no firm conclusions can be drawn from this observation, because of the small number of terms that could be compared.

Nomenclature

The way indigenous people group some insects and spiders is interesting and worth mentioning, though due to the relatively small number of terms collected, any conclusions must be regarded as tentative. For further studies on lexicographical treatment of folk taxonomies, see Conklin (1969).

As was pointed out earlier in this paper, some species of insects could have mythological associations, but since the locals were reluctant to give any information dealing with these forms, they were not investigated here. However, for the majority of arthropods one can conclude that species that are either harmful (i.e. sting, bite, smell, etc.) or beneficial (provide food and raw material, used for decoration, etc.) usually have distinct and specific names. Other insects, although sometimes comprising hundreds of species, are given just one general name if they do not have distinguishing characters other than those used by taxonomists. For example, the little nocturnal creatures that fly to the light at night (certain Lepidoptera, Neuroptera, Trichoptera, Coleoptera, Diptera etc.) are simply called “ki(u)wini” in Pintupi or “jimangi” in Walbiri; almost all butterflies and moths are called “beba” in Kiriwina.

Sometimes similarities in the behaviour of insects cause the natives to use one and the same word for two completely different creatures, e.g. in Chuave “toridi” means both flea and jumping spider (both leap), and in Walbiri “kalda-kalda” means both bull ant and wasp (both sting painfully).

In a number of cases female and male forms of the same species have different names, particularly if they look or behave differently, e.g. the Kiriwina terms “padidi” for male and “siekwapa” for female cicadas. It was found that in Kiriwina and Walbiri eggs, larvae and other immature forms belonging to the same species could have quite different names, particularly if they were in some way of importance to the people. This observation is reminiscent of reports on the very diverse vocabulary used by arctic or mountainous peoples to describe “snow” and “ice” (Basso 1972).

Very often the natives have one general name corresponding to our term “insect”, e.g. “bunje” in Onabasulu for all smaller flying insects, and then have a number of names for particular species within this group, using the distinguishing characters mentioned above. “Bingi” in Walbiri for example means “ant”, but “jirambi” (*Melophorus* honey ant: Meggitt 1962), “gadili gadili”, “nama” (2 different ant species), “kalda kalda” (bull ant) and “ingurani” (dark honeypot ant) are more specific terms.

These specific names may be quite different both from each other and from the more general term as was demonstrated for various ants in Walbiri, but they may also consist of added or exchanged parts of the general term. For instance, in Chuave “oremei” means small fly, but “oremei garumabu” means big fly and “oremei mam” is bumble bee. In Kiriwina “beba” is the term for butterflies and moths, “bebakoya” is the word for the female birdwing butterfly, “bebaim” that of the male, and “poula beba” that of the chrysalis. In the same language “tabuyusapi” means tree wasp and “tabuyuyuvi” ground wasp. The combination of one term with several other endings to describe a number of different species is probably a widely-used practice (Berlin 1972) and has also been reported for Mt. Hagen Highlanders (Strathern 1969).

It hardly need be emphasized that we are far from understanding native nomenclature, but to assume that these people have specific names for each and every insect which they find in their environment seems almost certainly wrong. The situation may be remotely similar to that of European peasants in the Middle Ages, who were unquestionably in much closer contact with Nature and her creatures than we are now, but who, very often, did not even know trivial things like numbers of legs in spiders and insects. The Natural History books of that time accurately reflect the state of contemporary knowledge of insects and spiders.

In conclusion we can say that the classification of insects and spiders based on their phylogenetic relationship to others is a relatively new concept, which has virtually developed into a scientist’s language. Speculations about the developmental background of ethno-botanical nomenclature have been presented by Berlin (1972), and similar mechanisms may be at work in ethnozoological nomenclature. In ethno-entomological terminology it appears clear that what the majority of people, Europeans and non-Europeans alike, are concerned with are the questions: Is it a harmful insect or spider? Is it a crop pest, a parasite or an edible form? If so, that species is likely to be given an individual name to distinguish it from the term used to describe a characteristic and similar form, or from the more general word applied to the group to which it belongs. Other issues, like mythological associations, could well be relevant, but were not investigated here.

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3.—Botany in Western Australia: A survey of progress: 1900-1971

Presidential Address, 1971

by Brian J. Grieve, M.Sc., Ph.D.¹

Delivered 26th July, 1971

Introduction

In selecting the above topic for this presidential address I have been very mindful of the important part played over the years by the Royal Society of Western Australia. Many of the discoveries and developments in botany in this State have been recorded through the Journal of the Society and several presidential addresses have been concerned directly or indirectly with the plant world.

The aim of this survey is to summarize what has been achieved in botany in Western Australia specifically relating to studies involving native plants, to try and indicate what imbalances have occurred and to suggest future approaches. The period from the start of the century up to the present time has been selected largely because it was in the early 1900s that facets other than purely descriptive ones in botany first began to be apparent here. To place the whole in perspective it seems desirable, however, to take a brief look at the history of pre-1900 botany in the State. Fortunately much of this has already been well documented. The fascinating story of the work of the early British and Continental botanical explorers has been recorded by Diels (1906), Gardner (1926) and Smith (1958). The human background of the painstaking collecting of native plants carried out by interested early settlers in Western Australia, notably James Drummond and Georgiana Molloy, has been illuminated by the researches of R. Erickson (1969) and A. Hasluck (1965), respectively.

The extent of scientific knowledge of the flora of the State from explorations and collections in the pre-1900 era was made known to the world in certain notable works from which three have been selected for comment. The first two related exclusively to Western Australian flora and the third to that of the whole continent. In his "A Sketch of the Vegetation of the Swan River Colony", Lindley (1839) summarized the then available knowledge regarding the flora. This was derived from a study of an herbarium of about 1000 species comprising the collections mainly of James Drummond and of J. and R. Mangles which had been forwarded to England. Lindley described a large number of new species and listed the synonymies of others in the light of botanical development at that time. The second work dealt with the specimens collected

by the German botanist L. Preiss during his stay in Western Australia from 1838-1842. His plant collections were expeditiously worked up and named by a team of outstanding European botanists under the leadership of Lehmann (*Plantae Preissianae* 1844-1848).

The third major work was that of Bentham, and it applied to the whole Continent (*Flora Australiensis* 1863-1878). This monumental work (which owes much to the co-operation of F. von Mueller in providing specimens and his published and manuscript descriptions of new species) gave an excellent picture of the West Australian flora at the time, although it would now appear that Bentham could have taken greater advantage of the data on the distribution of species documented in *Plantae Preissianae* (Diels and Pritzel 1904-5; Gardner 1926; Smith 1958), and of Brown's collections at the British Museum (S. Le Moore 1920-22).

Turning now to the history of botany in the post-1900 period, we note the beginning of a wider approach which followed up the visit of the German botanists Diels and Pritzel in 1901-1902. Their first publication, "*Fragmenta Phytographiae Australiae occidentalis*" (1904-5) was essentially concerned with taxonomy. Many new species were described and they also extended our knowledge of the distributions of known species. In addition their analyses led to the formulation of the boundaries of the botanical districts of south-western Australia which, with relatively minor modifications, have survived to the present day. But it was in "*Die Pflanzenwelt von West Australien*" (Diels 1906) that the full impact of the then current European botanical thought was felt. Diels applied many of the ideas expressed in Schimper's "*Plant Geography upon a Physiological Basis*" (published 1898; English edition 1903) to the West Australian scene. He first surveyed the then known plant world of the whole of Australia and used this as a framework for a more detailed account of the western region so as to bring into prominence those vegetative features which give to Western Australia its greatest individuality. He described and discussed the vegetation formations south of the tropic of Capricorn, their ecology (relationship to climate and soil) and distribution, the morphology and anatomy of characteristic plants and the taxonomic relationships and possible lines of evolution of the flora. The impact of these two great works on Western Australian botany appears, however, to have been quite

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limited at the time, due no doubt to their having been published in German. There is no mention of them for instance in the account of the State's flora given by East in "*The Cyclopaedia of Western Australia* (1912). But both works, and particularly that of Diels' have since become veritable source books as taxonomic, ecological and eco-physiological botany developed.

Although botanical exploration and description of new plants by numerous workers proceeded actively over succeeding years, there was a long gap between Diels and Pritzel's books and the appearance of another really significant integrative botanical work. The main reason for this appeared to be that for many years the main thrust of botanical investigation was directed more towards economic aspects, particularly the study of poison plants and of fungal diseases and nutritional problems in crop plants, as increasing areas of land were opened up for agricultural development.

The stage for a more balanced botanical development, however, began to be set in 1926 when Dr. W. Carne (Government Economic Botanist and Plant Pathologist) read a paper at the A.N.Z.A.A.S. meeting in Perth, stressing the need for consolidating the basic floristic knowledge accumulated in the past and advocating the building of a central Herbarium to incorporate collections currently separately housed in the Departments of Forestry and Agriculture² and at the State Museum. He also urged the need for preparation of a Handbook to the Flora, pointing out that Western Australia had fallen far behind the other States in this regard. Following Carne's departure from the State in 1928, his views bore fruit. The position of Government Botanist was in effect recreated, the incumbent of which was to be concerned primarily with flora and vegetation, while the separate position of Government Plant Pathologist was to deal with disorders and diseases particularly in plants of economic importance. One may speculate that the lack of a State Flora long after every other State had such publications, was due partly to the bias towards economic botany from 1910 onwards but perhaps more importantly to the unfortunate fact that successive Government Economic Botanists did

not stay long enough in the State to build up an adequate background of knowledge of the flora. The same was true of University appointed botanists. Between the critical years of 1910 and 1928 seven professional botanists came and went. The Economic Botanists, Drs. Herbert and Carne, for instance left after stays of three and six years respectively. The measure of their potential importance for Western Australia had they stayed longer is apparent from the quality of their later work elsewhere in Australia. In the University Professor Dakin and Dr. Cayzer, despite the distraction of World War I, which commenced shortly after their arrival, began to lay the foundations for a newer approach to the flora. (Cayzer for instance had commenced a Key to the Flora of the Swan Coastal Plain area, while Dakin as well as translating Diels' book was studying the biology of the Albany pitcher plant.) However by 1920 both had left the State to carry on their main life work in other universities.

Be the above as it may, with the appointment of C. A. Gardner as Government Botanist in 1929, the short-term pattern of stay changed, allowing a long, uninterrupted build up of knowledge of the flora. Gardner³, who had already been involved for some years in the study of Western Australian plants, first in the Forestry Department, then in the Department of Agriculture where he became Assistant Botanist under Dr. Carne, was soon to provide an important botanical landmark. This was his publication in 1930 of the "*Enumeratio Plantarum Australiae Occidentalis. A Systematic Census of the Plants occurring in Western Australia*". This listed all the then known native and introduced species (5578 and 275 respectively) in the State. Even more importantly it provided a bibliography listing the authors, journals and dates of publication of the original papers describing the species, and sorted out many nomenclatural difficulties. Over the next three decades C. Gardner was to describe (mainly through the Journal of the Royal Society of Western Australia) a host of new species and to acquire a unique knowledge of the flora. Much of his accumulated knowledge, particularly in relation to the distribution of plants, was contained in his presidential address to this Society in 1942, the title being "The Vegetation of Western Australia with special reference to the Climate and Soils". It is worth noting here that during the 1930s there had also been remarkable developments in the cognate discipline of Soil Science. Dr. L. Teakle, who had spent several years studying soil patterns in Western Australia, in 1939 summarized his results in his presidential address to this Society. His paper entitled "A

¹ W. Dakin (Professor of Biology in the newly opened University of Western Australia, 1914) quickly appreciated the value of Diels' work and was responsible for a large part of its translation. Owing to his return to England in 1920, however, the work was not completed. A copy of the manuscript, together with some additional translatory notes apparently by Dr. Bennett (Biology Department) and Dr. Herbert (Economic Botanist) was found among early papers in the Botany Department when the writer was appointed here in 1947. Because of its obvious value for teaching and research purposes, the translation was completed. It is currently being updated with a view to its possible publication.

Further note.—A second typed copy of the original translation with additional notes by D. Herbert and C. A. Gardner has recently been sighted in the State Herbarium Library. This was bequeathed to the Herbarium following the death of C. A. Gardner in 1970.

² Dr. Sutton (Director of Agriculture) first expressed this view in 1923.

³ Dr. Herbert (verbal communication) tells the story of how he first discovered C. A. Gardner. One weekend in 1919 in the Public Library he came across a young man (then a Bank Clerk) who was laboriously copying out keys from Bentham's "*Flora Australiensis*" in order to be able to identify plants in the field. Finding that his ambition was to become a botanist, Herbert when unable to have him appointed to his own staff, recommended him successfully for a position as botanical collector in the Forestry Department.

Regional Classification of the Soils of Western Australia" apart from mapping and defining soil zones, led to a better understanding of aspects of plant distribution in the State.

Having now provided a background by outlining the more important historical botanical landmarks in so far as descriptive botany is concerned, we may next turn our attention to examining in detail progress in the different facets of botany. In relation to this survey and assessment of progress it is necessary to appreciate that since 1900 there has been a continuing and accelerating tempo of change in the pattern of botanical interests, in concepts and climate of thought leading to the development of many new branches. Modern botany is in all its ramifications a huge field and partly because of this it is subject to differential development. Professor Bower (1938) in reviewing 60 years of Botany in the United Kingdom, makes an apt analogy to illustrate this development of botanical study as a whole.

He describes it as being similar to the progress of a flock of sheep advancing fan-like over a large plain. The irregularities of formation which develop are defined either by individual enterprise or by the varying richness of the pasture. In a similar way botanists stimulated by individual originality or by opportunity may develop some part too far and too fast; other parts may lag behind unduly as being relatively unfashionable so that individual branches of specialisation may lose touch with one another and an imbalance develops. If this picture be representative of the growth of botany in a major world centre showing that certain imbalances do occur, how much more likely would it be expected to show up and in a more extreme form in a geographically isolated State with so few working botanists. In fact, such imbalances have occurred. Fortunately in our time with the wider representation of different major branches of modern botany active in the University, the State Herbarium, the King's Park Botanic Gardens and the Regional Division of C.S.I.R.O., imbalances if they occur are now less likely to persist. But it is a position that needs constantly to be reviewed. The sub-branches or divisions of modern botany which have relevance for this review are numerous. We may now proceed to examine these to assess wider scientific aspects of botanical achievement in Western Australia.

Classical or Alpha Taxonomy

Over the period of time covered in the preceding largely historical review, taxonomy dealt mainly with the study of classification or the ordering of plants into classes essentially on the basis of their morphology. The fitting of distinct latin names to each of the classes recognized in a classification is referred to as nomenclature. Over the years a "code" of rules governing the application of names to plants had been developed. The basic unit was the "species" which was accepted at the time as having objective reality and some degree of permanence. The methods of description were based on individuals and the "type" concept.

Before proceeding to discuss newer aspects of taxonomy some further comments regarding the status of basic descriptive taxonomy in Western Australia may be made. At the time that Diels and Pritzel came to Western Australia in 1901-1902, the lay opinion was that there was little or nothing more to be learnt about the flora. When, however, Diels and Pritzel's extensive collections were worked up, 55 new species were described and they provided also much new data on distribution and growth forms of earlier described plants. Although over succeeding years many new plants continued to be discovered the lay view persisted that the flora had been thoroughly dealt with. Both Carne and Gardner in the mid-1920s had occasion to deprecate this. A vindication of their view is contained in the fact that since the publication of Gardner's "*Enumeratio Plantarum Australiae Occidentalis*" in 1930, several new genera and at least a hundred new species have been found. Interestingly enough also, the majority of these were found in the better explored south-west botanical province. When the flora north of the Tropic of Capricorn comes to be more intensively collected there will no doubt be a very highly significant increase in the number of taxa. This should dispel any idea that taxonomists spend much of their time working over "old hay". So far, a State Flora has not eventuated.¹ However, now that the State Herbarium is housed in its own specialist building with excellent back-up facilities, its scientific staff can give more time to research and the outlook is hopeful. The publication for instance in the Herbarium's new journal "*Nuytsia*" of revisions of key genera in the family Rutaceae (Wilson 1970) and the check list of the Orchidaceae (George 1971) are essential steps towards the preparation of a regional flora which might precede and so pave the way for any new "Flora Australiensis".

It seems appropriate here also to refer to the contribution to the knowledge of the south-western flora by the amateur botanist, Dr. W. Blackall. Exercised by the fact that by the mid-1930s there was still no current handbook available on how to identify flora, Blackall (who had collected extensively on joint expeditions with the Government Botanist) conceived the idea of producing illustrated keys for this purpose. He had made considerable progress with this work but unfortunately he died in 1941 before the project could be completed. As the Government Botanist and his staff, committed as they were to the State Flora, could not complete it, the work lay dormant for several years. Fortunately the Senate of the University of Western Australia on being presented with the manuscript in 1948 was persuaded of its potential value and commissioned the Head of the Botany Department to complete it with a view to publication. The work proceeded and Part I was published by University of W.A. Press (as by Blackall, edited by Grieve) in 1954, Part II (Blackall and

¹ Part 1. The Gramineae, by C. A. Gardner was published in 1952.

Grieve) in 1956, Part III (Blackall and Grieve) in 1965, while the final volume is nearing completion. The publications by R. Erickson providing descriptions and keys for the identification of Orchids (1951, 1965), Trigger Plants (1958), Droseras (and other insectivorous plants) (1968), constituted another highly valuable approach. Mention must also be made of the publication in 1965 (revised 2nd edition, 1970) of "*A Descriptive Catalogue of Western Australian Plants*" edited by Dr. J. Beard, Director of King's Park and Botanic Gardens. This provided an up-to-date listing of the species housed in the State Herbarium together with notes on their habitat, habit of growth and flowering period.

The above publications helped to make more generally accessible the accumulated floristic knowledge in the State. The corpus of the more recent scientific material which they incorporated was built up by a large number of botanists from the post-Bentham-Mueller era to the present time. These researchers include C. Andrews, L. Diels, K. Domin, A. Ewart, W. Fitzgerald, D. Herbert, K. Krause, J. Mildbraed, S. Le Moore, A. Morrison, C. Ostenfeld, E. Pritzel, A. Purdie and O. Sargent, who were active between 1900 and the early 1920s.¹ Over the period 1922-1942 (and to a lesser extent up to 1964) the local taxonomic scene was dominated by C. A. Gardner with his numerous publications, particularly in the Royal Society of Western Australia. N. Burbidge, working in Western Australia, studied and published papers dealing with the *Triodia* grasses between the years 1938 and 1944 (also up to 1960 from the eastern States after joining C.S.I.R. [now C.S.I.R.O.]). Over a wider period and extending up to the present the contributions of eastern States based botanists and of overseas botanists studying pan-Australian genera are notable. Prominent among these are C. Ali, A. Barlow, R. Belcher, S. Blake, J. Black, B. Briggs, G. Benl, H. van Bruggen, N. Burbidge, R. Carolin, G. Davis, H. Eichler, E. Ising, L. Johnson, F. Kraenzlin, N. Lothian, R. Melville, C. Norman, C. Rao, A. Orchard, H. Rupp, R. Schodde, A. Schindler, V. Summerhayes, D. Symon, M. Tindale, J. Vickery, L. Watson, J. Willis, and E. Wimmer. The decade 1960-1970 was marked by a significant number of taxonomic publications appearing from members of the staff of the State Herbarium (R. D. Royce, P. Wilson and A. George), from G. Smith (University) and co-workers, from Dr. N. Brittan (University) and his research students and from a visiting botanist from U.S.A., S. Carlquist.

In all, the above adds up to an impressive amount of progress in descriptive taxonomy. From current observations it is apparent that the discovery and description of new species is continuing at an active rate, while the review and redefining of older ones is receiving increasing attention. The stronger emphasis on monographic studies of families and genera is also an encouraging trend.

¹ For a complete list see C. A. Gardner, (1926) under Early Works.

Experimental Taxonomy or Biosystematics

The last 30-40 years has seen the rise of what has been called Experimental Taxonomy which co-exists with and overlaps descriptive Taxonomy. The term Biosystematics is also used and this perhaps indicates more clearly the emphasis which is placed on the application of cytogenetic, biochemic, morphologic, anatomic and statistic procedures on the identification of evolutionary units, the use of experiment to determine their genetic inter-relationship and the part the environment plays in their formation. By its nature this work involves considerable use of laboratory techniques and its development in this State so far has consequently been closely associated with the Botany Department in the University of Western Australia with its specialist in this field (Dr. N. H. Brittan) and his higher degree students. Some of these latter one may note belong to the State Herbarium staff so that these newer approaches may be expected to develop further there. Dr. Brittan concentrated on the variation, classification and evolution of flowering plants with particular reference to the genus *Thysanotus* in the Liliaceae. His study of this genus has provided evidence of variation at single gene mutation level (flower colour) and of polyploidy. This topic provided the subject for his presidential address to the Royal Society of Western Australia in 1962. In addition, his comparative anatomical and other investigations of *Thysanotus* species have proved very helpful in Descriptive Taxonomy (1960, 1971). Three of Dr. Brittan's research students have also made definitive contributions. J. Green (1960) examined the Haemodoraceous genus *Conostylis* and studied its inter-generic relationships with *Blancoa*, *Anigozanthos*, *Macropidia* and *Tribonanthes*. It is of interest to note that recently a Netherlands botanist, Geerinck (1969) has implemented a change foreshadowed by Green involving the suppression of the genus *Blancoa*, placing the single species under *Conostylis*. E. Bennett (nee Scrymgeour) (1970) has studied the taxonomy and cyto-taxonomy of all the Australian species of *Hybanthus* and the work has led to the erection of a new species. Ten Choo (1970) dealt with the genus *Lomandra* in the Xanthorrhoeaceae, and showed that anatomical features of the leaf were helpful as a supplementary basis for classification. Study of the variation in the inflorescence led to the postulation of possible lines of evolutionary development.

The above researches on experimental taxonomy have allowed a clearer understanding of the limits of the genera so far studied and have as well clarified many points at the species level. It is hoped that this newer experimental approach will intensify in the future.

Plant Geography

Knowledge of the distribution of plants is naturally closely related to taxonomy but it is also part of the study of regional communities and merges into ecology. In its wider aspects

the plant geography of Western Australia can not be considered independently of that of the whole of Australia, while the Continent itself has to be fitted into the overall scheme of world plant geography. Our appreciation of plant distribution is affected by our knowledge of the changing distribution and extent of land masses and oceans throughout geological time and by theories such as Continental Drift. The words of Shakespeare's Henry IV apply very aptly for Australia:

“Oh God! that one might read the book of
fate,
And see the revolution of the times
Make mountains level, and the continent,
Weary of solid firmness, melt itself into the
sea!”

Western Australia owes much of its vegetative uniqueness to just such a sea encroachment. The first post-1900 study involving Western Australia was by Diels (1906). He applied many of the new Schimperian concepts in discussing our vegetation scene and for a long time this account stood as the only analysis of plant distribution here, and of the State's floristic relationships with other parts of Australia. Gardner (1926, 1942) re-examined the plant geographical situation in the light of the additional evidence available to him from exploration and collection, and elaborated on Diels' analysis. It was not until 1947, however, that a further big advance came when Crocker and Wood in South Australia presented their findings arising out of the greater knowledge becoming available of the climatic and soil patterns of Australia and of the post-Tertiary historical sequences. They ascribed the high degree of endemism in south-west Australia to the fact that it had been effectively isolated by inundation of a large part of southern Australia in the Miocene. Then despite the retreat of the sea during the later Pliocene period the isolation of the flora had been maintained by edaphic factors (calcareous soils) and by climatic factors. The presence of lateritic soil in the south-west of Western Australia was considered to be the factor largely responsible for the selection of the Australian element there.

Burbidge (1960) in a re-examination of the phytogeography of the Australian region accepted the concept that floristically south-western Australia had been isolated by both geographic and climatic factors. She noted also that it was far from any well-marked migration route and lacked special affinities with South African flora, although this might have been expected under the Continental Drift hypothesis. She considered that it was because of the relative difficulty of communication with the tropical zone and with some other parts of the temperate zone, that a highly endemic flora had developed. These factors were also responsible for the persistence of many relicts. Burbidge emphasized the strong generic affinities with the South American flora strengthening the view that in the past there had been communication between the two land masses. In this connection the

discovery of the Rafflesiaceous parasitic plant *Pilostyles hamiltonii* (Gardner 1948) in the south-western botanical province has great significance.

Reference may also be made at this point to the valuable palaeobotanical work of Churchill (see pp. 40-41) in relation to the Plant Geography of Western Australia. J. Green (1964) presented details of distribution of discontinuous and presumed vicarious species pairs in south-western and south-eastern Australia. Selected species are discussed in relation to the geological and climatic history of Australia. He considered that while the discontinuity for most of the species could be explained on the basis of Crocker and Wood's or Burbidge's hypotheses the possibility that some disjunctions may have their explanation in long-distance wind dispersal should not be ruled out. In connection with the above problem of discontinuous distribution the work of Anway (1969) and of J. A. McComb (1966) in the Cytogenetics and Genetics section (pages 43-44) should be consulted.

One of the important features of the Western Australian flora is its high degree of endemism. Gardner (1959) and Royce (1965) have pointed out that the endemism is especially noticeable in the south-western vegetation province and they have estimated it to be as high as 75 per cent. The most recent study of endemism at the species level has been carried out by Beard (1969). He analysed data for the three Western Australian vegetation provinces and found the values to be as follows:— South-western 79 per cent, Northern 77 per cent and Ereman 45 per cent. With regard to the plant geography of the Northern province, Gardner (1942, 1959) described the salient features indicating the importance of the Indo-Melanesian (Palaeotropic) and Madagascan elements in relation to the dominant Australian element in the flora. Beard (1967) in connection with his study of northern vegetation types, has provided the most recent comment. It seems clear that much more collecting work needs to be done and data on taxa and distribution patterns built up to allow more meaningful conclusions to be made regarding the overall plant geography of the Northern province.

Ecology

Plant ecological studies have gone through a series of phases from the early descriptive investigations where habitat and soil relations of vegetation were examined, through the successional, the edaphic and eco-system approaches, becoming increasingly quantitative and sophisticated. Some of these phases are represented in larger or smaller degree in ecological research in Western Australia and will now be considered. The first descriptive eco-plant geographical study of the south-west and adjacent eremean areas we owe to Diels (1906), who outlined and named the main plant communities, discussed adapta-

tions of plant groups, and in the light of the then available knowledge of climate and soil assessed their relation to the environment.¹ A closer delineation of the forest formations in south-west Australia was made by Gardner (1923-1927), by Kessel and Stoate (1936), and by Brockway (1941). Gardner (1923, 1925) also provided an account of the forest formations of the north-west region.

In the 1930-1942 period, with one important exception (Williams 1932) and apart from Gardner's generalized descriptive account of all the vegetation provinces in Western Australia (1942), no ecological studies in depth were carried out here such as characterized this period in the eastern States. There the earlier accepted views on the relationship between vegetation and its habitat were questioned and tested. Ecological aspects of succession, of climate, and edaphic climaxes, the nature of associations, consociations, societies and forest types were debated, and considerable increases in knowledge of Australian plant ecology and modifications of earlier accepted theory developed (Wood 1939; Pidgeon 1942). The exception mentioned above to the general missing out of this phase in Western Australia was however an important one, and one which if circumstances had favoured its continuation and extension might well have anticipated by several years the break-through on the edaphic climax association made by Wood in South Australia. The work was a small-scale analytic approach with emphasis on the edaphic factor carried out by Williams (Botany Department, University of Western Australia, and under the direction of Dr. Armstrong) in the Darling Range and was supplemented by a further study commenced in the Beraking area. Williams' investigations appear to have been catalysed by the work of the soil scientist, Prescott, in South Australia, who in 1931 had produced the first soil map of Australia and had recognized that the extensive lateritic formations in Western Australia were a fossil soil representing the remains of an ancient B horizon. In his study of the composition of the vegetation in the valleys and on the hill tops in the Darling Scarp area at Darlington, Williams formulated the view that the *Eucalyptus marginata* association was adapted for laterite and lateritic gravel and that as the plateau became dissected by water courses and as valley formation continued, the *E. marginata* association was being locally destroyed and replaced by an *E. calophylla*-*E. redunca* association. Work on the related Beraking area had also been commenced by Williams in 1932 but

was interrupted due to his transfer interstate on joining C.S.I.R. (now C.S.I.R.O.) later that year. The field work for the Beraking study was completed when he came back later on a brief visit to Western Australia and the paper was communicated to the Royal Society of Western Australia in 1944 but due to the war was not published until 1948. The conclusions he reached were that the distribution of plant communities could be determined by edaphic factors such as soil type (determined by the underlying rock formations), the maturity of such soils and the soil water relations, as Wood (1939) had by then thoroughly worked out in South Australia. Williams in his paper points up an imbalance, commenting rather sadly on how Western Australia had lagged far behind the other States in these aspects of the study of ecology.

It is appropriate also to note here a further development in the soil science field in Western Australia which had an impact on ecological aspects of vegetation study. Trakle (1938), building on the foundations laid by Prescott (1931), described nine main soil zones and thirty-three regions into which the State could be divided. He showed that the known vegetation types were related to the soil zones and regions and both were closely related to the climatic rainfall factor. Teakle's work was followed by that of Gardner (1942-44) who summarized existing knowledge of the overall vegetation formations of Western Australia and discussed their relationship to climate and soil. During the 1940s also several helpful descriptive ecological accounts were given by Burbidge of vegetation in the north-eastern goldfields area (1941-42), the De Grey-Coongan area (1942-45)² and the Eighty-Mile Beach (1941-44)² before she too left the State on joining C.S.I.R. From about 1950 onwards more attention was focused on ecological work by the University Botany Department and a series of studies were made by different research students under the direction of B. J. Grieve and A. M. Baird. A. Holland (M.Sc. Thesis 1953) studied the ecology of *Eucalyptus* formations in the south-west and southern eremean regions. He found the edaphic factor to be dominant over the climatic factor in maintaining associations and suggested that the vegetation was possibly selective with respect to micro-nutrient elements, since N and P were low in all vegetation zones examined, and pH was not a factor. In commenting upon the existence of outliers of *E. marginata* (near Kulin) and of *E. diversicolor* (at Porongurups and Mt. Manyeaks), and on the occurrence of fossil podsoles and of wave platforms cut in the shore line, Holland suggested that climatic fluctuations had taken place with a warm wet period occurring possibly between 4000 to 8000 years ago. It may be interpolated here that D. Churchill (Ph.d. Thesis 1961, published in part 1967), using a palaeo-ecological approach provided confirmatory evidence indicating that climatic fluctuations had affected distribution of *E. diversicolor* and *E.*

¹ In the wider sense as affecting overall Australian forest ecology, it is of interest to note that, as recently claimed by Specht (1970), an early misinterpretation of the application of Diels' expression "Sclerophyllen-Wald" to the forest tree stratum rather than to the lower storey vegetation and the consequent introduction of derivative terms such as "dry sclerophyll" and "wet sclerophyll" in describing southern and south-eastern Australian forest vegetation, has caused much confusion. To overcome this Specht has proposed the term "Shrubby open-forest" for Diels' "Sclerophyllen-Wald".

² Publication delays due to the war.

calophylla. The climate appeared to have been wetter from 4 000-3 000 B.C. and then gradually became drier, with further fluctuations between wet and dry up to the present time.

N. Speck (M.Sc. Thesis 1952) dealt with the ecology of the metropolitan sector of the Swan Coastal Plain. He recognized two formations, dry sclerophyll forest and scrub. *E. gomphocephala* (tuart) was found essentially only on the Cottesloe Soil Association, while *E. marginata* occurred on the yellow sands of the Karrakatta Soil Association, the deeper sands of the Cottesloe Association and the gravelly sands of the Forrestfield Association. Other plant associations, consociations and their faciatiations were also shown to be closely associated with particular soil types. Climate, notably rainfall, was found to affect distribution, while bush fires were recognized as the most important biotic factor operating. Speck's work also included an ecological study of the University Botany Department reserve at Cannington. This area, subject to flooding in winter and severe dryness in summer, provided an ecological niche for many unusual plants which now appear to be at risk due to changes in drainage arising out of increasing urbanisation. The vegetation of the Darling and Irwin botanical districts was also studied by N. Speck (1958) who concluded that while climate was the over-riding factor in the selection of vegetation of the area as a whole, the edaphic factor determined the distribution of communities within the area. He confirmed that the 17.5 cm winter rainfall isohyet, as indicated by Gardner (1942) more clearly defined the limits of the south-west floral elements than the original 30 cm line (average yearly rainfall) of Diels and Pritzel (1904-5). Speck also modified Diels and Pritzel's outline of the Avon botanical district, separating the more northerly part to form a new district which he called Lesueur. The line of separation was clearly marked by a change in soil type. Dr. Brittan, with his research student Silstury (1955), in studying the ecology of *Kennedia*, showed that within a single climatic zone the edaphic factor (podsollic or lateritic soils of inherently low fertility) was the most important. The vegetation and soils of Garden and Carnac Islands were described by W. McArthur (M.Sc. Thesis 1952, published 1957). Following a disastrous fire on Garden Island in 1956, the process of regeneration of the *Acacia*, *Callitris* and *Melaleuca* communities was studied by A. M. Baird (University, Botany Department staff), the work being published in 1953.

It may be noted here also that Miss Baird has for several years been making a study of the effect of fire on regeneration of native species on the mainland with special reference to the Swan Plain area and specific plots in King's Park. It is anticipated that findings from this work will be published in due course. Regarding the effect of fires on vegetation, Gardner (1959) noted the fact that some plant communities included a number of species which were apparently well adapted to periodic fires.

The vegetation patterns on other islands off the south-west and southern coasts have been recorded by a number of workers as follows:—Rottneest Island, Storr, Green and Churchill (1959); Abrolhos Islands, Storr (1960, 1965); Bernier and Dorre Islands, Shark Bay, Royce (1962); Recherche Archipelago, Willis (1953). Descriptive accounts of the ecology of various arcas in the lower south-west have also been made. G. Smith (University Botany Department staff) dealt with the vegetation of the Porongurups (1952), while J. S. Beard (King's Park Botanic Gardens) noted relationships between "stripe" patterns in plant communities and soil conditions in the Ravensthorpe area. The work of Holland (1953) in this area has already been mentioned. Lange (1960), in an autecological study of the relationship of twelve tree species in an area of transition near Narrogin, found that the incidence of the species related to soil surfaces and to rainfall.

Sand dune vegetation in the region approximately 20 miles north and south of Perth has been studied by G. Smith (1957, 1970), while Sauer (1965) has surveyed the seashore vegetation over more extensive northern coastal areas.

The study of "wetland" ecology has attracted relatively little attention so far despite the fact that such studies are clearly becoming urgent. A valuable pioneering study in depth has however been made by Drs. J. A. and A. J. McComb (University Botany Department) dealing with the Loch McNess fresh water lake area in Yanchep National Park (1967). They recognized sedge swamp and sedge fen and showed that these were similar floristically and structurally to those found in wetlands elsewhere in Australia and abroad.

Turning now to more northern botanical areas we may note the descriptive accounts of W. Fitzgerald (1916) and Gardner (1923, 1925, 1942). Gardner and Bennetts (1956) delineated more precisely in map form the boundaries of the botanical districts north of the Tropic of Capricorn. Burbidge, in addition to her earlier mentioned descriptive ecological studies in the north-west, also published on the Pilbara area (1959), and described the ecological succession after fire in *Triodia* grasses (1943), while Royce (1964) discussed the relation of soil and climatic conditions on Depuch Island near Roebourne. More detailed ecological accounts of the vegetation of the North Kimberley and West Kimberley regions and of the Meekatharra-Wiluna area have been given by the C.S.I.R.O. botanists Perry (1970), Speck (1958, 1960, 1963), and Speck and Lazarides (1964).

With regard to inland desert areas we may note first the work of E. R. Johnson and A. M. Baird (1970) who gave an account of the flora and vegetation of the Nullarbor Plain near Forrest, and of J. Willis who described vegetation in the Eucla district (1959). Dr. J. S. Beard (1968, 1969) has made a special study of the ecology of desert regions, namely:—the Great Sandy Desert, the Gibson Desert, the Great Victoria Desert and the Nullarbor Plain. These

comprise about two-fifths of Western Australia. He subdivided these desert areas into botanical districts or natural regions each of which has its own characteristic landscape and vegetation. The principal vegetation types present are *Triodia* hummock grassland, Mulga scrub (on red loams) and Mulga parkland (on laterite). In a further development of his ecological studies Beard is currently systematically describing and mapping the vegetation of Western Australia (1969a, 1971). In addition the first of a series of vegetation maps in colour together with an explanatory memoir (commenced while Dr. Beard was Director of King's Park and Botanical Gardens and continued in association with Professor Webb, Geography Department, University) is being prepared for publication. The extension of this approach has great importance for our knowledge of the overall ecology of the State.

Finally mention must also be made here of the work done by a State Sub-Committee (under the chairmanship of Dr. Ride, Director of the Museum, and appointed by the Australian Academy of Science) in listing details of all National Parks and Nature Reserves throughout the State (1963). This compilation is of great value for future vegetation studies as well as recording the present degree of conservation of State flora and fauna areas.

Statistical Ecology

The use of statistics in the analysis of distribution of individual species within communities and in relation to the classification of plant species began to find application in Europe and the United States of America during the early 1930s. In the post-war period this approach intensified and methods were rapidly developed whereby vegetation could be described quantitatively. Such descriptions could then be used as a basis for classification or ordination. Dr. Goodall (while with C.S.I.R.O. in Perth and Hon. Reader in Botany in the University of Western Australia) published many papers in this field (1963, 1964, 1966, 1967). Although most of these were theoretical in approach and so applied to statistical studies of vegetation in general, we may note that part of the data on which they were based had been obtained in the course of his study of Western Australian vegetation. One of Dr. Goodall's research students in the University (W. A. Loneragan) is currently applying selected statistical procedures in a study of portions of the Jarrah forest and across the ecotonal region to the Wandoo woodlands (1966). J. Havel (W.A. State Forestry Department) has also used the objective statistical approach method to analyse and assess through the native vegetation the potential of the northern part of the Swan Coastal Plain for the growth of *Pinus pinaster* (1968). The production of a computer map of the flora of Western Australia is now highly desirable. In this connection it may be noted that Dr. Goodall has made surveys and samplings of vegetation through a selected region of Western Australia with a view to commencing the production of such a computer map.

Barrow Island, off the north-west coast, has already been so mapped. Unfortunately this work has been interrupted by Dr. Goodall's departure to take up a Chair of Ecology in the United States of America, but it is hoped that the project may be resumed at some later date.

Palaeobotany, Palynology and Palaeoecology

In discussing the origin of the present Australian flora, Herbert in 1950, could still only conjecture that in the early Tertiary there must have been something like a pan-Australian flora from east to west and so it would have been possible for Beech (*Nothofagus*) forests to extend to Western Australia where now they could not exist. He makes the comment "The fossil record is however silent on this point". By 1954, Dr. Cookson, a palaeobotanist in Melbourne was able to break this "silence". Already familiar with the micro-flora from the older Tertiary coal seams in Victoria and South Australia, she was able to find matching forms in material sent to her from a carbonaceous deposit obtained from a bore in the Nornalup Inlet area on the south coast of Western Australia. Thus she provided strong evidence that during the early part of the Tertiary (Eocene), the floras of the eastern and western portions of Australia were essentially similar. The scene now changes back to Western Australia where D. Churchill (a Ph.D. student in Botany) had developed a new method for concentrating pollen grains (1957) which facilitated the study (carried out in collaboration with Dr. Balme of the University Geology Department) of pollen grains in carbonaceous sediments at Coolgardie. Pollen grains of Beech (*Nothofagus*) and pollen of proteaceous and podocarpaceous affinities were identified (1959). Also at this time McWhae et al. (1958) had found *Nothofagus*, *Araucaria*, *Bankisia* and *Gleichenia* in Tertiary (Eocene) sediments near Kōjonup. Thus Cookson's discovery was confirmed and extended. Balme and Churchill were also able to suggest that in Eocene times the sea when at its most transgressive phase, must have reached as far north as Coolgardie.

Churchill (1959) next applied his pollen analysis technique to a study of a bore sample of submerged freshwater peat from 68 feet below sea level at the site of the "Narrows" bridge over the Swan River. He was able to show that pollen of *Eucalyptus wandoo* and *E. gomphoccephala* (Tuart) together with pollen of *Casuarina*, *Acacia* and other genera were present. Radio-carbon dating of the peat gave an age of ± 7900 years B.C. The results indicated that at that time the bed of the Swan River was more than 68 feet below its present level and that clay soils supporting Wandoo and nearby calcareous soils supporting Tuart were present along the river banks. An interesting point made by Churchill was that when the sea was at this low level, Rottnest, Carnac and Garden Islands would have been connected forming high ridges on a coastal plain extending out from the mainland. He believed that the

separation of Rottnest from the mainland must have occurred between 4 000 and 5 000 years B.C. It is also of interest that Churchill, from his studies on fossil wood from Rottnest Island, showed that *Xanthorrhoea* (Blackboy) which had not been found on the island since white settlement began, was at least represented there before the separation of the island.

In his major thesis study Churchill (Thesis 1961, published in part 1967) used pollen analysis to investigate the prehistoric past of three *Eucalyptus* species (namely *E. marginata*, *E. calophylla* and *E. diversicolor*) growing near the south-west coast. Fossil pollen was examined from a variety of areas but particularly from the Boggy Lake area near Walpole. Past changes in the relative eucalypt pollen frequencies were dated by radiocarbon assay and were found to cluster around certain dates. Keeping in mind the moisture requirements of the trees (a wetter climate for instance favouring a high *E. diversicolor*/*E. calophylla* ratio and *vice versa*), it became highly probable that the climate was responsible for the long-term changes in pollen frequencies. It was inferred from the strong occurrence of *E. diversicolor* from at least 4 000 B.C. to 3 000 B.C. that the climate was favourable to this species, and so wetter than at present. Thereafter the ratios suggested that fluctuations in climate occurred up to 1 500 A.D. from which time climate has remained more or less as at present. These studies support Holland's conclusions (see page 38) which were reached on other grounds. They also support those of Lange (1960) who in discussing the disjunct distribution of certain tree species in the south-west area considered that increasing aridity was important. He suggested that the species studied had continuous distributions over the area under the rainfall and soil conditions preceding the most recent aridity. The conclusions from the work by Churchill discussed above have wider significance in relation to plant geography and eco-physiology. It is relevant also to note here that Churchill's fossil pollen analyses indicated, in contrast to the views of Pryor and Boden (1962) in eastern Australia, that *Eucalyptus* pollen was dispersed by wind as well as by insects. It agrees with the work of N. Speck, who noted in a survey of monthly incidence of pollen in the Perth area (1953) that *Eucalyptus* species contributed 9 per cent of the atmospheric pollen. From the above it is clear that palaeobotany, palynology and palaeoecology have made significant contributions to the understanding of the Western Australian vegetation scene, and emphasizes the advantages of interdisciplinary studies.

Algology

In 1854 the algologist W. Harvey visited Western Australia and made extensive collections around the south-western and southern coasts. The published results (1854, 1858-1863) constitute the basic reference points for algal taxonomy. There was a long interval before fresh floristic and ecological studies of algae were made. These were commenced by G. G. Smith

of the University Botany Department staff. His work (M.Sc. Thesis 1951) involved a study of the algal ecology of the Cockburn Sound and Rottnest Island regions, and resulted in the classification of the marine plant communities into twelve plant associations arranged in two formations. Analysis of the causal factors controlling algal distribution suggested that reef terraces played an important part. In further researches, Smith (1956) has described the ecology of *Siphonales* occurring near Perth and in Hodgkin, Marsh and Smith (1959) has given an account of the algae present around Rottnest Island. In "Seaweeds of our Coast" (Smith 1964) he has also given a general account of marine plant life around the south-west and southern coasts. Two of G. Smith's research students, B. Allender (M.Sc. Thesis 1971) and S. Koh (M.Sc. Thesis 1971) have carried algal ecological studies in Western Australia further. Following up observations by Royce (1955), Allender investigated the macroscopic benthic marine flora of the Swan River estuary, describing the major plant communities of the sand, mud and rock formations. The increasing salinity and higher temperatures of spring and summer were found to be responsible for the occasional "bloom" conditions in some species which caused minor pollution of estuary beaches. Koh made a taxonomic and ecologic study of the *Dictyotales* group comprising ten genera and twenty-five species growing along the south-west coast. Five new species were described, while culturing studies showed that in some genera no sexual plants but only diploid (tetrasporic) plants were present. In other genera both sexual and tetrasporic plants were present but the latter predominated. Marine life studies are being extended to include the study of the sea grasses (*Posidonia* and *Amphibolis*) by another of G. Smith's students (M. Cambridge). *Posidonia australis* is of particular importance in the ecology of the Cockburn Sound area.

Apart from the above taxonomic and ecologic studies on marine algae it is relevant here to mention certain other developments concerning them which have arisen out of the overall growth hormone studies initiated in plant physiology by Dr. A. J. McComb. With one of his research students (R. Jennings) he found gibberellins to be present in the red alga (*Hypnea*) growing in the Swan estuary and on ocean beaches near Perth (1967). Further work by Jennings (see under Plant Physiology, page 47) led him to suggest that growth regulating substances may have arisen early in algal evolution. Jennings (1967) also provided an interesting addition to our knowledge of the life history of *Ecklonia radiata* (the only representative of the *Laminariales* found in Western Australian waters). He succeeded in growing the gametophyte and the young sporophyte under controlled conditions and showed that both male and female gametophytes were very reduced with most female plants having no vegetative filaments.

There is considerable need for further studies of marine algae to extend our knowledge of

their distribution, life histories and overall ecology. In this connection the work of Womersley in South Australia who has included in his study the Western Australian representatives of *Cystophora* present along the south coast (1964), may be noted.

Mycology

The economic importance of fungi as disease agents in crop plants was early recognized in the State by the appointment of a mycologist, and many important studies were made. It is outside the scope of this survey, however, to consider the plant pathological work which has been done in relation to crops, fruit trees and other introduced plants of economic importance. But fungal organisms have also been found which attack native plants and studies on these may be considered here. A list of diseases recorded on native plants was first compiled by W. Carne (1925, 1927) and later revised by Macnish (1963). The list is extensive, 42 genera and 70 species being known to be subject to attack. Where the native plant is of horticultural importance investigations have been extensive. In the early 1930s a canker disease was found to be attacking *Eucalyptus ficifolia*, the Red Flowering Gum. This tree, which in its natural state is confined to a small area on the south coast, had become widely planted in Perth as an ornamental tree. The fungus causing the canker was isolated and described by the Government Plant Pathologist, H. Pittman, in 1935, being named *Sporotrichum destructor*.

W. Cass-Smith, who succeeded H. Pittman as Plant Pathologist, continued the study and found that the canker disease in a milder form was naturally present on *Eucalyptus calophylla* which was common on the Swan Plain and metropolitan area, and that this had served as the source of infection for *E. ficifolia*. Despite continued study up to the present time no effective chemical or genetic means of control of the disease on the valuable Red Flowering Gum has been found (Cass-Smith 1970).

Another investigation dealing with fungal decay in a eucalypt, *E. marginata* (Jarrah), was carried out by N. Tamblin in the University Botany Department. He described five rot conditions and two abnormalities occurring in jarrah as a result of fungal attack (1937). Owing to the lack of any means, at the time, of determining the specific identity of the attacking fungi, the work remained incomplete. It is only in quite recent times that the problem has been taken up again in the Botany Department, and some success achieved in developing identificatory methods for dealing taxonomically with wood-attacking gill fungi. Mr. R. N. Hilton (Botany Department staff) and his research student (H. C. Broughton) are now combining the study of the microscopic features of the sporophores of genera in the families *Pleurotaceae* and *Polyporaceae* with microscopic and macroscopic features of pure cultures, to give full characterisation (H. C. Broughton, M.Sc. student 1966).

In another economically serious pathologic condition in *E. marginata* known as "dieback", a break-through has fairly recently been made by Commonwealth and State workers. This involved the isolation of the fungus *Phytophthora cinnamomi* and proof of its pathogenicity by Podger, Doepel and Zentmeyer (1965). The study of basic aspects of the biology of the fungus and of the forest microflora, which is essential in order to develop a method of control of the disease, is proceeding actively at the present time, both at the Commonwealth Forestry Research Laboratories at Kelmscott and at the University Botany Department under a State Forestry Department research fellowship.

A severe disease of native *Acacia* plants caused by gall-rust (*Uromycladium tepperianum*) formed the subject of study by J. Goodwin (M.Sc. Thesis 1966). She recorded 60 *Acacia* species which were susceptible to infection and 118 host species (previously the number of these known was 58). She also increased our knowledge of the life history of the fungus causing the gall formation.

In the course of studies of the pathogen *Sclerotinia sclerotiorum* another research student (R. Henderson 1962) added considerably to our knowledge of parts of the life history of this fungus.

In other areas of Mycology, research students directed by E. R. L. Johnson and R. N. Hilton have made interesting descriptive and experimental studies. Thus L. H. Tai (M.Sc. Thesis 1964) showed that species of *Saprolegnia* could be infected by the fungus *Olpidiopsis saprolegniae*, being particularly susceptible during their vegetative phase. It was found that nitrogenous materials and xylose as a carbon source tended to increase the resistance of the hosts.

H. K. Tan (M.Sc. Thesis 1966) made a study of the fascinating adaptations which facilitate the trapping of nematodes by a particular group of fungi. He isolated and described 32 species of these nematophagous fungi from Western Australia, three of which were new to science. C. S. Fang (M.Sc. Thesis 1968) extended the scope of earlier work dealing with air-borne pollen (see Speck 1953) by making a detailed study of the diurnal and seasonal changes in the concentration of fungal spores in the air in the vicinity of Perth. Basidiospores were found to be the major wet-air spore type in the air around Perth and two hitherto unrecorded groups of these were registered.

The systematic study and naming of field and forest fungi characterized by the presence of macro-fruiting bodies has lagged behind the specific studies on largely parasitic fungi described above. This has been at least partly due to the difficulty of collection and preservation of suitable diagnostic material. E. R. L. Johnson (Botany Department) commenced a mycological herbarium in 1964 and began the process of precise identification. Under the guidance of her successor (R. N. Hilton) the collection is being actively augmented. The preservation of speci-

mens has been facilitated by the application of a new freeze-drying technique. Further study should allow the compilation of a definitive census within the next few years.

With regard to Lichens it may be noted that a definitive list of those known to occur in Western Australia was compiled by P. Bibby and G. Smith (1954).

Plant Anatomy

L. Diels (1906) in "*Die Pflanzenwelt von West Australien*" touched upon and illustrated the leaf and stem anatomy of certain native plants which showed xeromorphic modifications such as thick cuticles and sunken stomata. Shelton (1921, 1934) also illustrated leaf sections showing these modifications. The first really detailed study of a Western Australian plant, however, was carried out by the Economic Botanist, D. Herbert (1919). This dealt with the leaf, stem and root structure of *Nuytsia floribunda*. It arose out of the discovery that the fine rootlets of this tree were parasitizing roots of other plants. As well as showing the nature of the parasitism the anatomic work explained certain other strange features in *Nuytsia* such as the habit of stem growth and the unusual brittleness of the branches. These were shown to be related to the unusual and remarkable method of secondary growth of the tree. No further histological studies in depth of Western Australian plants were made until Burbidge (1946) described the foliar anatomy of members of the grass genus *Triodia*. She described the way in which the leaf traces passed between the sheath and the nodes, the arrangement of bundles within the sheath, the differential distribution of stomata in grooves in different species and the mechanism of the closing of the grooves on both sides of the lamina during periods of water shortage. The collated information incidentally enabled Burbidge (1946a) to recommend that the name *Triodia* R.Br. be confined in use to Australian species.

A further long interval occurred before Dr. N. H. Brittan and his research students commenced a series of anatomical studies which were necessary for the elucidation of certain biosystematic problems. Dr. Brittan in the course of his study of 27 species of *Thysanotus* established a correlation between anatomical characters and morphological groupings (1970). J. Green made a study of the anatomy of *Conostylis* species which helped him to develop an identificatory key (1959), while two other research students demonstrated the value of the anatomical approach as an aid to separation of species in *Hybanthus* (Bennett 1970) and in *Lomandra* (Choo 1976).

Using the techniques of both standard and scanning electron microscopy, Dr. Brittan is currently continuing his anatomic studies of *Thysanotus* species. Dr. A. J. McComb and his student C. H. Wong have also employed the electron microscope in their study of cell structure in *Callitriche* (see under Plant Physiology).

Mention may also be made of anatomical studies carried out by overseas or eastern States botanists using preserved material collected in Western Australia. Thus C. Wilson (visiting Professor from U.S.A.) studied the floral anatomy of several local species of *Hibbertia* to assist him in enumerating, on the basis of structural features, the probable characters of the archetype of this genus (1965), while S. and D. Carr studied species of Western Australian eucalypts in their investigation of glands and ducts (1969).

Many of the anatomic studies undertaken within the State so far appear to have been designed to help in the elucidation of problems arising out of investigations in cognate branches of botany. While this is of course often necessary and desirable there still appears scope for more thorough-going anatomical studies in their own right dealing with characteristic genera and species, particularly those that are endemic to Western Australia.

Life Histories and Embryology.

Up to 1930 little was known of the details of the life histories of native plants. About this time Miss A. M. Baird (Botany Department staff), having observed the interesting work of Buchholtz in the U.S.A., commenced a study of the embryology of gymnosperms native to Western Australia. The first investigation dealt with *Actinostrobus* (1937) where she showed that cleavage polyembryony was a constant feature and that distinctive differences from the embryology of other genera in the Cupressaceae were recognizable. The second investigation dealt with *Macrozamia riedlei* where a new type of polyembryony together with unusual features of pollen formation were reported, enabling her to classify *Macrozamia riedlei* as one of the more primitive Cycads (1938).

The life histories of several species of *Callitris* were next studied. A highlight was the finding that in this genus there was a very long interval (often up to 2 years) between pollination and fertilization. The comparative studies also enabled her to determine which species were primitive and which were relatively advanced (1953).

Indian botanists working on the embryology of families with representatives in Western Australia, have utilized preserved material of Western Australian plants sent on request. One investigation of particular interest for Western Australian botany dealt with the embryology of *Nuytsia floribunda* (Narayana 1958).

Cyto-genetics and Genetics

Investigations in the areas of Cytogenetics and Genetics are concerned primarily with understanding genetic mechanisms in the biology of plants which have a bearing on evolutionary processes. In the early 1950s, a frequent visiting scientist at the University of Western Australia, was Dr. Smith-White of the Sydney Botany Department. He was studying the question of the possible lines of evolution in certain pan-

Australian plant families and while here made extensive collecting trips to enable him to make chromosome counts on Western Australian representatives in the families Myrtaceae, Rutaceae and Epacridaceae (1955, 1959). This work with his studies of the eastern States representatives enabled him to conclude that the hardwood genera in Australia were established during the early part of the Tertiary and that differences in chromosome number must have been characteristic of these genera then as now (1959). Two of Smith-White's research students (S. H. James 1965, and B. Barlow 1959) have worked on Western Australian plants. Dr. S. H. James was appointed to the staff of the Botany Department, University of Western Australia in 1963 and with his own research students has continued the genetic evolutionary study of Western Australian plants he began in Sydney. His main published work (James 1963, 1965, 1969, 1970) has dealt with *Isotoma petraea* which species occurs in small isolated populations inhabiting granite outcrops in the Bullfinch-Laverton area. Between these populations migration and gene exchange are greatly restricted. The species is self-pollinated and in-breeding, and James has been able to show that complex hybridity (or ability to breed true) has evolved in the south-west niche. He suggested that this complex hybridity was maintained by the presence of a balanced lethal system acting at the zygotic level (James 1963, 1965). One of his research students I. C. Beltran (1970) studied embryo-sac formation and the embryogeny of the species and with James has been able to confirm experimentally the presence of a balanced lethal system, the operation of which may be expressed by the abortion of the affected seeds before or after differentiation of the testa has begun (James and Beltran 1970). In attempting an explanation of the development of complex hybridity in *Isotoma petraea* James (1969) postulated that it probably arose as an adaptive adjustment and was incorporated through natural selection.

Another of James' students (Dr. J. A. McComb, nee J. Chessell) in a study of the evolution of sex has analysed the sex forms in plants of the south-western and south-central Australian flora (1966). Although these two regional floras have been substantially isolated since at least the mid-Tertiary, no significant sex form differences were found between them. This suggested that following isolation, factors such as climate and soil were not important here. A visiting student from U.S.A. (J. Anway) also working under the direction of Dr. S. H. James studied *Calectasia cyanea* which extends in distribution from south-western Australia to western Victoria. He noted little variability within the populations, the eastern and western parts of which had been separated since Miocene times. He ascribed the relative lack of variation to the presence of a stabilizing mechanism in the ninth chromosome (Anway 1969).

L. Bousfield (Ph.D. Thesis 1971) of King's Park Botanic Gardens staff, studied under Dr.

James the cytogenetics and distribution of *Dampiera linearis* in the south-west botanical province. He found that the forms occurring on the laterite (a fossil soil developed in the Tertiary) in the Busselton region were diploid while those on younger soils were tetraploid. It appeared that the development of tetraploidy enabled them to colonize these new areas. Hexaploids which were later derived from the tetraploids are now found to be widely distributed in the south-west.

Following Carlquist's suggestion (1969) that adaptations to pollination vectors and soil mosaic patterns were possible factors concerned in the high degree of speciation characteristic of the genus *Stylidium* in Western Australia, Dr. James and his research students (in as yet unpublished work) have found cytogenetic factors (chromosome number variation and lethal systems) also to be involved.

The above examples of cytogenetic research which highlight the evolutionary and taxonomic complexities within a genus or a single species of a genus need to be continued and widened in scope since such work has great potential value for an adequate understanding of the evolution of our flora. In this connection the researches of eastern States botanists who have included the Western Australian representatives of pan-Australian genera in their studies, on evolution, are relevant (cf. Rao 1957, Pryor 1959, Johnson and Briggs 1963, Carr et al. 1971 and Barlow 1971).

The important results from the above cytogenetic researches indicate the pressing need for conservation of vegetation in selected areas. The warning sounded by Williams (1948) for ecological studies and relating to increasing and indiscriminate land use and the risk of fiercer bush-fires, applies even more cogently to cytogenetic studies. If species are placed at risk and face extinction, priceless genetic material could well be lost.

Eco-Physiology

As stressed by Wood (1939) the question of drought resistance is of primary importance to Australia since some four-fifths of its area comes within the 25 cm annual rainfall isohyet. Eco-physiology studies the effects of climate and soil on physiological processes in plants with the aim of throwing light on any apparent physiological adaptations, and of determining whether there is functional significance in any morphological modifications present. Morphological modifications such as sunken stomata, thick cuticle, hairy or waxy leaf coverings, and reduction in leaf area or complete aphyllly collectively are described as xeromorphy. Many theories, including an early one that long, continued water stress was a causal agent, have been put forward to explain their origin. The fact, however, that xeromorphy occurs not only in plants growing in dry areas but also in areas not necessarily subject to water stress (as in parts of eastern Australia), has in more recent times downgraded the adaptation to aridity theory and led to increasing emphasis being placed on the

soil phosphate mineral deficiency theory (Beadle 1954, 1968). But regardless of the causes which may have brought these xeromorphic modifications into being in the remote past the question still remains whether, when they are present in plants growing in areas subject to severe summer drought, they have any functional significance for survival.

Diels (1906) emphasized that xeromorphic modifications were a conspicuous feature of plants growing in the summer-dry south-western area of Western Australia. He however did not completely espouse Schimper's view (1898-1903) that such xeromorphic modifications were necessarily adaptations for reducing transpiration to a minimum. Shelton (1921) became interested in this problem and described the xeromorphic modifications in the leaves of several south-west species. He elaborated on these features and their apparent significance in his presidential address to the Society (1934). On the basis of the morphological features alone, however, he considered that restriction of water loss was favoured, enabling such plants to survive the succession of long dry summers. Ashby (1933) in considering the overall problem of xeromorphy pointed out, however, that conclusions regarding reduction of transpiration rested on insecure foundations, unless and until they had been tested by experiment. Accepting this viewpoint the writer together with his research students (Holland, Doley, Pearman and Hellmuth) has carried out experimental studies on the field physiology (water relations, photosynthesis, heat resistance and reflectance) of selected native plants. For sclerophylls it was in general found that with increasing summer stress the rate of water loss decreased while osmotic potential and water potential values fell (Grieve 1953, 1955; Grieve and Hellmuth 1970). An important exception was the Jarrah (*Eucalyptus marginata*) which showed some reduction of water loss by mid-summer, but due apparently to its deep-rooting system managed to avoid any severe stress (Doley 1967). Non-native mesomorphs grown under similar conditions in the field, failed to control their water loss and finally showed permanent wilting and died. In native plants of the south-west botanical province, whether scleromorphs or mesomorphs (such as *Phyllanthus calycinus*), the drought-tolerating or drought-avoiding mechanisms noted included stomatal control and progressive defoliation under stress.

Hellmuth (1967, 1968, 1969, 1971) extended the researches into a very dry environment at Cue in the Austin botanical district. He made comparative studies of the field physiology (transpiration, photosynthesis, osmotic quantities and heat resistance) of characteristic sclerophyll, semi-succulent and mesomorphic plants. He demonstrated that these plants displayed considerable physiological diversity and that a variety of adaptations including stomatal control and presence of thick cuticles affecting survival, operated. Pearman (1965) showed that leaves with hairy or waxy covering (which are also a feature of many plants in south-western

Australia) possessed a high reflectance value. In such plants also he noted that as their water deficits increased so did their leaf reflectance values. These results suggested that those morphologic features and physiologic factors which enhanced reflectance were of ecological advantage to the plant.

The results of the overall eco-physiological experiments so far, suggest that regardless of their original causation the xeromorphic features present do have functional value as adaptations assisting survival under summer stress conditions in south-western Australia. In those cases where external xeromorphic features are lacking and yet the plant survives without defoliation in summer (cf. *Hibbertia pungens* with marked xeromorphy and *H. tcretifolia* without, both growing in the same habitat) clearly internal physiological factors operate. What Ashby (1933) described as a possible "tuning" of the protoplasm needs investigation. In this connection it may be noted that Holland (M.Sc. Thesis 1953) showed that for *Eucalyptus calophylla* (Marri) there was something innate to the plant in drought resistance in terms of resistance to desiccation and in recovery after prolonged wilting. Hellmuth (1969) obtained a similar result for *Acacia craspedocarpa*. There is obviously still much to be explained here and further studies on such aspects as drought resistance, epharrosis in leaves, leaf aphyllly, root growth and salt and water uptake are desirable for a better understanding of the overall field physiology of native plants. Such studies would have considerable relevance to future decisions on land use for agriculture, forestry and mining.

Plant Physiology.

In considering research which comes within the scope of plant physiology we may note first that basic and highly valuable research directed essentially towards growth and nutrition (including nitrogen, phosphorus and trace element) relations of crop plants has been proceeding for a long time in the State Department of Agriculture, in the Institute of Agriculture at the University and in the Regional Laboratories of C.S.I.R.O. However these researches will not be considered here as they are held to lie outside the scope of this essentially botanically oriented review. Here we shall confine discussion to those plant physiological studies which relate to native plants or which use proven "guinea-pig" indicator plants not considered in any crop context.

Shortly after his appointment in 1914-15 Professor W. Dakin (Biology Department, University of Western Australia) became interested in the biology of the Albany Pitcher Plant (*Cephalotus follicularis*). He found that the pitchers captured insects in large quantities and that a protease type ferment was present which might facilitate very slow digestion of the insects (Dakin 1919). Further researches which he foreshadowed were not completed owing to his return to England in 1920. Another unique West Australian plant, the Christmas Tree (*Nuytsia floribunda*) was the subject of a detailed study by Herbert (1919). He was able

to prove that its roots were parasitic upon those of other plants, attachment being by way of collar-like haustorial structures. He also noted the fact that although seed production was high seedling plants were very rare and generally died off young. Those that survived were assumed to have made early connection with a host root. Main (1947) concluded from field observations that non-finding of a host root was not the essential factor causing the death of the young *Nuytsia* plant; he believed faulty root formation was involved and attempted by the use of root-hormones to activate sound root growth. Some of his treated seedlings survived and grew successfully without a host for at least a year or so. He considered that further extensive trials would be necessary to clarify the situation.

In 1958 the writer commenced a study of the physiology of *Nuytsia floribunda* with special reference to germination and growth without a host plant. Although the work has not yet been published apart from a brief article in 1963, the following is a summary of results.

Germination in surface sterilized and depericarped seeds remained high (90-100 per cent) for nine months. The usual early death of seedlings could be deferred by up to eighteen months in sand-nutrient-tap water culture. Treatment with a range of growth factor chemicals produced a favourable response. The most effective was gibberellic acid (100 p.p.m.); treated seedlings survived without a host for up to three years.

Following the discovery in 1963 of an unusual case involving production of haustorial collars of *Nuytsia* roots on underground plastic covered electric cables a study was undertaken by Doley and Grieve. This also is as yet unpublished but the main results are as follows. The formation of the parasitic haustorial collars has been shown to be a response to chemical stimuli and not just a mechanical effect following contact. *Nuytsia* roots consistently by-passed pieces of wooden dowelling and lengths of rough and polished glass rod, while they vigorously "attacked" lengths of several different kinds of cable. Coverings of butyl rubber, red nylex, nylon, polythene and termite-resistant PVC all had haustorial collars formed around them. In additional experiments it was also observed that *Nuytsia* roots actively "attacked" plastic flower pot containers, but the haustorial cushions were flat structures. Some evidence was obtained to suggest that ethylene or ethylenic compounds might be the stimulating substances involved in inducing attack by the *Nuytsia* roots on plastic covered electric cables.

Keeping to the subject of unique Western Australian plants and their physiology mention may also be made at this point of the work of Drs. A. J. and J. A. McComb (University Botany Department) on *Pilostyles hamiltonii*. This plant is completely parasitic upon its hosts (*Daviesia pectinata*, *D. polyphylla* and *D. rhombifolia*), its flowers appearing from protuberances on their stems (Gardner 1948; Smith 1951). Because of its importance in plant

geography (see page 12) it appeared desirable to try and learn further details of its life history. With this in mind the above workers carried out experiments designed to induce development apart from its host, in aseptic culture. Results so far have not proved rewarding but the experiments are proceeding.

In this section also we may perhaps mention the work of Lloyd on the mechanism of action of the insect traps in *Utricularia*. Professor Lloyd spent some time collecting and examining species of *Utricularia* in our south-west area and was able to extend his findings. He describes the operation of the traps as follows (Lloyd 1936). By glandular action of the walls, water is pumped out from the interior of the trap, so that the walls become concave with the reduced pressure. When the tripping mechanism of projecting stiff bristles on the door surface is activated by a slight touch, as by say a copepod bumping against them, the door opens, the water rushes in, and carries with it the offending animal.

The main area of plant physiology which has developed in Western Australia, in terms of the defined area of comment as set out earlier, relates to growth hormone work. Since his appointment to the University Botany Department in 1963, Dr. A. J. McComb and his research students have concentrated on gibberellin growth hormone physiology.

McComb (1965) first found that gibberellic acid stimulated internode expansion in floating rosettes of the aquatic plant *Callitriche stagnalis*. Floating shoot parts had been observed in nature to be shorter than submerged shoot parts and the effect of gibberellin was found to be due to its ability to offset the effect of water loss by transpiration in such shoots. In a further anatomical investigation into the effects of gibberellic acid on the expansion of *Callitriche* shoots, McComb with his research student C. H. Wong, was able to show, using light and electron microscopy techniques, that the greater internode length was due to increase in both cell length and cell number (Wong and McComb 1967). In a study of the effect of gibberellic acid on unvernallized rosettes of *Centaureium minus* held under long day and short day conditions, McComb (1967) observed that only under long day, did stem elongation followed by flowering occur. The results of further experiments suggested that it was only under long day that the production of endogenous gibberellins was stimulated in the flower primordia.

Using intact dwarf pea seedlings McComb (1966) was able to show that the addition of gibberellic acid brought about an increase in the rate of dry weight incorporation into expanding internodes. This theme was then elaborated with one of his research students, the emphasis being on how the gibberellin acted. It was found that gibberellin stimulated protein synthesis and cell wall synthesis and increased the amount of soluble nitrogen in expanding internodes (Broughton and McComb 1967). Broughton (1969) extended the scope of this work to include study of the relations between DNA,

RNA, protein synthesis and the cellular basis of the growth response in gibberellin treated pea internodes. One of the main discoveries was that in treated internodes there was at least a doubling of the total RNA and protein and that the length of the internodes was closely related to the content of these metabolites. Continuing this line of study Broughton and McComb (1970) showed that the overall effect of gibberellic acid on enzymic development was to provide more substrate (particularly glucose) to general cell metabolism and wall synthesis in elongating internodes of *Pisum sativum*. In a further study Broughton, Hellmuth and Yeung (1970) advanced the hypothesis that gibberellic acid actively directed glucose supply towards elongating internodes.

Another area of enquiry relating to growth-hormone physiology was directed towards their implication in the growth of marine algae. Dr. McComb and his student (R. Jennings) made an interesting extension of our knowledge regarding the importance of gibberellins as endogenous growth regulators in a red alga (*Hypnea musciformis*), in a green alga (*Enteromorpha prolifera*) and in a brown alga (*Ecklonia radiata*) (Jennings and McComb 1967; Jennings 1968). In further work by Jennings (1968, 1969, 1970) the presence of cytokinins as endogenous growth regulators in the abovenamed red and brown algae and the presence of a regulatory gibberellin antagonist in the brown alga, *Ecklonia radiata*, were reported. The overall data led him to suggest that growth regulating substances may have arisen early in algal evolution.

An interesting sidelight on early physiological plant pathologic studies in New South Wales on the fungus *Gibberella fujikuroi* var *subglutinans* and its effect on the germination of grain and elongation of internodes in Maize carried out by Edwards (1935) has been provided by McComb and Rizvi (1968). Edwards had suggested that the fungus might produce a growth promoting substance similar to that produced by *Gibberella fujikuroi* attacking rice as described in the Japanese literature. McComb and Rizvi were able to confirm this by isolating gibberellin from cultures of the fungus. As they point out, if Edwards had been able to continue his work the knowledge of gibberellins might well have become widely known outside Japan (publications there commenced in 1926) before its late discovery by the rest of the scientific world in 1951 and consequently the history of thought concerning plant growth control might have been very much altered.

Two other quite different areas where basic plant physiological approaches have been applied by Dr. McComb and his research students may finally be mentioned. The first, verging on ecophysiology, was concerned with the relation between germination requirements and the composition of summer and winter annuals in an arid zone. J. Mott (Ph.D. student) has shown that in the grass *Aristida contorta* which normally germinates after summer rain and sets seed in autumn, dormancy was maintained largely by mechanical means in the glumes until

the following summer. In the case of the composites, *Helipterum craspedioides* and *Helichrysum cassinianum* seeds were produced in spring, remained dormant over summer and germinated with winter rains. The dormancy mechanism here was shown to be an endogenous after-ripening effect. Heavy rain in the case of both grasses and composites appeared essential for germination while temperature in the seed bed also played an important part in determining germination once dormancy had been broken.

The second area of investigation centred round the study of the importance of proteoid roots (dense clusters of rootlets produced in many taxa of the family Proteaceae) with particular reference to their occurrence in *Hakea* species. B. Lamont (Ph.D. student) in a projected series of publications has described their morphology and anatomy and the effect of soil nutrients on their production. Proteoid roots have been shown to be produced by the youngest roots in the root system, and to be relatively short-lived surviving for only two to three months. It has also been shown that endophytic organisms are not normally associated with them. In an interesting extension of the study it has been demonstrated that proteoid roots also occur on the legume *Viminaria denudata*. This may allow new insights into whether these structures have any special function.

Concluding remarks

This completes the outline of this review. It is apparent that over the period 1900-1971, during which time many new facets of modern botany developed, there has been a highly significant increase in the extent and depth of our knowledge. This survey has ended at an arbitrary point in time determined by the date of a presidential address. This is not that important. What is important is that the science of botany will keep advancing. While it would be futile to attempt to predict, in terms of Bower's fan-like development concept, which facet or facets of modern botany will be involved in the next big push forward, one may venture to hope that in the future, developing imbalances will be controlled, that some of the more obvious lacks in our botanical knowledge will be remedied, and that current promising lines of enquiry will be brought to fruition.

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Appendix

History of the development of botanical institutions in Western Australia

In the course of the preceding survey emphasis naturally has been upon developments in botanical research in the different fields. But it may perhaps be helpful to illustrate how the advancement of botany has been related to personnel and establishments.

Dealing first with the official Government appointments it may be noted that the positions of Economic Botanist (Stoward, 1911-17; Herbert, 1918-21; Praaf, 1921-22; Campbell, 1922-23; Carne, 1923-28), Government Botanist (Gardner, 1929-60) and Officer-in-Charge, Botany Section, and Curator of the Herbarium (Royce, 1960+) were held within the State Department of Agriculture. The State Herbarium has been successively housed in part of the Observatory Building (1933-58), in the Department of Agriculture Laboratories, Jarrah Road, South Perth (1958-69), and finally from March, 1970, in its own new building. Currently a staff of nine professional botanists is engaged on taxonomic and ecological studies. A new journal "*Nuytsia*" provides for the publication of the results of their researches.

Botany in the University of Western Australia developed in the Biology Department, commencing in 1914. Professor W. Dakin (primarily a zoologist but with an interest in the physiology

of plants as shown by his study of *Cephalotus follicularis*, the Albany pitcher plant, and his translation of a large part of Diels' "*Die Pflanzenwelt von West Australien*") and Dr. Cayzer (taxonomic botanist) comprised the staff. Professor Dakin was succeeded by Professor Nicholls (zoologist) in 1921 and Dr. Cayzer by Miss E. Reed about the same time. Towards the end of the 1920s Botany achieved autonomy and moved from the Biology building north of Stirling Highway to a separate building on the main campus at Crawley. Dr. Armstrong succeeded Miss E. Reed as Head of Department in 1930-31 and with Miss A. M. Baird, (who was appointed to the staff in 1934), continued until world war II commenced in 1939. On the outbreak of war Dr. Armstrong joined up and Miss Baird acted as Head of Department from then until 1947 when the influx of ex-servicemen necessitated expansion of staff. Dr. B. J. Grieve was appointed as Head in 1947 and foundation Professor in 1956.

In 1970 a new Botany building well equipped for studies in descriptive and experimental botany was completed and occupied on Hackett Drive at the southern end of the campus. A

small teaching botany garden was developed being laid out to show a possible evolutionary sequence of plant development and incorporating a variety of ecological niches. The professional staff at that time numbered nine and the major facets in Botany were represented by specialists.

In 1959-60, following a report by a Government appointed committee and a further recommendation by Dr. W. Stewart, Director of the Los Angeles State and County Arboretum (who at the time was a Fulbright Scholar in the University Botany Department), a Botanic Gardens essentially for native plants was approved for establishment in King's Park. In 1961 Dr. J. S. Beard was appointed as the first Director. Following four years of development the Botanic Gardens was officially opened in 1965.

Botanists both professional and amateur, through publications in the Royal Society of Western Australia, the Western Australian Naturalists' Club and a variety of specialist Australian and overseas scientific journals, have contributed considerably to the development of botany in this State as outlined in the course of the preceding presidential address.

4.—New finds of sand fulgurites from the Perth Basin, Western Australia

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Abstract

The first fulgurite recorded in Western Australia was recovered from West Popanyinning in 1931. In 1974 fulgurites were recorded from Willetton, East Victoria Park, Canning Vale and near Broome, and they are now reported from Jandakot, Lynwood, Welshpool, Malaga, Beechboro, Upper Swan, Wanneroo, Guilderton and near Northampton. Eleven of the fourteen localities are in the central Perth Basin, and ten are near Perth. The spate of recent finds near Perth is due to close local investigation. Fulgurites are also probably fairly common in the rest of the central Perth Basin, which is similar in its topography and sandy soil, and has about the same annual lightning frequency. The fairly common association of Aboriginal artifacts with fulgurite fragments in sand blow-outs is probably generally fortuitous, because both remain as lag when sand is removed. However, isolated fulgurite fragments do not necessarily post-date associated artifacts.

Introduction

Sand fulgurites are glassy, tube-like bodies fused from sand by lightning on or near the Earth's surface. Reports of fulgurites seen to form from lightning strikes have been presented by Pfaff (1822), Wicke (1859), Van Bastelaer (1883), Wood (1910), Simpson (1931), and Fenner (1949). Beadle (1940) has shown fairly conclusively that bushfires do not attain the temperatures necessary to fuse quartz (Rogers 1946) and thus simulate fulgurites.

Fulgurites generally consist of vesicular lechatelierite with a mean refractive index close to 1.461 ± 0.002 , and have a smooth, translucent, vitreous lumen with a rough, opaque, commonly flanged exterior containing embedded quartz grains, or partly fused quartz grains. Most fulgurites recovered recently from Western Australia are fragmentary, probably because of sand movement after the fulgurites formed, and represent parts of tube walls and flanges. The original appearance of the fulgurites can be reconstructed from two that were found *in situ* and unbroken, namely the West Popanyinning fulgurite (Simpson 1931) which was tubular, highly flanged, vertical and about a metre long, and the East Victoria Park fulgurite (Glover 1974) which was tubular, vertical and may have been over two metres long. Tube walls are commonly one or two millimetres thick, and generally contain vesicles with their long axes normal to the surfaces. It has been shown on chemical grounds that fulgurite fragments from

Willetton were formed from the fusion of the white sand in which they were found (Glover 1974).

The newly recorded material, which is all fragmentary, is described briefly, and its significance is discussed. The colours and corresponding numerical designations refer to the Rock-color Chart distributed by the Geological Society of America (Rock-color Chart Committee 1963). Each fulgurite fragment, or group of fragments from one locality, has been allotted a number by the Geology Department of the University of Western Australia, with the exception of the Wanneroo object, on loan from the Commonwealth Scientific and Industrial Research Organisation, Floreat Park. The distribution of the fulgurite localities is shown in Figures 1 and 2.

Petrography

General

Most of the fulgurite fragments have been recovered from sand blow-outs, or from commercial sandpits, and because of probable sand movement, their precise stratigraphic position is uncertain. It is clear in some places, however, that they come from about a metre or less below the original surface. Aboriginal artifacts, dominantly quartzite and chert flakes, have been found at ten of the fourteen localities.

The newly recorded material consists mainly of irregularly shaped, crinkled to roughly flat fragments up to 4 cm x 2 cm x 1 mm in size, but there are some tubular fragments up to 4 cm long. One side of each fragment is almost invariably vitreous, translucent, smooth and somewhat mammillated: this side is always the lumen in tubular fragments. The other side is rough, opaque and contains embedded sand grains. The glass is not uniformly coloured even within the one fragment, and the smooth side of the fragments commonly ranges from very light grey (N8) to light grey (N7), but other colours including white (N9), pinkish grey (5YR8/1), greyish orange (10YR7/4), dark yellowish brown (10YR4/2), medium dark grey (N4), and greyish black (N2) have been observed. Dark grey (N3) to black (N1) schlieren about one mm long, or smaller spots, are commonly found in the light-coloured glass. The overall colour of the rough outer surfaces is generally a little different because of embedded sand grains and superficial iron staining.

Under the microscope, some quartz sand grains show cracks filled with glass, or grade

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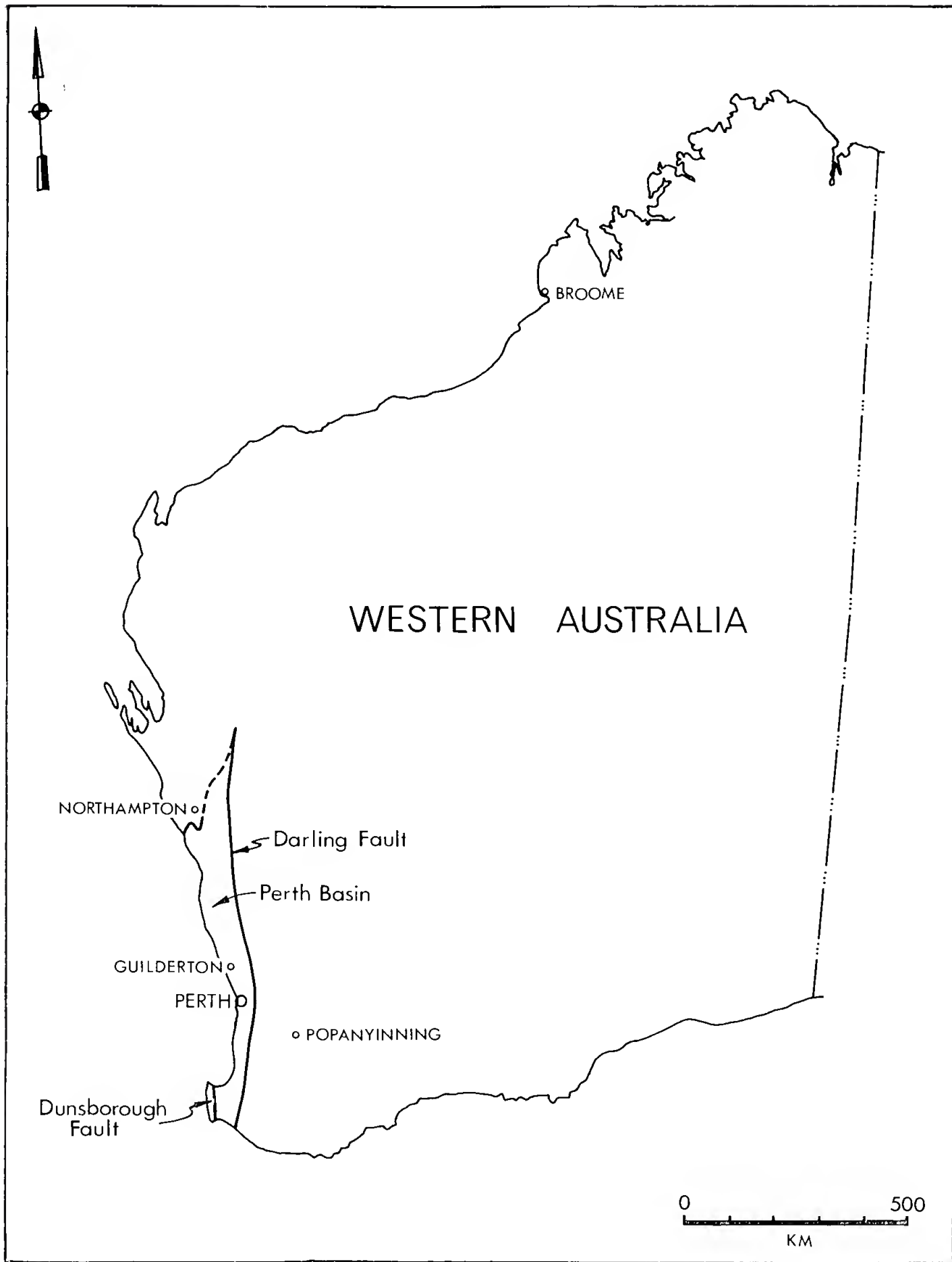


Fig. 1.—Locality map of Western Australia showing Perth Basin.

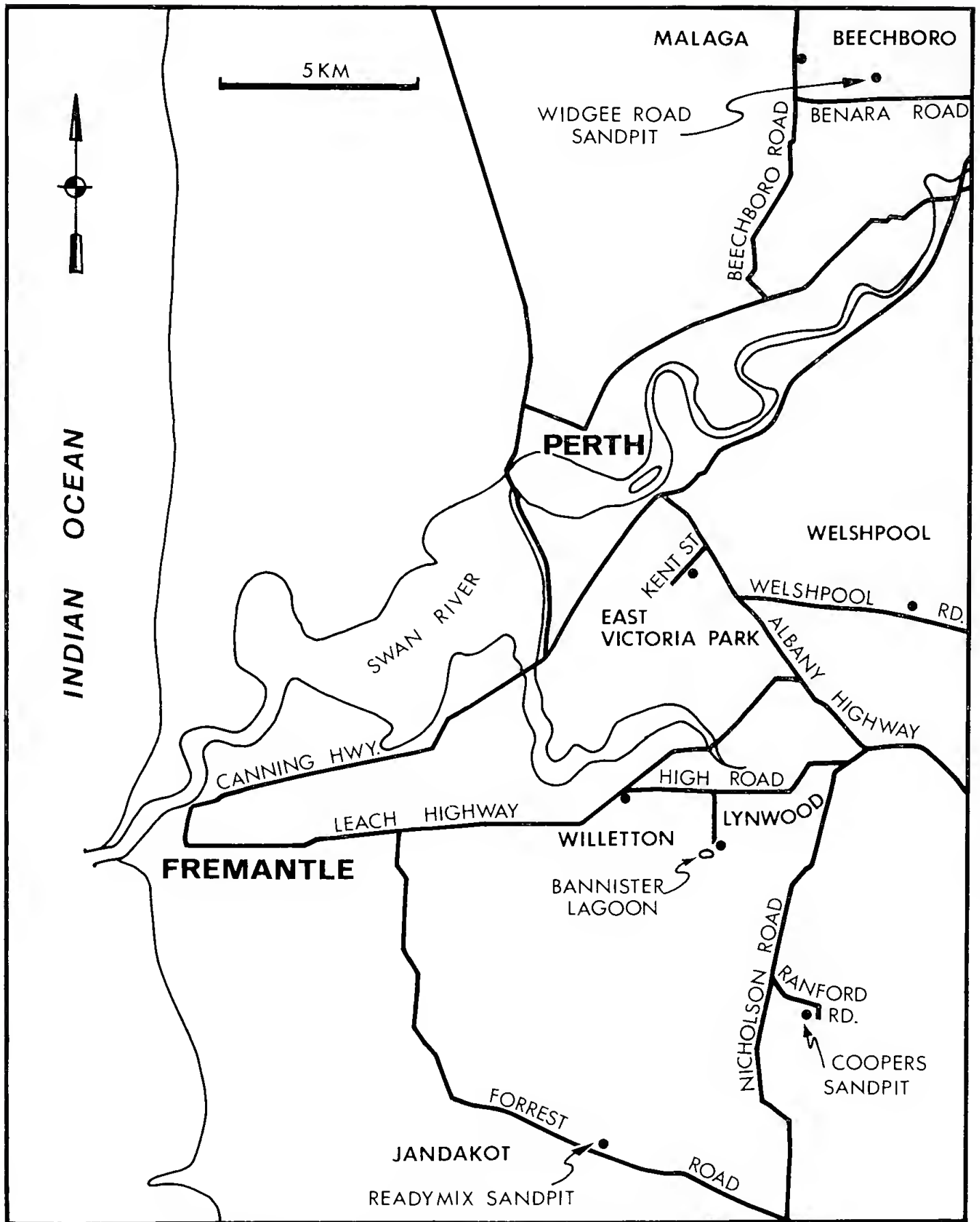


Fig. 2.—Map of Perth area showing fulgurite localities (small solid circles).

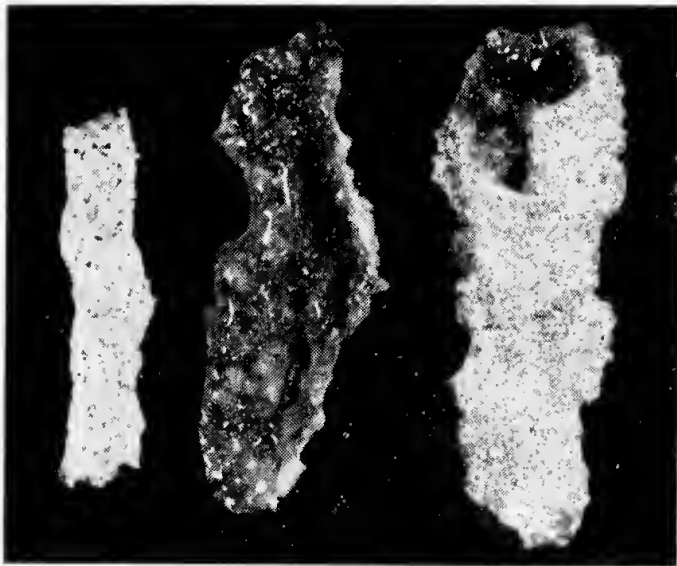


Fig. 3.—Wanneroo fulgurite (left) and two fragments from the Widgee Road Sandpit, Beechboro (centre and right). Note the holes in the Wanneroo material. The Widgee Road material has a smooth, shiny inner surface, and a rough outer surface with embedded sand grains. Length of Wanneroo tube 2.3 cm.

into glass, and the glass of the walls is finely vesicular. The mean refractive index of the glass ranges from 1.460 to 1.467 ± 0.002 , but is most commonly within the range 1.461 to 1.463 ± 0.002 . Dark glass from a parti-coloured fragment commonly though not invariably has a slightly higher refractive index than colourless glass from the same fragment.

The Wanneroo object, listed with the others below, is unique. It is an unflanged tube in which the lumen is smoother than the outer surface, but the clearly discernible sand grains characteristically embedded in the outer surface of other Western Australian fulgurites are not evident. The tube walls are unusual in containing a network of irregularly shaped holes up to 2 mm in diameter (Fig. 3).

The localities and main features of the newly recorded material are listed below.

Jandakot Lechatelierite, Geology Dept. No. 73365

Locality: Jandakot Readymix Sandpit, Forrest Road (see Fig. 2).

No. of fragments: Two (includes one tube). Associated artifacts.

Colour: Very light grey (N8) to light grey (N7) with a few black (N1) spots.

Mean refractive index: 1.460 ± 0.002 .

Lynwood Lechatelierite, Geology Dept. No. 73366

Locality: Sand blow-out north of Bannister Lagoon on Riley Road (see Fig. 2).

No. of fragments: One. Associated artifacts.

Colour: White (N9) to very light grey (N8) with a few black (N1) spots.

Mean refractive index: 1.461 ± 0.002 .

Welshpool Lechatelierite, Geology Dept. No. 73367

Locality: Sand blow-out north side of Dowd Street near its eastern end, north of Welshpool Road (see Fig. 2).

No. of fragments: Two (includes one tube). Associated artifacts.

Colour: Light grey (N7) with a few black (N1) spots.

Mean refractive index: 1.461 ± 0.002 .

Malaga Lechatelierite, Geology Dept. No. 73368

Locality: Road cutting in sand, east side of Beechboro Road, 1.6 km north of King Road (see Fig. 2).

No. of fragments: One. Associated artifacts.

Colour: Pinkish grey (5YR8/1) with medium dark grey (N4) to black (N1) spots.

Mean refractive index: 1.461 ± 0.002 .

Beechboro Lechatelierite, Geology Dept. No. 73369

Locality: Disused sandpit, Widgee Road (see Fig. 2).

No. of fragments: 250, with numerous tubes (see Fig. 3). Associated artifacts.

Colour: Light grey (N7) to greyish black (N2).

Mean refractive index: 1.463 ± 0.002 .

Upper Swan Lechatelierite, Geology Dept. No. 73545

Locality: 20 km N.N.E. of Perth, Bell Bros. Sandpit, northern side of Gnangara Road, 2.1 km west of West Swan Road turn-off. North of area covered by Figure 2, and not shown.

No. of fragments: Three. Associated artifacts.

Colour: Very light grey (N8) to light grey (N7) with dark grey (N3) to black (N1) spots and streaks.

Mean refractive index: 1.462 ± 0.002 with some darker glass close to 1.464 ± 0.002 .

Wanneroo Lechatelierite, C.S.I.R.O. No. 9073

Locality: Sand at Wanneroo, about 25 km north of Perth, precise locality not recorded.

No. of fragments: One tube.

Colour: Very light grey (N8) with rare small black (N1) spots.

Mean refractive index: 1.463 ± 0.002 .

Guilderton Lechatelierite, Geology Dept. No. 73370

Locality: Sand blow-out near mouth of Moore River, south bank, opposite Guilderton (see Fig. 1).

No. of fragments: Five. Associated artifacts.

Colour: Greyish black (N2) to dark yellowish brown (10YR4/2).

Mean refractive index: 1.461 ± 0.002 .

Northampton Lechatelierite, Geology Dept. No. 73371

Locality: Sand blow-out 3 km west of Howatharra Homestead, which is 22 km south of Northampton on Highway No. 1 (see Fig. 1).

No. of fragments: One. Associated artifacts.

Colour: Dark grey (N3) to greyish orange (10YR7/4).

Mean refractive index: Mainly close to 1.463 ± 0.002 , but ranging from 1.461 to 1.467 ± 0.002 .

Discussion

Some sandy areas of the Earth, such as the south-eastern portion of the Kalahari Desert in southern Africa, are notable for their concentration of fulgurites, and Lewis (1936) in his discussion of the region guessed that there were not less than 2,000 fulgurites within an area of about 20 sq km. He thought it reasonable, after questioning local inhabitants, to assume that the area had been struck recently only about once every fifty years by lightning. He therefore proposed that the sands might be about 100,000 years old, if there had been unchanged climate throughout.

Meteorologists chart thunderstorm activity by isobronts, lines that join places of equal annual thunderstorm activity. The central Perth Basin occupies a 20 to 30 isobront area, a thunderstorm frequency described by the Bureau of Meteorology (1967) as "relatively high", and exceeded in Western Australia only in the tropical northern part of the State. The Western Australian statistics suggest a far higher annual frequency of lightning in the central Perth Basin than that now experienced in the south-eastern Kalahari area, if the assumptions of Lewis are accepted. It should be added, however, that the isobrontic map of Ramakrishnan and Rao (1955) shows a higher thunder frequency in the Kalahari than around Perth. The Western Australian statistics suggest a far higher annual frequency of lightning in the central Perth Basin than that now experienced in the south-eastern Kalahari area, if the assumptions of Lewis are accepted. It should be added, however, that the isobrontic map of Ramakrishnan and Rao (1955) shows a higher thunder frequency in the Kalahari than around Perth.

Ten of the fourteen known Western Australian fulgurite localities are also rich in Aboriginal artifacts. There is not necessarily any significant connection between the association of artifacts and fulgurites: the former are normally sought in blown-out sandy areas because they are concentrated as wind removes the sand, and the fulgurite fragments, which are similarly concentrated, were found when the localities were examined for artifacts. The time of artifact manufacture in Western Australia ranges from the ethnographic present back 25,000 years and probably longer (see Dortch and Merrilees 1973). It is known, in the light of the West Popanyinning event, that fulgurites are forming at present, but it cannot be assumed that isolated fulgurite fragments are necessarily younger than the artifacts with which they were found. It is not possible to say what proportion of the recovered fulgurite material formed under the current climatic regime.

The recent spate of fulgurite finds in the Perth area, which is similar in its topography, sandy soil and meteorology to the surrounding region of the central Perth Basin, is probably a reflection of the high number of studied sites of former aboriginal occupation, rather than any special abundance of fulguritic material. Fulgurites are therefore probably fairly common throughout the central Perth Basin. Other sandy areas in Western Australia, such as the

Gibson Desert and part of the Great Victoria Desert, are of equal isobrontic frequency, and the northern part of the Great Sandy Desert has a higher frequency. These areas will almost certainly contain numerous fulgurites.

Acknowledgements.—Fulgurite fragments from Guilderton, Upper Swan and Jandakot were supplied by Mrs. S. J. Hallam, Department of Anthropology, University of Western Australia, and the Welshpool material was supplied by Miss A. D. McConnell, Department of Geology, University of Western Australia. The Wanneroo material was loaned by Dr. D. R. Hudson, Commonwealth Scientific and Industrial Research Organisation, Floreat Park.

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5.—Geometric microliths from a dated archaeological deposit near Northcliffe, Western Australia.

by C. E. Dortch¹

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Abstract

Preliminary examination and a test excavation made in a sandy podzol overlying a silcrete formation near Northcliffe, Western Australia, established that prehistoric man quarried the silcrete and used the immediate locality as a factory for manufacturing stone tools. Two radiocarbon dates based on charcoal samples collected at the excavation site indicate that geometric microliths were manufactured there from about 6000 to about 3000 years BP, and that the site had been a silcrete quarry-factory for some time previous to this. Analysis of pollen samples taken from the dated deposit show that *Eucalyptus diversicolor*, *E. calcophylla*, and *E. marginata* existed in the locality prior to about 6780 years BP and that the two former species and possibly the latter were present at times since.

Introduction

Geometric microliths are very small, abruptly retouched stone tools known in many Old World stone industries dating to the terminal Pleistocene and Recent periods, and they are a characteristic feature of stone artifact assemblages from many districts in the southern two-thirds of Australia (Mulvaney 1969, Fig. 28). Radiocarbon assay has shown that geometric microliths were used in Australia from about 5000 to 6000 years BP until Modern times (Pearce 1974, Table 2). Various prehistorians (e.g. Mulvaney 1969) have interpreted the introduction of geometric microliths and a range of other distinctive forms of flaked stone tools (e.g. tula adze flakes and invasively flaked points) into the archaeological sequences of a number of Australian sites as a definitive event marking the beginning of a phase or period in continental prehistory.

The Northcliffe quarry-factory site

Several years ago Mr. G. Gardner, a naturalist from Northcliffe, W.A., identified an outcropping formation of sedimentary rock located about 10 km west of Northcliffe (Fig. 1) as an Aboriginal stone quarry. The rock has since been identified as silcrete (J. E. Glover, *pers. comm.*).

On different occasions Mr. Gardner collected quarrying *débris* and stone tools from an area of several hectares around the silcrete formation, and he found silcrete artifacts in the section of a bulldozed cutting in a sandy soil overlying the formation. In 1973 I took a char-

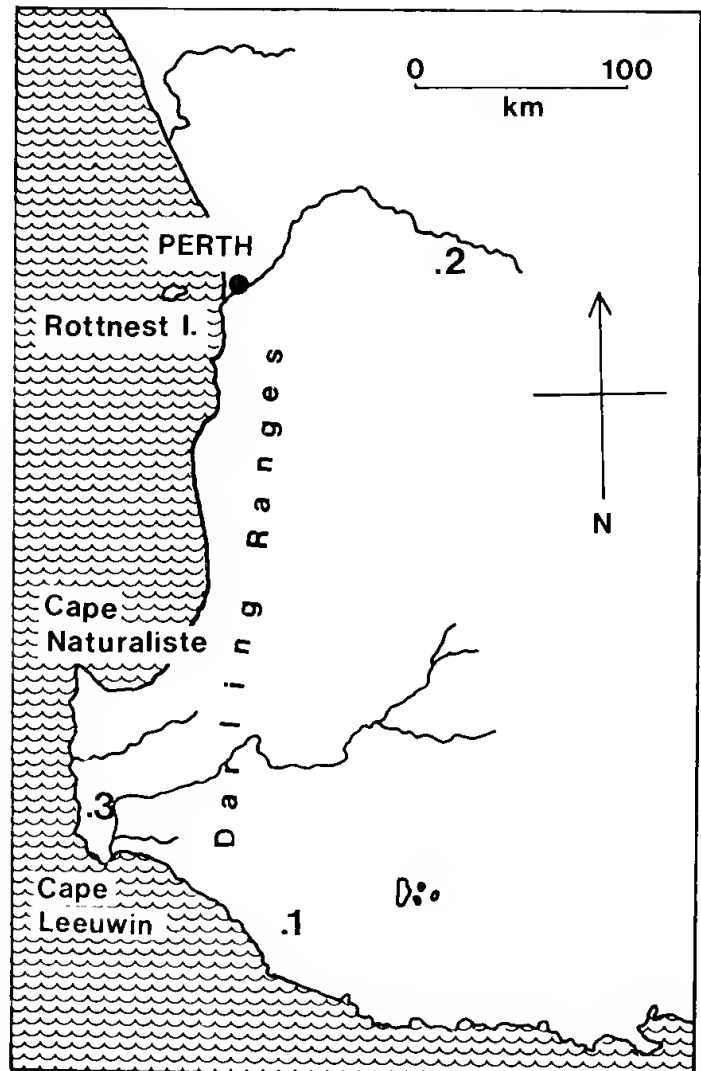


Figure 1.—Map of the south west, Western Australia showing locations of archaeological sites mentioned in the text. 1, Northcliffe quarry-factory; 2, Frieze Cave; 3, Devil's Lair.

coal sample from the upper part of the cutting face at a position (50 cm below a datum level later established at the site) where several artifacts (B1716) were visible. The sample, KS 1 (Table 1), has since been radiocarbon assayed at 3080 ± 75 years BP (ANU 1131: H. Polach, *pers. comm.*).

Mr. W. M. McArthur of the Division of Land Resources Management, CSIRO, Perth, who was present at the site, identified the sandy deposit

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as an iron humus podzol (*pers. comm.*). He also found several flakes (B1715) 30-40 cm deep (i.e. at about the same depth as the artifacts visible in the section) in a 15 x 20 cm test pit dug into undisturbed soil about 2 m away from the cutting. He and I regard these flakes as evidence that occupation took place on the surface of the sand as it accumulated, and that the artifacts we found in the face of the cutting are *in situ*.

In February 1974, Mr. Gardner, Miss A. McConnell and I excavated a 1 x 1.5 m test trench (Trench 1) in the bulldozed cutting at the position where a year previously I had collected charcoal for sample KS 1. We excavated Trench 1 in two, three and four cm arbitrary levels and screened all excavated material through three or five mm sieves. The deposit as shown in the north section of Trench 1 (Fig. 2) shows a

surface plant fibre and leaf zone overlying a dark humic zone about 20 cm thick. This merges into a leached zone about 50 cm thick. At the base of the leached zone is a five cm thick layer of dark sand which in turn rests on a hard pan of iron stained, cemented sands.

The first stone artifacts we excavated in Trench 1 were in the upper part of the leached zone at a depth of 46 to 51 cm below datum. Below this, the number of artifacts increased to a depth of about 75 cm and continued in smaller numbers to the surface of the basal cemented sands (Fig. 2, Table 2). This surface contained several pits or channels 10 to 30 cm deep, and a few stone artifacts were excavated from these. We did not continue systematic excavation into the cemented sands; we screened about 20 kg of these sediments through a five mm sieve but found no archaeological material.

Table 1

Radiocarbon dates based on charcoal samples collected from Trench 1, Northcliffe quarry-factory site, Western Australia

Sample	Date	Radiocarbon age in years BP	Provenance, with depth below datum
KS 1	ANU 1131	3 080 ± 75	upper part of leached zone, 50 cm
KS 2	SUA 379	6 780 ± 120	lower part of leached zone, 85-95 cm

Table 2

Distribution of stone artifacts in Trench 1, Northcliffe quarry-factory site, Western Australia

Radiocarbon dates	Depth in cm below datum	Geometric microliths ¹	Notched flakes and other re-touched tools	Silerete artifacts					Artifacts of other stone		
				Blades	Blade-lets	Flakes	Chips ²	Cores	Debris		
ANU-1131 3080 ± 75	46-51					2					
	51-53					2	6+				
	53-57	1 atypical	1			3	39	47+			
	57-59	2 atypical	2			2	48	57+			
	59-60		2			6	57	110+			1 quartz chip
	60-62		3	2		2	76	50+		2	2 quartz chips
	62-64	2	1			1	54	50+			1 quartz flake
	64-66		2	6		5	81	50+		3	1 quartz bladelet
	66-70	6,2 atypical	2	3		11	149	250+			
	70-72	4,1 atypical	2	4		2	106	250+		2	6 quartz flakes and fragments
	72-74	2	4	5		1	97	250+	5		1 pebble
	74-78	1 atypical	3	1		11	112	250+	4	1	3 quartz fragments
	78-82	3		1			38	100+	1		2 quartz fragments
	82-85	1				1	14	20+			1 fragment of gneiss
SUA 379 6780 ± 120	85-90		2				5	20+	1	1	8 quartz chips
	90-96		1				5	2+	1		1 quartz fragment
	96-98						5	9+			1 quartz flake
	98-103						7	1+			1 quartz core
	103-c,120						5	4+		2	1 quartz flake
		18 typical 7 atypical	25	22	46	903	1526+	12	11	40	2 quartz bladelet
											2 quartz flakes
											2 quartz fragments
											1 quartz fragment
											2 quartz flakes
											2 chert flakes

¹ atypical indicates irregular or partly retouched specimens.

² + indicates that total chips were not recovered.

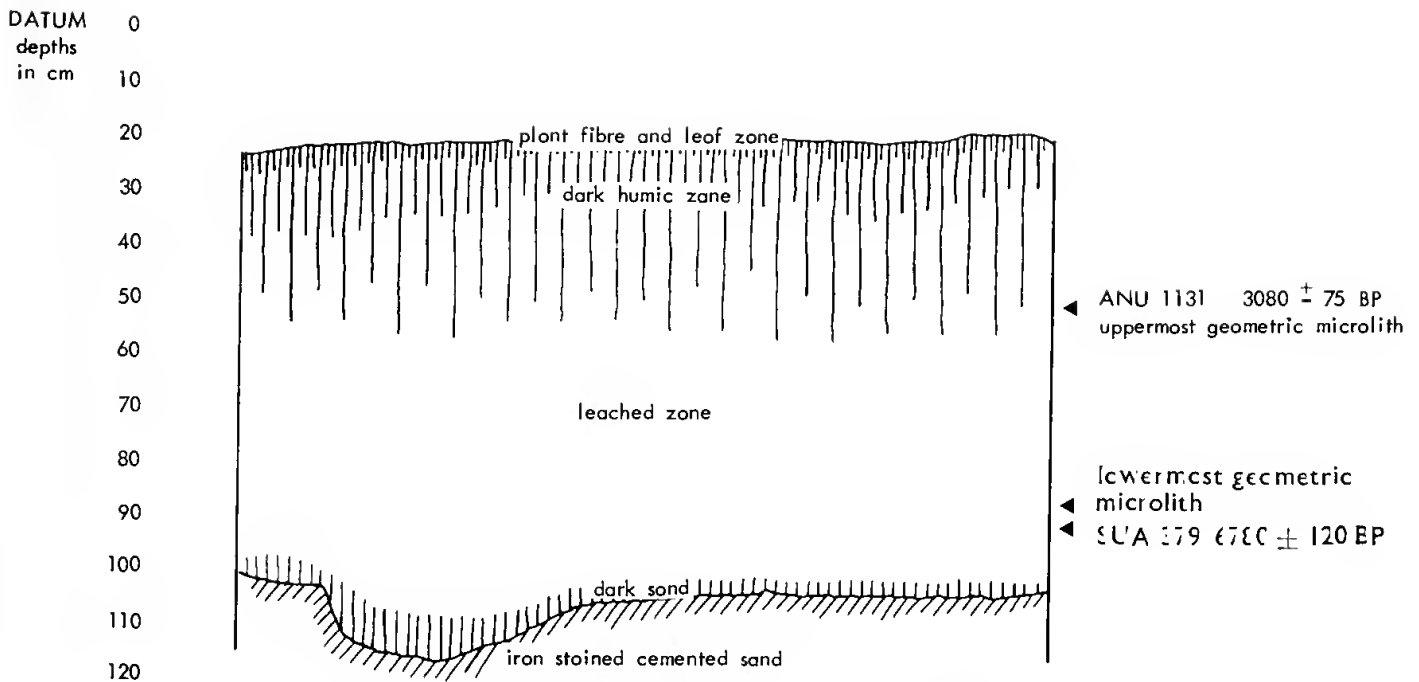


Figure 2.—North section of Trench 1, Northcliffe quarry-factory.

Trench 1 contained no vertebrate remains or mollusc shells. Charcoal occurred in varying quantities throughout and we collected several samples for radiocarbon assay. One of these samples, KS 2, taken from a depth of 85 to 95 cm in the lower part of the leached zone (Fig. 2), was submitted for dating and yielded an age of 6780 ± 120 years BP (SUA 379: R. Gillespie, *pers. comm.*) (Table 1).

Stone artifacts

The largest quantities of stone artifacts were in the leached zone between 65 and 80 cm (Table 2). The assemblages from arbitrary levels at this depth comprise retouched tools, large irregular flakes or fragments, numerous small flakes and very many tiny chips. These last are flakes which have a maximum dimension of less than one cm; many of these (measuring $< .5$ cm) were not retained. There are also many blades and bladelets which, following Tixier (1963, p. 38), can be distinguished on the basis of width, bladelets having a maximum width of 1.2 cm (e.g. Fig. 3d). No blade cores were recovered from Trench 1 though these have been collected from other sites in the district. Some of the blades and bladelets are snapped short, perhaps deliberately. None is retouched.

All of the 13 cores from Trench 1 were used in flake production. One of these, from 74 to 78 cm depth, is a typical discoidal core. There are also a number of short (2-4 cm long) flakes with broad, thick faceted butts and oval or triangular forms which were probably produced on discoidal cores. The single quartz core (depth 96-98 cm) is of bipolar or scalar type (White 1968).

Half of the retouched tools are geometric microliths of trapeze (Fig. 3a), crescentic (Fig. 3b) or triangular form (Fig. 3c). We recovered 18 typical geometric microliths from Trench 1. Almost all of the other retouched tools are flakes with one or two notches, the exceptions being retouched flakes. The very high proportion of *débitage* ranging from flakes or fragments to hundreds of tiny chips probably resulting from the manufacture of finely retouched tools such as geometric microliths, as well as the retouched tools themselves, indicate that the site is not only a quarry but also a factory where geometric microliths were one of the main products.

Only two flakes, both made of silcrete, occurred above the position of ANU 1131. The uppermost geometric microlith came from a depth of 53 to 57 cm or about three to seven cm below the sample position of ANU 1131 (Fig. 2, Tables 1, 2). The lowermost geometric microlith (this piece is illustrated in Fig. 3b) was recovered one to three cm above the upper limit of the level from which we collected charcoal for SUA 379 (Fig. 2, Tables 1, 2). These radiocarbon dates thus show that geometric microliths were being manufactured at the factory from about six thousand to about three thousand years ago.

Relatively few artifacts were found below the sample position of SUA 379. However the silcrete artifacts from this depth and below are similar (i.e. quarried fragments, tiny chips and flakes of small size, some with small butts and parallel dorsal flake scar ridges) to the silcrete *débitage* in the assemblages containing geometric microliths higher up in the sequence, thus sug-

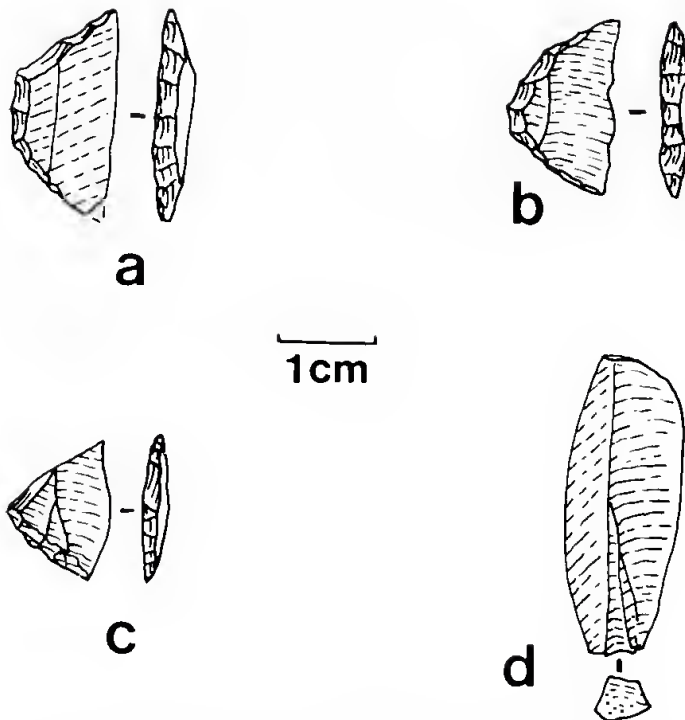


Figure 3.—Geometric microliths and a bladelet excavated from Trench 1, Northcliffe quarry-factory.

gesting that essentially the same industrial activity took place. It is possible then that a larger artifact sample from the lower part of the deposit would contain geometric microliths.

Most of the artifacts from Trench 1 and all of the retouched tools are made of silcrete, the few exceptions being quartz pieces (e.g. B2418), a fragment of gneissic rock (B2412) and two flakes (B2418, B2420) made of a distinctive form of fossiliferous chert (J. E. Glover, *pers. comm.*). This chert is similar to that used for artifacts from many sites in the Perth area (Fig. 1: Glover and Cockbain 1971; Hallam 1972) and in the late Pleistocene layers of Devil's Lair (Fig. 1: Dortch 1974; Dortch and Merrilees 1973; Glover 1974). One of the two chert flakes comes from a deep depression in the surface of the basal cemented sands (Fig. 2) and the other comes from dark sand just above the basal sands. These flakes may be considerably older than the artifacts in the leached zone, and they may have dropped down to the hardpan during the deflation of an earlier soil. Hallam (1972, pp. 14-15) has postulated that fossiliferous chert of this kind predominated in the early assemblages from sites on the coastal plain to the west. However on the south coast there is evidence to suggest that here fossiliferous chert continued to be used in quantity during the later prehistoric period. Gardner has collected numerous fossiliferous chert artifacts from surface sites in the Northcliffe area which also contain quantities of geometric microliths and bladelets of silcrete and quartz typical of later Australian stone industries. He has also located an outcrop of fossiliferous chert about ten km east of Northcliffe which would have been accessible during the later prehistoric period. It seems likely then that fossiliferous chert was used until relatively recent times in the Northcliffe area.

Pollen Analysis

Pollen samples were taken at different depths in Trench 1. These were submitted to Dr. B. E. Balme of the Geology Department, University of Western Australia for analysis. His report (B. E. Balme, *pers. comm.*) stated that a sample from a depth of 47 cm contained pollen grains, the dominant species being *Eucalyptus calophylla* and *E. diversicolor* though some grains "of *E. marginata*-type were also fairly common". A sample from 68 cm contained a similar plant microfossil assemblage to that of the previous sample. The next sample from 87 cm contained no pollen. The lowermost sample from the dark sand resting on the basal cemented sands (depth 121 cm) contained pollen grains of the three above *Eucalyptus* species with *E. diversicolor* appearing to be "relatively more abundant" than in higher samples.

These three *Eucalyptus* species are at present dominant in the Northcliffe area. The pollen analysis suggests then that climate in this locality was at various times during the Recent period much the same as it is at present. In his recent study Churchill (1968, p. 146) concludes that "the climate [of the extreme south west] from 4000 to 3000 B.C. was favourable for *E. diversicolor*". The oldest Northcliffe pollen sample above suggests that conditions were favourable for *E. diversicolor* even earlier during the Recent period.

Western Australian Museum catalogue numbers of silcrete artifacts illustrated in Fig. 3

a. B2410	b. B2414
c. B2413	d. B2410

Stone artifacts excavated from Trench 1 at the Northcliffe silcrete quarry-factory are listed in the Western Australian Museum register under catalogue numbers B2401-B2421. All catalogue numbers mentioned in the text pertain to the Western Australian Museum register.

Discussion

Hallam (1972, pp. 16-17) has published four self consistent radiocarbon dates ranging from 3090 ± 240 years BP (ANU 830) to 110 ± 70 years BP (ANU 827) which are associated with tool assemblages containing geometric microliths excavated at Frieze Cave near York, W.A. (Fig. 1) some 300 km north of Northcliffe. The Frieze Cave dates and those from the Northcliffe quarry-factory (Table 1) indicate that the use of geometric microliths in south western Australia persisted from about 6 000 years ago until the Modern period, this being the longest duration for microlithic industries yet recorded for Australia (see Pearce 1974, Table 2).

The Northcliffe dates do not support Pearce's recent hypothesis (1974, p. 307), based on previously available radiocarbon dates (e.g. ANU 830), that "the introduction of backed blades [geometric microliths] was earliest in New South Wales and progressively later away from that area". The earlier date from Northcliffe shows that geometric microliths are not a relatively late innovation in the south west, and that it is possible that they occur here earlier than in south eastern Australia. Until more data be-

come available I see no reason to assume that the beginning date of the microlithic industries in Western Australia differs greatly from that of the microlithic industries in eastern regions.

The dates reported here from Northcliffe, those from Frieze Cave (Hallam 1972), and the sequence of radiocarbon dates from Devil's Lair (Dortch 1974; Dortch and Merrilees 1973) provide a radiocarbon dating sequence for south western prehistory which extends from about 25,000 years BP to Modern times. A relatively recent date SUA 364: 6490 ± 145 years BP (R. Gillespie, *pers. comm.*), has been obtained from a charcoal sample collected during the 1973 excavation of Devil's Lair, Trench 7 (Dortch 1974). The sample on which this date is based comes from layer G (Dortch 1974, Fig. 3), a sandy deposit containing a quartz flake (B1846), some mussel shell (e.g. B1846) and other faunal remains, and some possible bone artifacts (e.g. B1847). No stone tool forms of great diagnostic value are associated with this date from Devil's Lair or with the older date (SUA 379) from Northcliffe. Nevertheless it is possible that SUA 364 and SUA 379 relate respectively to an early phase assemblage left by some of the last occupants of Devil's Lair, and an initial late phase assemblage marking an early period of quarrying and tool manufacture at Northcliffe. If this is true, then the early-late phase transition in south western Australia took place over 6000 years ago. Further investigations at these two sites should provide more data relevant to the age and significance of this transition.

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Dr. D. Merrilees, Dr. J. P. White and Mr. R. J. Lampert who read the *MS.* I thank Miss A. McConnell and Mr. W. M. McArthur for their help in the field, and I wish to thank Mr. G. Gardner for his co-operation and hospitality. Last I wish to express my gratitude to the Australian Institute of Aboriginal Studies for sponsoring the radiocarbon dates referred to here.

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6.—Nitrogen oxide levels in suburbs of Perth, Western Australia

by G. A. Bottomley¹ and F. C. Cattell²

Manuscript received 22 October 1974; accepted 19 November 1974

Abstract

Nitrogen oxide determinations are reported for two residential suburbs southwest of the central city area of Perth, Western Australia. Daily measurements for the period 10 a.m. to noon during 1971, 1972 and 1973 show that the levels of nitrogen oxides in the atmosphere are low in comparison with overseas major urban areas. The day to day values fluctuate considerably but periodogram analysis detects a seven day cycle which reflects local traffic flows with highest values on Fridays and the lowest on Sundays. The thirty day moving average shows a seasonal pattern where average values are low from about August to April and rise to a pronounced peak in May and June (late autumn). Data is given for autumn evenings when local meteorological conditions often result in shallow inversions about sunset. These inversions are coincident with peak traffic flow and concentrations of NO_x as high as 47 pphm have been detected on such evenings. Some limited monitoring of photochemical conversion of NO to NO_2 and production of ozone has been undertaken.

Introduction

The residents of Perth, Western Australia, ordinarily enjoy atmospheric quality and clarity which are remarkably good for a city with more than three-quarters of a million inhabitants. Partial explanations are adequate mixing and good ventilation (the mean wind speed is 15.6 km/hour) and the location and control of industrial and other pollutant sources. In the City and most residential suburbs the levels of smoke, sulphur dioxide and particulates are modest. However, motor vehicle use has risen sharply in the last decade and the trend continues. Because of the intense and prolonged sunshine (average 2 850 hours annually) pollution from car exhausts and photochemical effects are of public interest. We report here concentrations of oxides of nitrogen at three suburban sites recorded chiefly in 1971, 1972 and the first half of 1973.

Relevant geographical information

General

The City proper and much of the Metropolitan residential areas are on the Swan Coastal Plain at elevations less than 70 metres above sea level. Fifteen kilometres to the East the Darling Scarp rises sharply to above 300 metres. Most traffic generated by the business and residential areas is within a radius of fifteen kilometres of the City centre.

Recording sites

Air samples were taken at about two metres above ground level at three locations (see Figure 1).

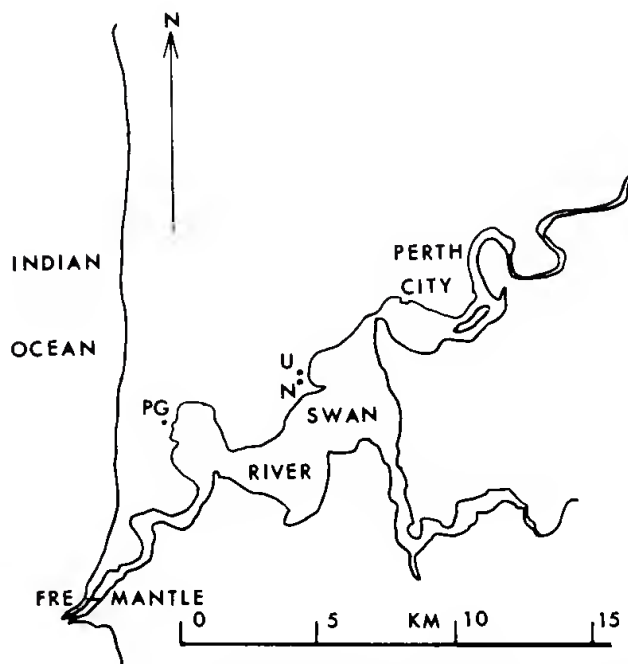


Figure 1.—Map showing University site (U), Nedlands Site (N) and Peppermint Grove Site (PG) in relation to Perth.

University site.—The University of Western Australia campus five kilometres South West of central Perth business area. Most of its forty hectare area is grassed but it includes car parks for about two thousand vehicles. To the North East is four hundred hectares of Kings Park with bush, botanic gardens and open space and to the East and South East there is a broad stretch of the Swan Estuary, hereabouts two or three kilometres wide. On the West the University is flanked by residential areas.

Nedlands site.—A private residential area about three hundred metres to the South of the University sampling site.

Peppermint Grove site.—A private residence ten kilometres South West of the city centre, within one and a half kilometres of the Indian Ocean and close to the open reaches of the lower Swan. The area includes much open space and is not near any recognisable industrial sources though domestic gas and oil appliances are in normal use for water and space heating, as at the other two sites.

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Analytical procedure

Saltzman's method (Katz 1968, p. 80) with permanganate oxidation of the nitric oxide was used to determine total nitrogen oxides NO_x . Air was usually sampled at about twenty litres per hour and for two hours. The absorbing reagent, N-(1-naphthyl)ethylene-diamine dihydrochloride with sulphanic acid in aqueous acetic acid solution was kept in very subdued light during prior storage and until the spectrophotometric determination was completed. Direct sunshine degrades the red azo compound.

The values are cited as parts per hundred million by volume (pphm) of the combined oxides NO plus NO_2 unless a distinction is made in the context. The conversion factor is:

$$18.8 \text{ pphm} = 1 \text{ microgram metre}^{-3} (25^\circ\text{C})$$

Measurements at the University of Western Australia

Two hundred determinations on outside air at the University Site were taken sporadically between June 1970 and June 1971 at various times of the day and night. Table 1 summarises these exploratory results in histogram form.

Table 1

General results in preliminary survey at University Site 1970-1971

NO_x at University Site (mean value over period)	Number of Observations June 1970—June 1971
pphm	
0.0 to 0.99	27
1.0 to 1.99	63
2.0 to 2.99	39
3.0 to 3.99	11
4.0 to 4.99	16
5.0 to 5.99	9
6.0 to 6.99	6
7.0 to 7.99	4
8.0 to 8.99	1
9.0 to 9.99	3
Above 10.00	2
(16.4, 23.6)	181

The low values are evidence for the ability of Perth air to disperse contaminants. Particularly in South Westerly air streams in winter and during the regular afternoon sea-breeze (the Fremantle doctor) in summer, values as low as 0.2 pphm have been recorded. However, there are occasional periods of calm air and poor mixing conditions which correlate with higher levels of NO_x . Table 2 sets out the highest values recorded June 1970 to June 1971 together with comments on atmospheric conditions. We consider it most unlikely that these occasional measurements would have detected the highest levels experienced that year. Newspaper reports of the highest value recorded, 23.6 pphm, 8 a.m. to 10 a.m. April 29, 1971, provoked external criticism that emissions from a small oil-fired boiler in the University grounds were responsible, a view the authors do not endorse. To eliminate this possible bias sampling was transferred to the Peppermint Grove residential site.

Table 2

Highest values in preliminary survey at University site 1970-1971

Date	Approx. Time	Value NO_x pphm.	Comment
1970			
June 18	4-6 p.m.	5.4	
June 23	8-9 a.m.	6.7	
	9-10 a.m.	7.1	
July 17	9-10 a.m.	9.5	
July 24	4-8 p.m.	8.2	
July 25	4-8 p.m.	5.4	
Aug. 3	6-8 p.m.	6.0	
Aug. 4	9-11 a.m.	9.1	Blue light-scattering material evident between University buildings.
	4-6 p.m.	5.2	
	6-9 p.m.	16.4	
Sept. 25	8-10 a.m.	5.9	
Sept. 29	7-9 a.m.	7.6	
Sept. 30	7-10 a.m.	6.0	
1971			
April 1	8-10 a.m.	6.0	
April 2	4-6 p.m.	5.2	
April 20	8-10 a.m.	6.8	Anticyclone continues for week, Herdsman Lake vegetation on fire two days previous
April 21	8-10 a.m.	7.2	
April 28	8-10 a.m.	5.8	
April 29	8-10 a.m.	23.6	City not visible from University (three miles) at 10 a.m. because of 'white-out' Clears partially by 11.00 a.m.
	10-Noon	7.8	
April 30	8-10 a.m.	9.0	'Blue haze' again
May 1	8-10 a.m.	6.5	
May 6	8-10 a.m.	5.8	'Grey-out'. City just visible at 10.00 a.m. from University.
May 7	8-10 a.m.	5.0	
	5-7 p.m.	5.8	

Peppermint Grove morning series

June 1971 to July 1972

Measurements were made 10 a.m. to noon each day for more than a year and the results are set out in Table 3. The daily values fluctuate considerably with the weather circumstances and include many very low values. The maximum values 15.0 and 12.7 pphm recorded respectively on May 12 and June 8 1972, bearing in mind the greater distance of the Peppermint Grove site from the City, approach comparability with the University maximum on April 29, 1971. The monthly averages and the maximum values each month show progressive variation in levels of NO_x with a pronounced maximum in autumn and early winter months. Figure 2 shows the 'thirty day moving' average as a function of the mid-date of the averaged sequence.

Our hypothesis is that NO_x is generated by emissions from vehicular traffic in the morning rush hour and that the recorded levels reflect the inability of the air in each day to disperse that chemical burden. Information supplied by the Bureau of Meteorology for the mean monthly 7 a.m. mixing depth (1966-1969 inclusive) shows values which range from one hundred and thirty metres to two hundred and ten metres, with the lower values in May-August. The routine radiosonde ascents may

Table 3

Results of year long survey of morning values at Peppermint Grove 1971 and 1972

pphm. NO + NO₂ = NO_x 10 a.m. to noon daily

(140a Forrest Street, Peppermint Grove)

DAY	June 1971	July	Aug.	Sept.	Oct.	Nov.	Dec. 1971	Jan. 1972	Feb.	Mar.	Apr.	May	June	July 1972
1	6.9	0.5	1.6	0.8	1.2	0.4	0.6	0.2	0.6	0.6	3.4	6.3	1.6
2	2.5	1.5	0.9	0.9	0.6	0.3	0.6	0.2	0.5	0.6	3.3	1.0	0.7
3	1.7	2.1	1.0	1.1	0.6	0.2	0.6	0.2	0.5	0.6	2.6	1.9	1.1
4	1.0	0.8	1.1	0.8	0.9	0.2	0.6	0.7	0.5	0.4	1.7	1.0	2.2
5	1.5	3.9	0.8	0.8	0.2	0.6	0.7	0.6	1.1	1.0	2.8	4.6
6	3.3	1.0	1.1	0.9	0.2	0.6	0.7	0.7	0.7	1.1	2.0	0.8
7	1.5	4.7	3.5	1.0	0.8	0.3	0.5	0.6	0.7	0.7	1.5	5.0	1.7
8	1.0	2.5	1.2	1.8	0.9	0.4	0.5	1.0	0.7	0.9	3.3	12.7	0.8
9	1.5	1.7	1.4	1.1	0.8	0.6	0.4	0.8	1.3	0.2	5.0	11.0	0.9
10	0.9	7.3	1.3	0.9	0.6	0.5	0.5	0.7	0.8	0.8	1.3	2.6	1.1
11	3.8	4.0	1.5	1.1	1.0	0.7	0.5	0.6	0.7	0.8	0.9	2.0	1.3	2.0
12	2.7	1.3	0.9	1.1	1.0	0.6	0.7	0.5	0.8	0.2	1.3	15.0	0.8	1.4
13	1.5	2.2	0.8	1.1	0.8	0.6	0.5	0.5	0.9	0.2	2.0	1.0	0.4	0.9
14	1.1	1.7	1.7	2.0	0.9	0.7	0.7	0.4	1.3	0.2	0.9	0.8	0.4	0.9
15	1.6	2.2	0.6	1.7	1.0	0.4	1.0	0.6	0.8	0.2	2.3	1.1	0.7	4.5
16	1.1	2.3	0.8	1.9	1.0	0.4	1.1	0.7	0.9	0.5	1.8	3.5	0.4	2.1
17	3.8	2.2	0.8	1.4	0.6	0.5	0.7	0.7	0.6	0.3	1.4	4.0	0.5	3.0
18	7.2	2.1	1.6	1.4	0.8	0.4	1.0	0.7	0.8	0.3	1.0	1.9	2.0	1.7
19	1.6	2.2	2.0	1.0	1.0	0.4	0.9	0.7	1.1	0.2	0.9	1.8	2.0	5.2
20	1.2	0.9	1.8	1.1	0.7	0.5	1.0	0.9	1.1	0.3	1.0	1.2	2.0	4.5
21	6.5	0.6	0.9	0.9	0.9	0.9	0.9	0.7	2.5	2.0	2.3	3.0
22	2.5	0.8	0.7	0.7	0.5	1.1	0.8	1.5	0.4	1.7	1.7	0.8	2.0
23	6.8	1.0	0.8	0.9	0.5	0.8	1.2	1.3	0.6	1.0	1.9	2.5	1.6
24	3.8	1.4	0.8	0.8	0.6	1.1	0.6	1.1	0.4	1.8	2.0	1.8	0.4
25	6.5	2.0	1.3	0.9	0.6	0.8	0.6	1.0	0.5	1.1	1.7	1.0	0.4
26	6.8	2.2	0.8	0.8	0.8	0.6	0.9	0.3	1.3	1.1	0.8
27	4.8	1.9	1.1	1.1	1.0	1.1	0.5	0.9	0.8	0.4	4.8	0.9	1.2
28	6.8	1.4	0.7	0.9	0.9	0.5	0.4	0.7	0.5	0.6	7.5	1.7	0.8
29	2.1	1.0	0.5	1.1	0.9	0.6	0.4	0.4	0.6	0.5	3.4	1.0	4.0
30	2.7	1.1	0.9	0.8	0.9	0.4	0.6	0.2	0.5	1.6	2.0	10.3
31	1.1	0.6	1.0	0.6	0.2	0.5	0.8
Av.	3.33	2.22	1.34	1.14	0.87	0.62	0.66	0.61	0.81	0.51	1.56	2.36	2.74	1.96
Max.	7.2	7.3	3.9	2.0	1.1	1.2	1.1	1.2	1.5	1.3	7.5	15.0	12.7	5.2
Min.	0.9	0.6	0.5	0.7	0.6	0.4	0.2	0.2	0.2	0.2	0.2	0.8	0.4	0.4

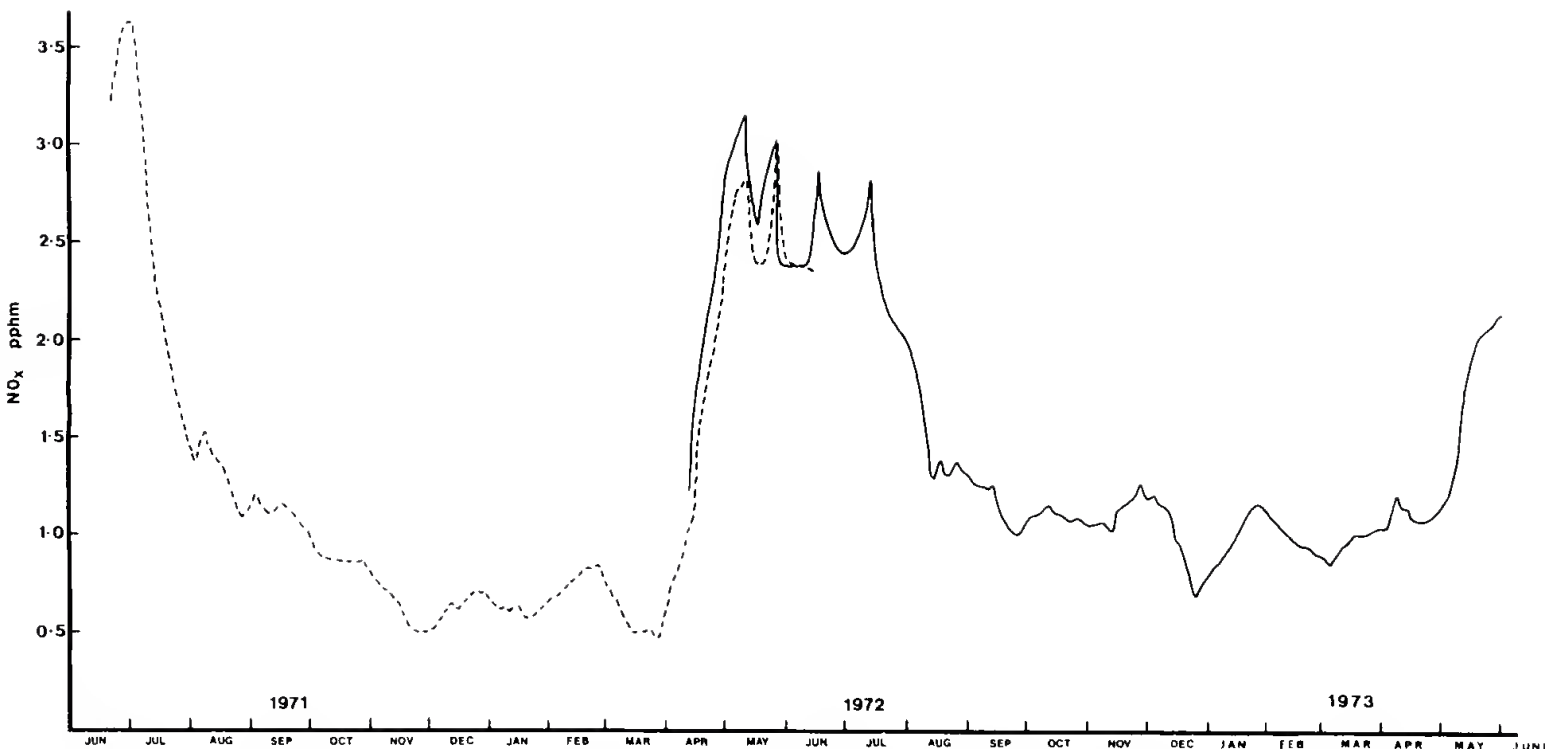


Figure 2.—Morning values of NO_x recorded at Peppermint Grove (dotted line) and at Nedlands (full line) expressed as a thirty day moving average.

not give particularly useful information about the lapse rate below the first hundred metres which is presumably the critical zone for dispersion of traffic exhausts.

Taken in the broad sense the dispersion of the air is rather generally governed by the energy flux from the sun which is very high here in summer. In the winter months the sun is at a relatively low angle and operates for less time before the start of the sampling period. The monthly averages appear to be governed substantially by this main driving force. Daily features of the synoptic weather pattern such as rain storm progressions and anticyclones are obscured by the thirty day averaging procedure but special features will be taken up later.

In general high nitrogen oxide levels correspond to days of reduced visibility, with suggestions of association with a special blue light-scattering quality. This does not require that the source of the nitrogen oxides is also responsible for the impaired visibility but indicates that at these times weather conditions are unfavourable for the dispersion of all pollutants. On days of poor visibility any photochemical destruction of the nitrogen dioxide would be slower.

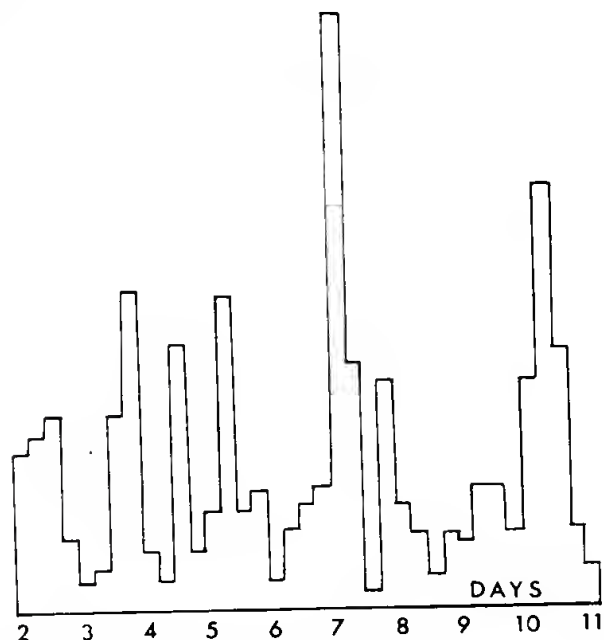


Figure 3.—Periodogram showing response against duration of cycle for the data given in Table 3.

The entries in Table 3 contain latent information which supports the car emission origin. It would be reasonable to suppose traffic flow to be substantially less on Sunday mornings in comparison with mid-week mornings. Emission release may therefore be cyclic, of period seven days, and of minimal amplitude on Sundays. The values in Table 3 were subjected by Schuster's method (Whittaker 1944) to a computer-assisted search for periodicities in the range two to thirty-two days in intervals 1/4 days. Part of the periodogram is shown in Figure 3. There is considerable evidence for a seven day component. For seven day periodicity the data can be succinctly expressed as the sum of the values recorded each Monday, each Tuesday, etc., through the week. The totals for fifty-five weeks are:

Monday	Tuesday	Wednesday	Thursday	Friday	Saturday	Sunday
70.6	67.3	72.7	90.2	98.3	75.2	58.6

a pattern which qualitatively reflects the traffic behaviour in the Metropolitan area.

Periodograms for the period March 1, 1972 to June 30, 1972 have also been run on data for twenty-four hours smoke values and sulphur dioxide values in the City. The patterns are not similar to that for the NO_x data so it is reasonable to conclude that the sources and dispersion characteristics of NO_x, SO₂ and smoke are dissimilar. In particular the seven day frequency component for the SO₂ measurements shows a mid-week rather than a Friday maximum.

Nedlands series

Mornings April 1972 to December 1972

Table 4 shows in summary form measurements 10 a.m. to noon at the Nedlands site from March 28, 1972 to June 14, 1973. Figure 2 summarises the trend of these measurements in the form of "thirty day moving averages" and displays the two series together. An interesting point is that the thirty day averages for the two sites five kilometres apart for the few weeks when simultaneous measurements were underway are similar in magnitude and in form.

A maximum mean concentration of 3 pphm in late autumn and early winter falls from the middle of July to about 1 pphm in September at both sites. In 1971 at Peppermint Grove there was a further decrease to an average

Table 4

Results of year-long-survey of morning values at Nedlands

		pphm. NO _x 10 a.m. to noon daily									
		Mar.*	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1972											
Average	1.51	1.70	2.67	2.95	2.23	1.38	1.18	1.15	1.11	0.97
Maximum	1.33	8.9	19.1	13.2	6.4	3.6	3.2	2.1	4.0	1.9
Minimum	0.7	0.4	0.4	0.7	0.6	0.7	0.4	0.7	0.7	0.5
1973		Jan.	Feb.	Mar.	Apr.	May	June*				
Average	0.96	0.99	0.98	1.08	1.88	1.76				
Maximum	2.2	1.5	1.5	2.6	5.3	3.1				
Minimum	0.2	0.4	0.6	0.3	0.7	1.0				

* Incomplete month.

concentration of about 0.7 pphm from November to March but at Nedlands in 1972 the average remained constant at 1 pphm. The relative contributions of the different sites and the different years to this difference cannot be estimated.

Periodogram analysis shows a similar frequency pattern to that of the Peppermint Grove data and again the totals over sixty three weeks for the weekdays are indicative of traffic origin:

Monday	Tuesday	Wednesday	Thursday	Friday	Saturday	Sunday
86.5	85.3	98.6	110.2	122.3	92.1	70.9

Figure 4 shows the daily inter-site comparisons of the 10 a.m. to noon values for a sample period in April and May 1972. The very close comparison between the rise and fall of the values above 2 pphm supports the view that both the long term average and the major observed effects are very probably typical of substantial parts of the Metropolitan area.

The correlation between the measurements at both sites for all days of the month can be estimated from the Spearman's rank correlation coefficient (Fisher 1958). If the days of the month are ranked according to nitrogen oxide values:

$$r = 1.0 - \frac{6 \sum d^2}{n^3 - n}$$

where $\sum d^2$ is the sum of the squares of the rank differences between the two sites and n is the number of days of the month. For April 1972, $r = 0.577$ and for May, $r = 0.879$, suggesting significant positive correlation. The probability, P , that such a correlation could arise by random

sampling from uncorrelated data can be estimated from Student's t test where

$$t = r \left(\frac{n-2}{1-r^2} \right)^{\frac{1}{2}}$$

which gives for April $t = 3.7$ and for May $t = 9.9$. For each month P is less than one in a thousand for a random occurrence. Again we conclude that the same controlling factors for nitrogen oxide concentrations seem to be operative at both sites, local uncorrelated sources can play only a minor part.

Results from measurements outside the 10 a.m. to noon period

The main sequence of measurements was deliberately taken so as to avoid the traffic peak emissions but some effort has also been made to measure the effects of these.

The principal meteorological factor leading to high concentrations of car emissions is the presence of a very shallow mixing layer in the air of the Metropolitan area. Particularly on late autumn afternoons with little or no wind, as sunset approaches inversion conditions set in as the layer of air close to the ground cools by radiation to temperatures substantially below that of air at a few tens or hundreds of metres. The onset of these conditions is often apparent to casual observers in that light smoke from domestic or garden fires is retained at shallow depth with otherwise very clear air above it. The same does *not* apply to emission from tall chimney stacks where the plumes carry well above this stagnation layer.

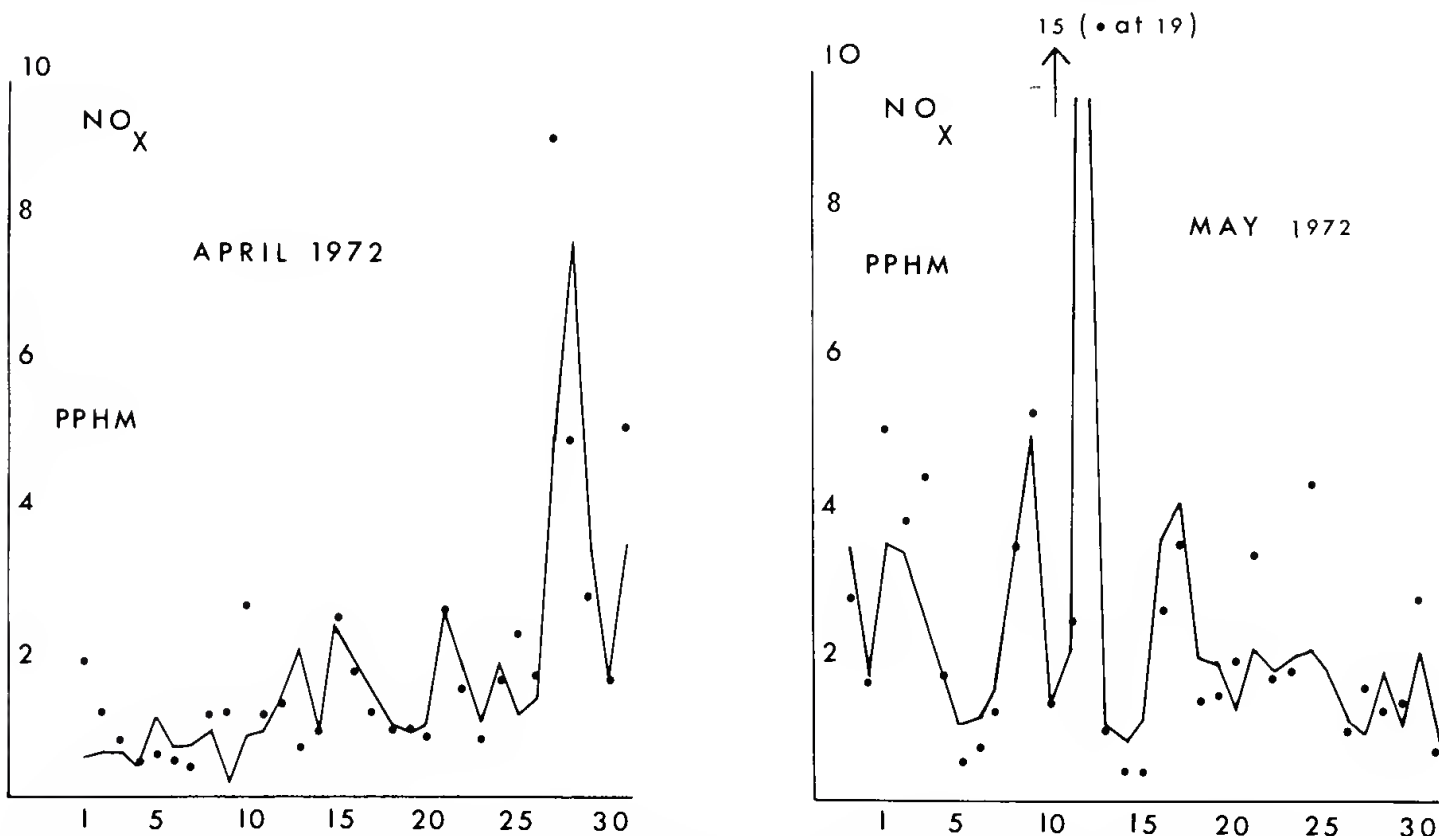


Figure 4.—Intercomparison of simultaneous morning values at Peppermint Grove (full lines) and at Nedlands (dots).

Measurements of NO_x levels were often purposefully taken during such actual or suspected (they are not visually detectable after dark) conditions. Observations outside the regular 10 a.m. to noon period were deliberately biased to times and days of anticipated higher levels and they do not represent an average overview of the early morning or evening conditions.

Table 5 lists pertinent but extreme data collected at the Nedlands site. Values taken at the same time in Peppermint Grove are broadly similar though the peaks tend to be somewhat lower and later consistent with a Westerly movement of contaminated air from the City centre across Nedlands to the coast at two to three kilometres per hour.

Table 5

Notably high measurements recorded in Nedlands 1972

<i>Saturday, 15th April</i>			
Above 20 pphm	1900 to midnight	5 hours
Above 25 pphm	2000 to midnight	4 hours
Peak 27.8 pphm.			
<i>Sunday, 16th April</i>			
Above 20 pphm.....	2100 to midnight	3 hours
Peak 23.8 pphm.			
<i>Friday, 28th April</i>			
Above 20 pphm.....	1900 to 2100	2 hours
Peak 32.5 pphm.			
<i>Saturday, 29th April</i>			
At 19.5 pphm.	300 to 500	2 hours
<i>Wednesday, 3rd May</i>			
Above 20 pphm.....	1800 to 2200	4 hours
Above 30 pphm.....	1900 to 2200	3 hours
Above 40 pphm.....	1900 to 2100	2 hours
Peak 47 pphm.			
<i>Friday, 12th May</i>			
Above 20 pphm.....	900 to 1100	2 hours
Peak 30.4 pphm.			
<i>Tuesday, 23rd May</i>			
Above 20 pphm.....	1813 to 2000	2 hours
Peak 30.7 pphm.			
<i>Thursday, 25th May</i>			
Above 18 pphm.....	1200 to 2210	10 hours
Peak 31 pphm.	(Data possibly of lower confidence limits)		
<i>Thursday, 1st June</i>			
Above 30 pphm.....	1800 to 0100	7 hours
Peak 37.3 pphm.			
<i>Thursday, 29th June</i>			
Above 20 pphm.....	1900 to 2300	4 hours
Peak 29.4 pphm.			

The 1972 mid April anticyclone and subsequent stagnation spells

Thursday, April 13th, 1972 brought a distinct layer of smoke over the Metropolitan area, with the Bureau of Meteorology issuing an air dispersion alert. Friday, April 14th, was similar with smoke haze extending many kilometres out to sea and persisting well into the afternoon: a dispersion alert was issued for Friday evening to Saturday noon. The smoke is said to have originated in burning-off operations on South West farms. This agricultural burning is common at certain times in Western Australia. Similar controlled burning of forest land occurs

at selected times; a major discussion of such bush-fire smoke is available (Vines 1971). Saturday and Sunday were much better optically. By midday Monday winds were affecting the City, clouds were gathering and after a calm period in the evening, wind sprang up again and rain fell early on Tuesday morning. The University wind records showed a forty hour calm starting 6 p.m. on Friday 14th. Alerted by some unexpectedly high values at Nedlands we obtained a considerable number of one hour and two hour duration measurements on April 15th, 16th and 17th. These are shown in Figure 5: similar information at other times in May and June 1972 appear in Table 5.

The extreme peak of 47 pphm on Wednesday, May 3rd, 1972 followed the formation at sunset of a very shallow stagnation layer containing smoke from domestic fires under almost calm conditions. The plume from a ship leaving Fremantle Harbour persisted virtually intact for twenty minutes.

Visual evidence that Perth's atmosphere can at times be incapable of dealing quickly with atmospheric contamination is given in Figure 6 which shows a view looking South from the University at 9.45 a.m. and 9.55 a.m. on June 7th, 1972. Smoke from a fire at a distance of about eight kilometres has risen to about two hundred metres and has spread horizontally over a distance of about five kilometres. Dispersion occurred quite suddenly two hours later.

Several of the evening events were preceded by an abnormally hot day for the time of the year, but such a feature is not essential. Thursday, June 29th was a day with a maximum temperature of 13.4°C, several degrees below average, but again there was a radiation inversion early in the evening to give exceptionally low ground temperature. Friday, May 12th produced quite high values in the morning, yet was associated with morning mist and light fog in Kings Park and slight rain clearing from the South West around 1 p.m.

It may be informative to make extremely simplified estimates of the amount of nitrogen oxide released. Assume a cylinder of contaminated air five kilometres radius, one hundred metres deep and of average concentration 20 pphm. This contains a volume of 75 x 10⁸ metre³ or 3 000 x 10⁸ moles of gas at one atmosphere pressure. At 20 pphm it will contain 60 000 moles of NO₂, which is some 3 000 kg. The amount of NO_x involved can also be approached from emission estimates. The "Freeway" Brochure produced by the Commissioner of Main Roads (1967) shows that Metropolitan Region traffic in an earlier survey amounted to 50 000 trips per hour over a five hour weekday period 3 p.m. to 8 p.m. This is 250 000 trips with an average of say four miles per trip each evening traffic rush period. Taking the Californian 1971 standard of 4 grams NO per mile gives 6 000 kg. NO_x. To the car emission after revision for annual growth we should add of course any NO_x from fuel oil and gas consumption but only that released at very low level. It then appears that the levels observed are achievable by car exhaust emissions within the

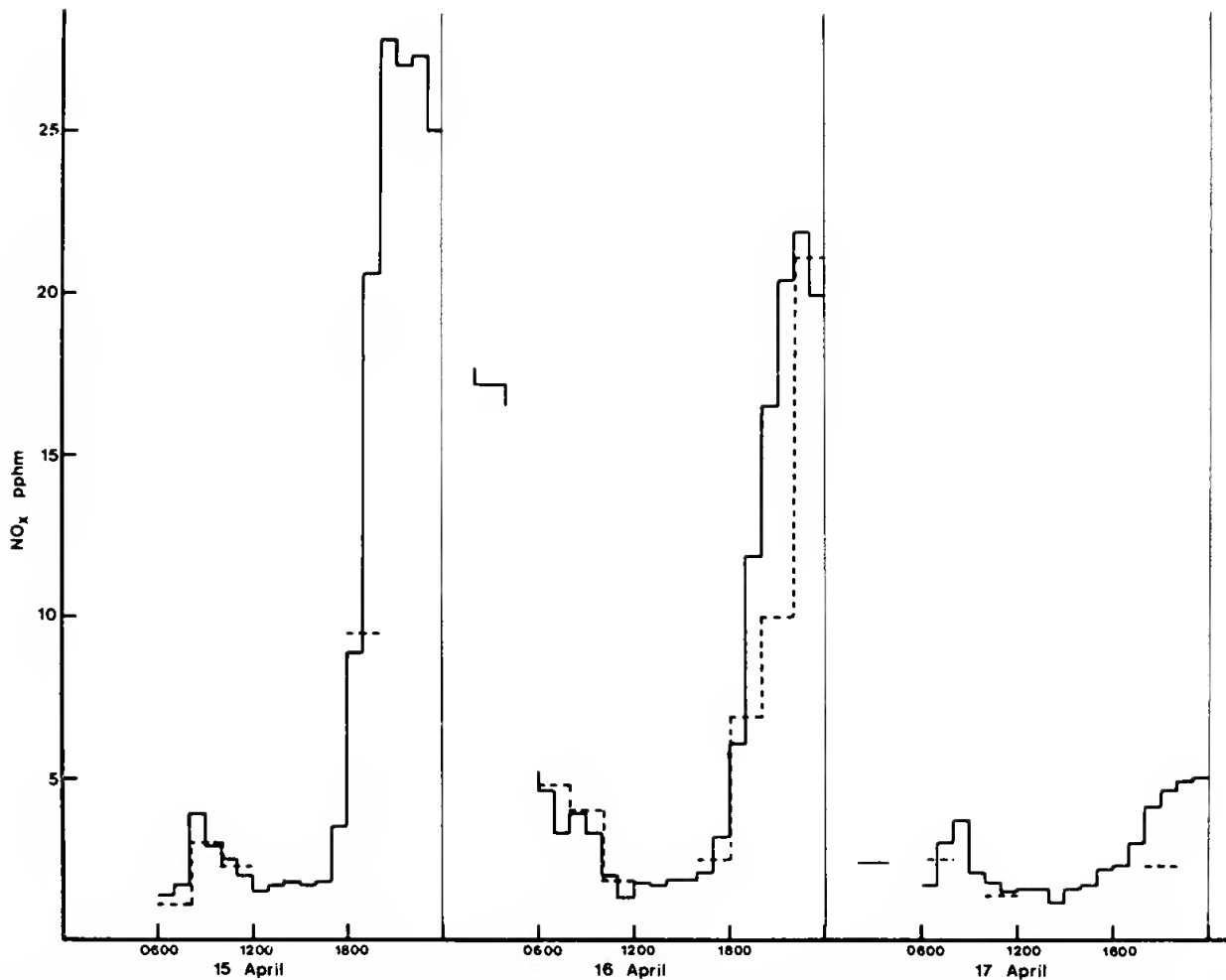


Figure 5.—Intercomparison of simultaneous values at various times for the special circumstances in mid April 1972. Full line Nedlands site, dotted line Peppermint Grove site.

Metropolitan area without invoking other sources such as bush fires which do not from other evidence (Vines 1971) appear to contribute NO_x though they may well produce smoke levels in Perth.

NO_x levels as indicators of photochemical and other pollutants

The NO_x values found as maxima in Nedlands compare at the one hour and eight hour level with those recorded as maxima for New Orleans (Zimmer 1965). This is disconcerting as it is most unlikely that the values measured at the particular sites correspond to absolute maxima in the Metropolitan area. The values justify commentary and further experimentation on other forms of car pollutants; carbon monoxide, photochemical oxidant and lead levels.

The national primary and secondary ambient air quality standards (Federal Register 1971) for nitrogen dioxide prescribed by the Environmental Protection Agency of the United States of America is 5 pphm annual arithmetic average. Our measurements even for the total oxides of nitrogen do not approach this figure and nitric oxide, for which there is no standard, predominates over nitrogen dioxide (See Figure 7) at least in the evening air for which the concentrations are greatest.

Although the nitrogen oxide concentrations are not in themselves of serious concern it is

possible from them to make inferences of the simultaneous concentrations of carbon monoxide. Overseas data for automotive emissions (Hurn 1968) and experimental observations from the Continuous Air Monitoring Programs (Zimmer 1965) suggest that the carbon monoxide concentration is typically about forty times the total nitrogen oxide level. If this is true also for Perth, as seems likely, then on four of the seven nights for which concentrations of oxides of nitrogen greater than 20 pphm were measured, the U.S.A. national primary and secondary carbon monoxide air quality standards (Federal Register 1971), 9 pphm maximum eight hour concentration not to be exceeded more than once a year, were violated in some suburbs West of the central Perth area.

The levels of 20 pphm NO_x recorded several times are certainly sufficient to induce photochemical smog given sufficient hydrocarbons, except that the observed incidents occurred in the late evening. Should such levels persist into two or three hours of sunshine we must anticipate photochemical effects with the characteristic lachrymatory effects and with visibility loss. The 8 a.m. to 10 a.m. April 29th, 1971 event was possibly just such a persistent wave.

Less nitrogen dioxide than nitric oxide is emitted from combustion processes. In the absence of other contaminants the conversion of nitric oxide (at pphm concentrations) to



Figure 6.—Smoke from fire South of Swan River on June 7th, 1972. Upper photo 9.45 a.m., lower photo 9.55 a.m. Nedlands site in foreground.

nitrogen dioxide is exceedingly slow. However, in the presence of hydrocarbon pollutants and sunlight the conversion is accelerated and typically takes one to two hours. In cities where photochemical smogs occur the nitric oxide peak, formed as a result of the morning traffic, decays and is replaced by a nitrogen dioxide peak. Nitrogen dioxide absorbs light and is removed with the formation of photochemical oxidant (mainly ozone) which has a maximum concentration about noon. This sequence although typical of photochemical smog formation is modified by weather conditions.

Photochemical oxidant concentrations were measured sporadically in 1972 by the neutral buffered potassium iodide method (Katz 1968, p 86). Measurements in Nedlands showed that nitric oxide, nitrogen dioxide and photochemical oxidant concentrations behaved similarly with time to atmospheres in which photochemical smog formation occurs (Tebbens 1968) except that pollutant concentrations are much smaller. For example, as shown in Figure 7, on the 7th June 1972 a morning nitric oxide peak of 5 pphm occurred between 8 a.m. and 9 a.m. a nitrogen dioxide peak of 2.5 pphm occurred between 11 a.m. and noon and an oxidant peak between noon and 1 p.m.. This suggested that

photochemical activity was occurring and is consistent with occasional subjective observations by experienced workers of a faint "Los Angeles" smell.

Oxidant concentrations were measured routinely on weekdays from October 1972 until the end of December 1972. In October, November and December maximum oxidant concentrations often occurred between 10 a.m. and 11 a.m. in the morning after which time they decreased rapidly and often remained relatively constant throughout the afternoon. The decrease which may be associated with the break up of an inversion or with the appearance of a sea breeze supports the belief that the oxidant is formed at low altitudes.

This pattern was not always followed and on 22nd November, 11th December and 16th December 1972, concentrations of greater than 6 pphm, which is the unofficial WHO goal (Bilger 1972), were measured. On the 11th December, as shown in Figure 8 an average oxidant concentration of greater than 8 pphm persisted for about two and a half hours between 1 p.m. and 3.30 p.m. This concentration is greater than that recommended by the U.S. primary and secondary air quality standards for photochemical oxidants and which is usually taken as the first indication of a mild photochemical

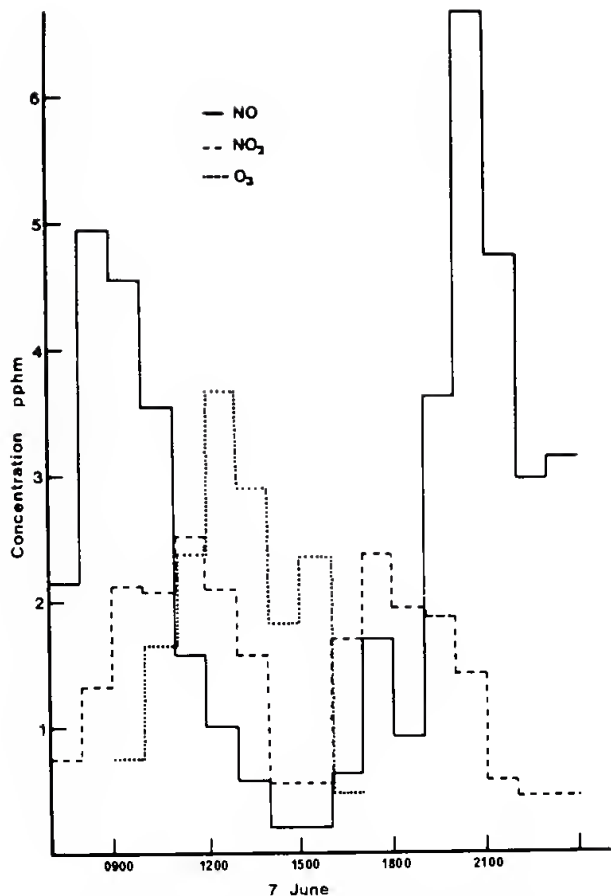


Figure 7.—Time dependence of ozone, nitric oxide and nitrogen dioxide on June 7, 1972.

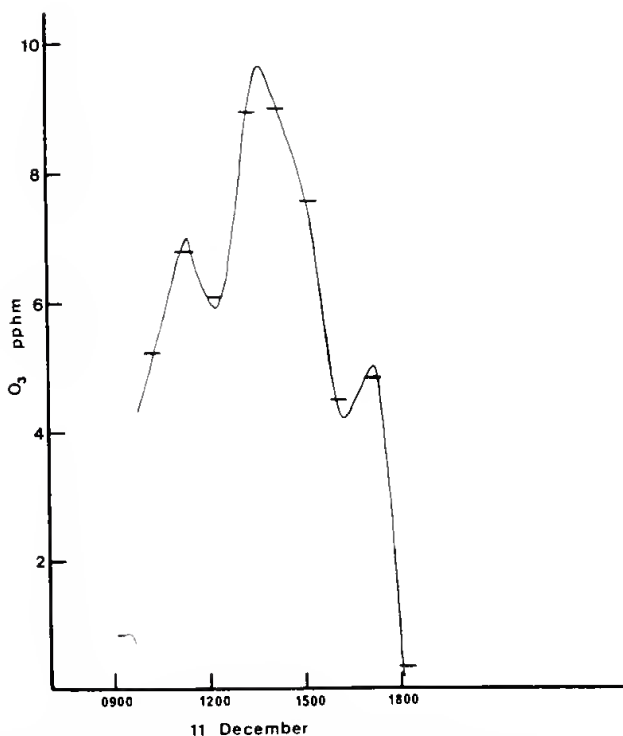


Figure 8.—Dependence of oxidant concentration on hour of day, 11 December 1972.

smog. This is the first unequivocal evidence for photochemical smog formation in Perth.

During 1973 a chemiluminescent detector, based on the reaction of ozone with ethylene was constructed. This detector follows most of the recommendations of the United States Environmental Protection Agency (Federal Register 1971), is specific to ozone and has a very fast response. Parallel measurements on a few days with the neutral potassium iodide method and with the chemiluminescent detector suggest that our earlier measurements may have underestimated the concentration of the photochemical oxidant by as much as 20%.

Studies were made of the variation with time of the ozone concentration (measured by chemiluminescence) outside the Chemistry Department. On 28th August, 1973, for example, the ozone concentration rose from 2.2 pphm at 9 a.m. to a maximum of 6 pphm at noon, remained relatively constant to 3 p.m. and decreased to 4 pphm at 5 p.m.

Occasional relatively high oxidant concentrations were measured on days on which bush fires were burning. However, insufficient measurements were made to test whether any positive correlation exists. It is possible that natural organic vapours may participate in the photochemical reaction leading to oxidant formation in which case the abnormal release of large amounts of these in bush fires could be important.

Topographic factors

Since the highest NO_x concentrations always seem associated with a shallow stagnant air layer which has accumulated pollution from vehicles and above which is clean air, the observed concentrations will depend very sharply on the precise location of the observing station. Accordingly, altitude changes of ten, twenty or fifty metres above ground levels or in buildings may be very significant especially when emissions occur over concave land surfaces. Tests should be instituted at such sites as: the Perth foreshore between the Narrows and the Causeway, Dog Swamp—a classical 'frost hollow' traversed by Charles Street, the vicinity of Cottesloe railway-station in a valley traversed by Stirling Highway (the fringe of this valley is the location of the Peppermint Grove Sampling site), and at Lake Monger, Perry Lakes, and Herdsman Lake. Sampling sites representative of the whole Metropolitan area may be difficult to select.

It was completely beyond our resources to undertake multisite routine measurements, but a preliminary investigation was mounted as follows.

About forty members of the University of Western Australia Clerical and Technical Staff Association co-operated in collecting simultaneous "grab samples" of air at different sites in the Metropolitan area. These grab samples were analysed subsequently. Because of the difficulty in converting nitric oxide to nitrogen dioxide these measurements are not completely quantitative and probably relate to the nitrogen diox-

ide component alone. However, they do provide a relative measurement and have shown that at any one time there is a wide variation in concentrations throughout the Metropolitan area. In general low values were found on the outskirts and highest values along a NW to SE corridor through the city. Some localities (e.g. Dog Swamp) consistently recorded high values and in general the ranking of sites in terms of NO_x concentrations did not vary much from day to day.

For instance, when twenty-four suburban sites were ranked accordingly to nitrogen oxides concentration at 8 a.m. on 27th April and also at 8 a.m. on 4th May, 1972 the rank correlation coefficient was 0.739 corresponding to a value of $t = 5.1$ and indicating a value for P of less than 0.1%. The correlation is apparently not as good when the concentrations of nitrogen oxides are lower. The correlation between twenty sites at 8 a.m. on 20th April and 27th April 1972 was described by a value of the rank correlation coefficient r of 0.424, a value of t of 2.0 suggesting a value of P of about 6%.

Strong correlation between sites often existed even when the measurements were made at different times of the day. For twenty-one suburban sites the rank correlation coefficient between measurements at 8 a.m. on 27th April and 9 p.m. on 17th April, 1972 was characterised by a value of $r = 0.477$, corresponding to $t = 2.4$ and $P = 4\%$.

The management of Strathern Apartments, Kings Park Avenue, kindly allowed 'grab samples' to be taken at ground floor, 14th floor and 23rd floor levels in an attempt to obtain information about vertical distribution of NO_x. No successful measurements were made even on days with well defined shallow stagnation layers. These inquiries should be prosecuted in future with fully automated equipment operating simultaneously at the three levels.

General Comment

To some extent 1972 was an exceptional year in terms of broad meteorological parameters, but 1973 was not an average year either. Whether the surprisingly high levels of NO_x measured on several days in 1972 were quite abnormal, perhaps the highest ever experienced, is a question which can only be answered by chemical measurements taken over the next

several decades. In the absence of extremely detailed meteorological information about the surface inversions which have occurred in the past history of Perth it would appear unwise to assume that 1972 was a wholly abnormal year with respect to chemical concentrations.

The special position of 1972 is perhaps sufficiently emphasised by the fact that ten air dispersion alerts were issued in 1972 by the Bureau of Meteorology, compared to two in the whole of 1973 and one only in the first nine months of 1974. Irrepective of future events, we contend that the analytical figures obtained in 1972 have merit in drawing attention to the special pollution features of shallow inversions and in providing a datum against which to measure any future year, typical or atypical.

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7.—The petrology and probable stratigraphic significance of Aboriginal artifacts from part of south-western Australia

by J. E. Glover¹

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Abstract

Aboriginal rock and mineral artifacts found in the southern Northampton Block, Perth Basin, Naturaliste Block, and areas around Albany and Esperance, consist of dolerite, actinolite-rich rock, granite, schist, quartz, quartzite, silcrete, siliceous and ferruginous shale and seven varieties of chert. The chert includes novaculite from the Proterozoic Coomberdale Chert, mottled chert probably from the Lower Triassic Kockatea Shale, two varieties of veined epidote-bearing chert from metamorphosed Precambrian strata, opaline and chalcedonic chert from the Middle-Late Eocene Plantagenet Group, similar chert from amygdales of the Neocomian Bunbury Basalt, and fossiliferous cryptocrystalline chert from an unidentified Middle-Late Eocene unit. Artifacts are particularly abundant in the Perth Basin.

The fossiliferous cryptocrystalline chert has been found in firmly dated contexts only at Devils Lair, in strata with radiocarbon dates of 19 000 to 12 000 B.P. It is widely distributed in a strip along the western coast and probably came mainly from the west when sea level was significantly lower than at present. Some flakes of fossiliferous cryptocrystalline chert in the southern part of the Perth Basin may have come from Plantagenet Group rocks. Most other artifacts in the basin were carried west from the Precambrian shield, but some in the north are of local origin. Fulgurite fragments are found in many artifact assemblages, but evidence of their utilization is lacking. Feldspar cleavage flakes are also rather common at some sites.

Introduction

The Perth Basin and adjacent shield areas in Western Australia contain numerous surface and near-surface accumulations of flaked stone artifacts (primary flakes and cores, utilized flakes and cores, and specific tool types). This paper describes their petrology, and that of the associated, less abundant ground stone material (axes and grinding stones). Shield areas near the Perth Basin covered in this report include the Naturaliste Block, the south-western part of the Northampton Block, and part of the Precambrian terrain along the southern coast, which is commonly covered by Plantagenet Group rocks. (See Johnstone *et al.* 1973 for a geological review of the region.) Many of the artifact sites listed in this paper were discovered by the author, or jointly by Mrs. S. J. Hallam and the author. Material from a few other sites was made available by Mrs Hallam, and by the Western Australian Museum.

The lithological composition of artifact assemblages at the sites was estimated by counting 100 or more flakes. The abundance of artifacts in the Perth Basin is notable, and as those revealed (mainly in sand blow-outs) must rep-

resent a practically insignificant proportion of the total, the volume of transported rock material is truly remarkable.

The rock types used include dolerite, actinolite-rich rocks (rare as artifacts), granite, schist, quartzite, silcrete, siliceous and ferruginous shale, and at least seven varieties of chert, including novaculite, mottled chert, two varieties of veined epidote-bearing chert, two varieties of opaline and chalcedonic chert, and fossiliferous cryptocrystalline chert.

Most of the artifacts described come from blown-out areas of sandy country and commercial sandpits, and their relative stratigraphic positions and times of accumulation have been established only in a broad way. According to Hallam (1972) sites assumed to be early on typological grounds are almost exclusively scraper assemblages and are very high in fossiliferous chert (the fossiliferous cryptocrystalline chert of this paper). Late assemblages contain many fabricators and are high in quartz. Intermediate sites have a high backed-blade component and are lithologically rather heterogeneous. Hallam also noted that near-coastal sites around Perth are rich in fossiliferous chert. This investigation shows that sites with abundant fossiliferous cryptocrystalline chert are concentrated within a belt in the central and northern Perth Basin that extends up to 40 kilometres inland. Flakes are commonly found where the coastal white or grey sand (the Quindalup Dune System of McArthur & Bettenay 1960) has been blown away to reveal underlying yellow or yellow-brown sand (Spearwood Dune System) commonly with emergent limestone pipes and pillars. Farther inland they are concentrated in blown-out areas of other sand formations. In commercial sandpits, artifacts are normally concentrated in the walls about 2 m below the original dune surface.

Patterns of lithologic distribution are fairly clear (Tables 1 and 2). Fossiliferous cryptocrystalline chert is found in almost all near-coastal assemblages between Gregory and Black Point some 700 km to the south. Between Gregory and Eneabba (about 220 km) the proportion of this chert in the assemblages is less than 10 per cent and commonly closer to 1 per cent. From the Eneabba area to Mandurah (300 km), referred to hereafter as the Eneabba-Mandurah belt, fossiliferous cryptocrystalline chert is invariably present and is abundant (above 10 per cent, locally above 75 per cent). South of Mandurah toward Black Point (about 200 km) the chert apparently composes part of most near-coastal flake assemblages, but the number of

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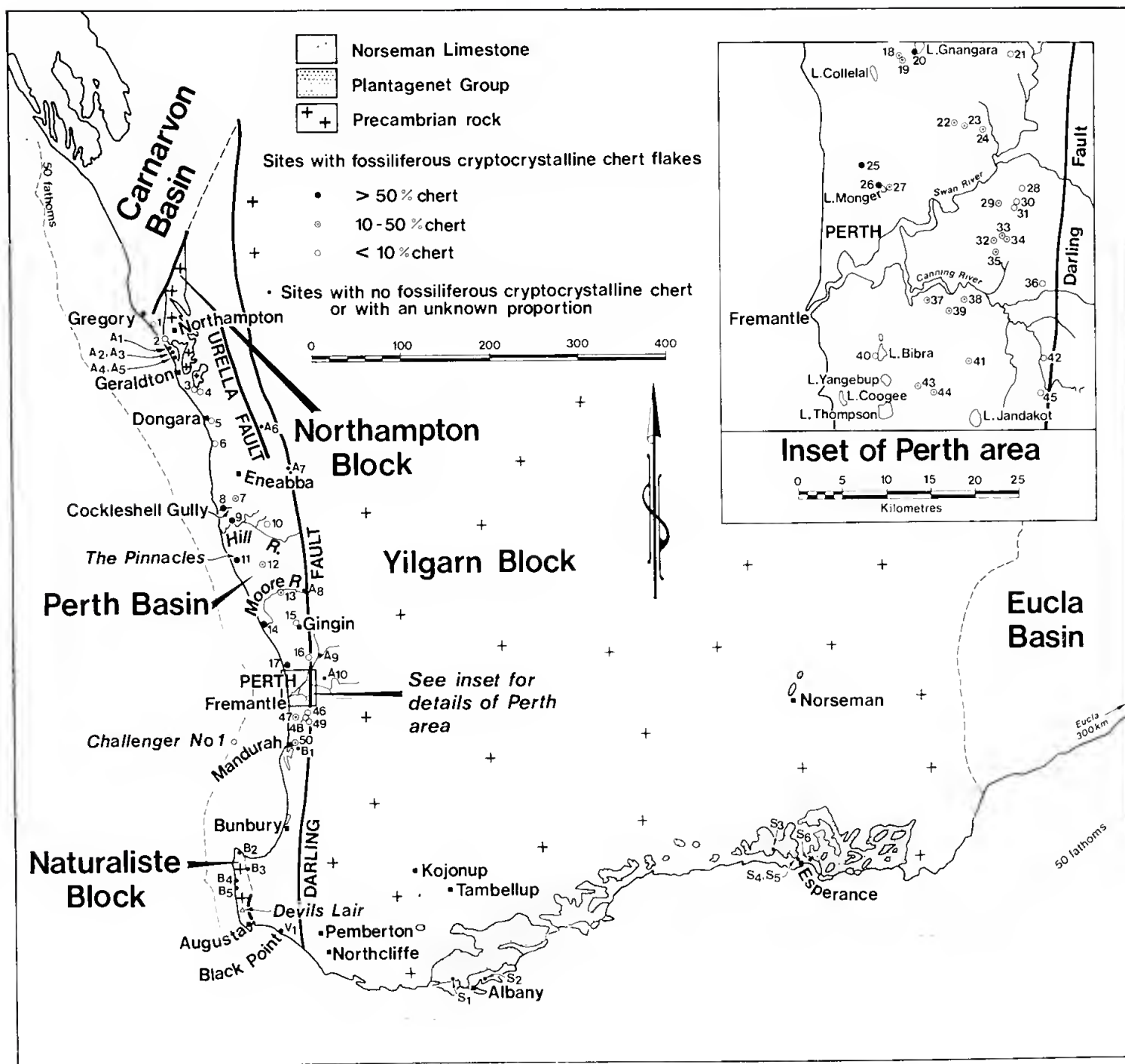


Figure 1.—Map of south-western Western Australia showing flake localities. See Tables 1 and 2 for details about localities. All scales in km.

flakes is normally small, and meaningful proportions cannot be given. Inland from the coast there is a general but uneven decline in fossiliferous cryptocrystalline chert: near the north-eastern margin of the Perth Basin it is absent, and near the central eastern margin it ranges from 0-5 per cent. There is insufficient information to generalize about the south-eastern margin. It should be noted that estimates are difficult at sites on the Precambrian shield, for quartzite flaked by Aborigines is hard to distinguish from chips formed by weathering of local rock.

Mottled chert, feldspar, and siliceous and ferruginous shale are restricted to the area north of Dongara, whereas opaline and chalcedonic chert is confined to sites near the south coast. Quartzite is the most widespread and abundant

material. Silcrete and veined epidote-bearing chert are also fairly widespread but are normally minor constituents. Novaculite is uncommon south of the Perth metropolitan area.

Man has been in Australia at least 32,000 years (Barbetti & Allen 1972) and perhaps far longer. In Western Australia excavations at Devils Lair, near Augusta, include artifact-bearing strata dating from about 12 000 to about 25 000 BP, and the bottom of the deposit has not been reached. Quartz artifacts are found in strata representing the whole time interval, but fossiliferous cryptocrystalline chert has so far not been found in strata older than about 19 000 years (Dortch & Merrilees 1973; Glover 1974a).

This paper is based on the examination of some 18 000 chips and flakes in handspecimen,

Table 1

Sites at which the proportion of fossiliferous chert is known.

Sites are located on 1 : 250,000 Series R 502 maps, and co-ordinates are based on grid references estimated to the nearest hundredth. Co-ordinates refer to centre points of large sites.

No.	Type of site	Map co-ordinates	Flakes counted	% fossiliferous chert
1	Sand blow-out, Ridley's Pool area	22744932	448	4
2	Sand blow-out, 3 km E Horrocks Beach	23444785	877	1
3	Sand blow-out, 2 km S Walkaway	27164108	376	1
4	Sandy patch, Wondado Springs	28404048	325	0
5	Sand blow-out 0.8 km E Pell Bridge	29453744	301	0.5
6	Sand blow-out E side L. Arromore	29843469	400	1
7	Road cutting in sand, Kooringa area	32002760	319	45
8	Sandy soil, N bank Cockleshell Gully	30372666	215	75
9	Sand blow-out, N bank Hill River	31492481	310	63
10	Sand spoil from dam about 1 km W. Dinner Hill	35772452	154	2.5
11	Sand blow-outs, Pinnacles area	31692063	2107	69
12	Sand near dam, Caro Station	34651927	249	41
13	Road cutting in sand, S bank Moore River, Regans Ford	36921652	133	17
14	Blow-outs in yellow sand near mouth of Moore River	34851205	886	86
15	Sand blow-out 2 km NNW Gingin Railway Station	38801260	406	3
16	Sandy area 6 km S Bullsbrook East	40370758	290	3
17	Blow-outs in yellow sand 1 km north Mullaloo Beach	37190695	127	87
18	Gnangara Sandpit	38370671	249	20
19	Brambles Sandpit	38410669	193	13
20	Sandy area, SW margin of Lake Gnangara	38550680	684	54
21	Bell Bros. Sandpit, Gnangara Road	39730675	309	5
22	Ready Mix Sandpit, Beechboro	39040592	307	23
23	Road cut in sand, Beechboro Road	39180588	228	29
24	Widgee Road Sandpit, Beechboro	39380584	291	16
25	Sand Patch, S side Talbot Way, Woodlands	37880540	373	71
26	Sand dune, NW of Lake Monger	38120517	344	58
27	Red sand, E shore of Lake Monger	38220512	642	44
28	Sandpit, Maida Vale	39880510	347	16
29	Exposed sand, airport runway extension	39600492	348	17
30	Rail cutting in sand near Wittenoom Road, Maida Vale	39820496	353	3.5
31	Sand blow-out near Bingham Street, Maida Vale	39800490	384	7.5
32	Exposed sand, Kewdale	39550449	669	32
33	Sandpit, Hardey Road, Cloverdale	39630455	717	23
34	Exposed sand, Newburn Road, Kewdale	39690452	413	19
35	Sand blow-out N side Dowd Street, Kewdale	39550434	318	21
36	Sandpit NE White Street, Orange Grove	40140397	306	6
37	Exposed dune, corner High Road and Leach Highway, Riverton	38700377	378	20
38	Exposed sand, Metcalf Road, Lynwood	39160377	181	14
39	Sand blow-out near Riley Road, Nicol Road, Lynwood	38980364	317	19
40	Snashall Bros. Sandpit, Bibra Lake area	38080308	394	17
41	Coopers Sandpit, Canning Vale	39220303	277	16
42	Hot Mix Sandpit, Gosnells	40110265	361	6
43	Ready Mix Sandpit, Forrest Road, Jandakot	38590273	299	29
44	Calzil Sandpit, Forrest Road, Jandakot	38780266	118	13
45	MWSS & DB Sandpit, Lillian Avenue, Armadale	40110266	359	0.25
46	Fremwells Sandpit, Hopkinson Road, Cardup	39710126	1589	4
47	Wellard Sandpit, Parmelia	38540114	174	18.5
48	Sand blow-outs, Lang's Farm, Mundijong	39820092	500	2
49	Sand blow-out, 0.5 km S railway bridge, Mundijong	40040058	374	7.5
50	Sandpit 4.5 km E Stake Hill Bridge, Mandurah	38049805	116	28.5

and microscopic study of 180 thin sections. The study was supplemented by several complete and partial chemical analyses, by X-ray determination of some silica minerals, and by examination of some silcretes with the scanning electron microscope.

Colour designations used in the lithologic descriptions are taken from the Rock-color Chart distributed by the Geological Society of America (Rock-color Chart Committee 1963), and are accompanied by a numerical code from the same source.

Lithologies

Dolerite

Dolerite was used for grinding stones and axe-heads, and is not common as flaked artifacts. The best dolerite for flaking is fine-grained and comes from small dykes or from the chilled

margins of large dykes on the Yilgarn Block. Waterworn boulders were a source of some dolerite.

Actinolite-rich rocks

Actinolitic rocks are rather rare as artifacts, and have so far only been found at Wondado Springs (site 4) and near Howatherra (Site A₂), where they compose less than 5 per cent of the flakes. The finer grained rocks are aphanitic, black (N 1) through greenish black (5G 2/1) to dusky yellow green (5GY 5/2) and are tough, with conchoidal fracture. They are made up mainly of interlocking actinolite grading to tremolite, with pyrite, magnetite, quartz, and other minerals. Coarser grained rocks tend to be greenish grey (5G6/1) with a less well developed conchoidal fracture, and are made up mainly of andesine and actinolite. They resemble uranitized dolerite.

Table 2

Sites at which the proportion of fossiliferous chert is not precisely known.

Some sites (A₁-A₁₀) may contain numerous fragments weathered from nearby rocks. Other sites (B₁-B₅, V₁) have yielded insufficient flakes, or have not been closely investigated. Museum sites have not been inspected by the author. Sites S₁-S₆ are near Plantagenet Group rocks and contain distinctive chert flakes. Map co-ordinates as for Table 1, except that sites B₂-B₅ are located on Sheet 1930 (Edition 1) Series R611.

Site No.	Type of site	Map co-ordinates	Fossiliferous cryptocrystalline chert*	Chert with colloform opal and/or abundant microcrystalline chalcedony*
A ₁	Sand blow-out 1.4 km W Oakabella Homestead	24824666	r	a
A ₂	Sand blow-out 1.5 km S Howatharra, 400 m S Royce Homestead	25234603	r	a
A ₃	Sand blow-out, Howatharra area, 3 km WSW Royce Homestead	25054596	r	a
A ₄	Small sand blow-outs in field, W side Highway No. 1, 0.8 km S Buller River	25214483	r	a
A ₅	Small sand blowouts, 0.5 km W locality A ₄	25144485	a	a
A ₆	Sandplain 2 km S Yandanooka near Government Windmill, Bundanoon	35413660	a	a
A ₇	Sand blowout about 3 km SW Winchester, 0.7 km NW Kileur Pool, near mill	39003096	r	a
A ₈	Sand blowout 4.5 km SSW Gillingarra, 0.5 km W highway	40331674	r	a
A ₉	Junction of Avon and Brockman Rivers	41210814	a	a
A ₁₀	S side Jane Brook, about 1.3 km E Stoneville	41870573	a	a
B ₁	Sandpit about 7 km N Pinjarra, North Dandalup Road	38739728	p	a
B ₂	Small sandpatch 0.4 km SSW Meelup Spring, S Dunsborough-Naturaliste Road	LH206816	p	a
B ₃	Sandpit E Bussel Highway at junction with Yelverton Road	LH296653	p	a
B ₄	Sand blowouts, Cowaramup Point	LH128509	r	a
B ₅	Small sand blowouts, S side Margaret River Road 1 km NE Wildcliffe House	LH157395	p	a
S ₁	Sand, N side Albany-Denmark Road 3 km W Torbay	56146730	a	p
S ₂	Road cutting in sand, Nannarup Road 3 km NNW Nannarup	60386803	a	p
S ₃	Sand on laterite, between Dalyup tennis courts and Dalyup River N side Esperance Albany Highway	46028345	a	p
S ₄	Railway cutting in sand, 0.5 km N Shark Lake Siding	48778275	a	p
S ₅	Sand blowout in dune, 0.25 km N Shark Lake Siding	48748274	a	p
S ₆	Sand blowout, S side Esperance Road 3.5 km W Mt. Edward	50128247	a	p
B1038	Yeagerup Dune, 16 km S Pemberton		p	a
B271	Cleared paddock, Half Moon Farm, 8.4 km SW Kojonup		Mainly silcrete, no chert	
B1763	Sand dune, E shore large lake, E side main road, 4 km SSE Lake Banks Hst. near Tambellup		p	a
V ₁	Sand blowout about 1 km E Black Point	35417488	Chert from volcanic amygdalites present	

* a = absent, r = rare, p = present

Granite and Schist

Fragments of granite and schist are found in some Perth Basin sites, and the rocks would have been carried westerly from the Yilgarn Block. Most of the material examined, because of its coarse grain size and poor coherence, was probably unsuitable for flaking, and was used mainly for grinders.

Quartz

Quartz (rock crystal) was used where available, and large clear crystals were not spared. Many chips resemble flaked window or bottle glass, from which they can be distinguished by their anisotropism and lack of bubbles. Rock crystal, though not abundant, is widespread near shear zones on the Yilgarn Block and no specific sites of origin have been determined.

Quartzite

The term quartzite is used for all polycrystalline quartz rocks because it is difficult to distinguish fragments derived from such diverse parents as large quartz-rich pods (the quartz blows of prospectors), metaquartzites, and highly silicified orthoquartzites such as those found interbedded with chert in the Proterozoic

Moora Group. It is not always easy, in fact, to distinguish quartzite and Coomberdale Chert without microscopic examination. Quartzite was widely utilized for grinding implements and flakes in south-western Australia, and is the main constituent at many sites in the Perth Basin. Source rock is abundant on the Yilgarn Block and on other Precambrian terrains, and the artifacts generally give no precise indication of their place of origin. Some have been broken from waterworn boulders, which would have saved the work of quarrying. In the northern part of the Perth Basin rounded pebbles and boulders from the Tumblagooda Sandstone and Mesozoic units seem to have served locally as sources.

Feldspar

A significant proportion (1-28 per cent) of flakes at some sites north of Dongara (sites 2, and A₁-A₅ inclusive) is made up of cleaved perthite. The flakes are commonly about 3 cm x 2 cm x 1 cm, but they vary in size between wide limits. The overall colour of many flakes is pale yellowish orange (10 YR 8/6) to greyish orange (10 YR 7/4) with the host micro-

cline coloured in shades of brown, pink and grey, and the abundant plagioclase veins in shades of yellow.

Feldspar has two perfect cleavages (001) and (010), and reflection from these smooth surfaces causes the flakes to glisten in the sun. The cleavages meet at an angle of 86° to form straight edges which would be useless for cutting. It is not known if the feldspar was used by the Aborigines.

Fulgurites

Fragments of lechatelierite (silica glass) from sand fulgurites have been found at ten artifact sites in the Perth Basin, and have been described in detail elsewhere (Glover 1974b, 1975). Sand fulgurites are narrow tubular bodies up to two or three metres long that resemble plant roots in external shape and orientation, and they form from the fusion of sand by lightning. The tubes commonly break into fragments of a few square centimetres in area, and remain as lag in dune blow-outs. Fulgurites that formed in sand blown over former artifact sites can thus be concentrated with the artifacts during subsequent deflation. Some older fulgurite fragments may have been carried to the site by Aborigines, but evidence of handling would be almost impossible to establish.

In handspecimen, non-tubular fulgurite fragments can be recognized by a smooth, translucent somewhat mammilated appearance on one surface, and a rough opaque aspect, with numerous embedded sand grains, on the other. Microscopically the glass is vesicular with a refractive index close to 1.461.

Silcrete

Silcrete fragments can be recognized in hand-specimen because they contain quartz grains, commonly in shades of light grey, in a uniform, porcellaneous cement that generally ranges between very pale orange (10 YR 8/2) and pale yellowish orange (10 YR 3/6). The rock has pronounced conchoidal fracture.

In thin section most of the silcrete fragments consist essentially of quartz grains in colourless or pale brown cement. A silcrete from the Northampton area (see Fig. 2B) has a more complex clastic assemblage and contains quartz (some grains with well-defined outgrowths), glauconite, microcline, leucoxene, tourmaline, and siliceous grains of unknown origin. The cement seems to be isotropic under the polarizing microscope, but X-ray powder photographs of a typical specimen (Uni. No. 74,628) from site 32 show quartz lines. The refractive index is close to 1.549 ± 0.002 , and the specific gravity is indistinguishable from quartz in heavy liquids. Scanning electron microscopy shows that the average grain size is about $1 \mu\text{m}$. It seems therefore that the mineral is quartz whose unusual optics are caused by its finely divided state.

Silcrete apparently forms in at least two ways (see Hutton *et al.* 1972) and can form from different kinds of rock. Silcretes from different sources are therefore likely to differ texturally and even mineralogically, in rather distinctive ways. Silcrete artifacts in the Perth metropolitan area, and at Gingin, resemble outcropping silcrete from the Kojonup area very strongly.

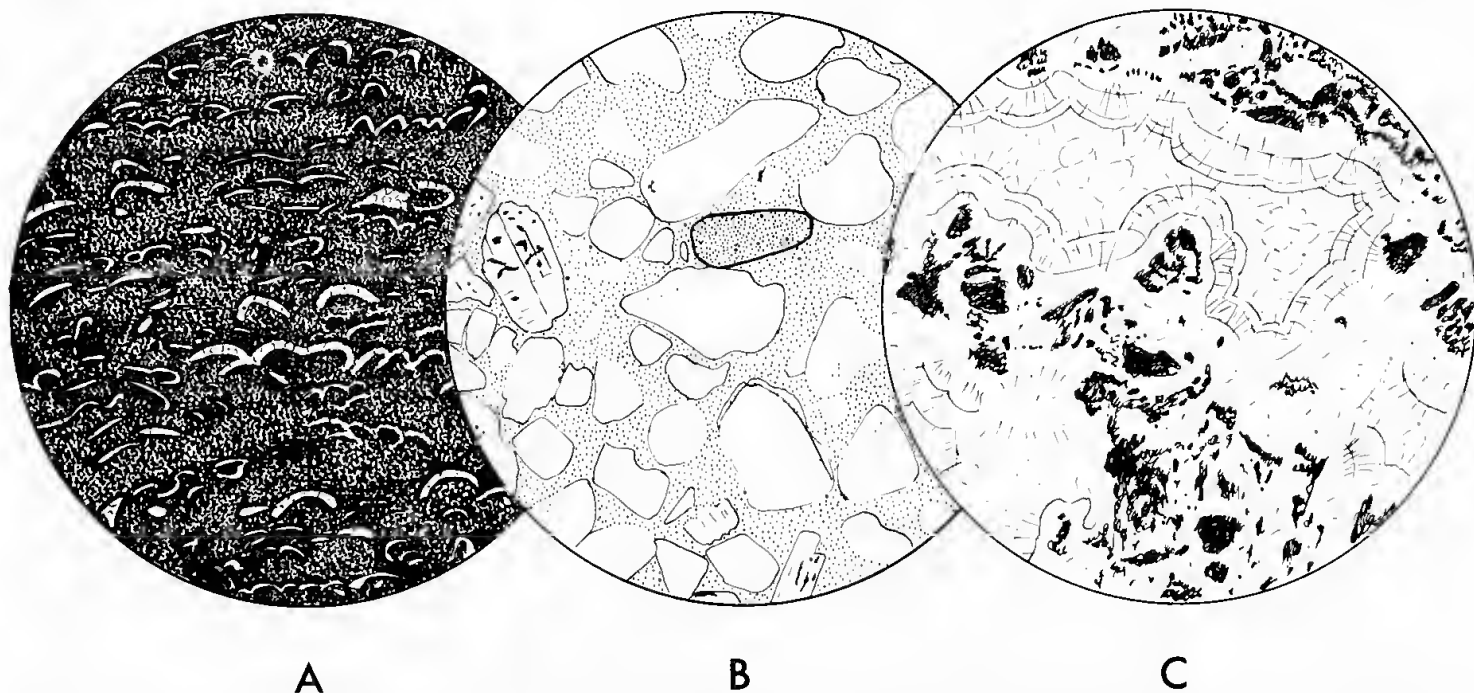


Figure 2.—Thin sections of flakes. A.—Siliceous ferruginous shale (Uni. No. 74451/1) from site 2, Horrocks Beach area. The curved siliceous bodies of microcrystalline quartz may be algal. Cement consists of hematite and goethite. Flake probably derived from Kockatea Shale. Diameter of field 1.3 mm. B.—Silcrete (Uni. No. 74501) from site A₃, Howatharra area. Colourless grains without cleavage are quartz, colourless grains with cleavage are microcline. Dark grain with high relief is tourmaline. Cement is very finely divided quartz. Diameter of field 1.3 mm. C.—Mottled ferruginous chert (Uni. No. 74481) from site A₅, Buller River area. Dark areas contain mixture of hematite, limonite and cryptocrystalline silica. Colourless areas contain radiating chalcedony with cores of microcrystalline quartz. Probably derived from Kockatea Shale. Diameter of field 1.3 mm.

Siliceous ferruginous shale

The siliceous ferruginous shale flakes are tough, laminated, have conchoidal fracture and range in colour from greyish red (5R 4/2) to moderate brown (5 YR 4/4 to 5 YR 3/4). Microscopic examination reveals that up to 15% of some flakes is made up of bodies with strongly curved to fairly straight walls from 0.01 to 0.05 mm thick, composed of microcrystalline quartz, in a cement of hematite and goethite (see Fig. 2A). This rock is found at sites 2 and A₂ and is apparently restricted to the northern part of the Perth Basin. It is the same as that illustrated by Karajas (1969, fig. 24, unpubl. data) from the so-called algal unit of the Triassic Kockatea Shale.

Chert

Classification

According to the hypotheses of primary origin, chert is deposited as silica gel, or forms by partial redistribution, *in situ*, of silica precipitated by organisms such as diatoms and radiolarians. Secondary origin can be demonstrated for many cherts by their field relationships or palimpsest microstructures, and generally involves replacement of calcareous rocks.

Though there is a considerable literature, advances in chert petrology have been slow (see Dapples 1967) and classification and nomenclature have not kept pace with other sedimentary rock groups, notably the carbonates. A descriptive nomenclature partly based on that of Williams, Turner and Gilbert (1954) is adopted to distinguish between the varieties of chert artifact described here. The common term *flint* used by some as a synonym for chert, and by Williams *et al.* and others for a tough grey or black variety of chert with conchoidal fracture, is unsatisfactorily defined, and is not used. The term *chert* is taken to include compact siliceous rocks composed of opal, chalcedony and cryptocrystalline or microcrystalline quartz, or a mixture of these constituents. Chert can be any colour, and can originate in several ways.

Chert composed mainly of microcrystalline quartz is called novaculite in this paper, a term used in parts of the United States and already applied to the Coomberdale Chert by Logan and Chase (1961). Apart from novaculite the descriptive terms opaline and chalcedonic chert, mottled ferruginous chert, veined epidote-bearing chert, and fossiliferous cryptocrystalline chert, have been used for distinctive local varieties. There is unfortunately disagreement about the size limits indicated by the commonly used terms "cryptocrystalline" and "microcrystalline" (see Bissell and Chilingar 1967, Table IV). This paper follows Pettijohn (1957, Table 18) in taking the boundary between the two at 0.01 mm, as it then forms a suitable dividing line between two distinctive varieties of chert found in Western Australia. Crystal size in cryptocrystalline chert is taken to be less than 0.01 mm, whereas microcrystalline grains are defined as being greater than 0.01 mm, but too fine for observation with the naked eye.

Novaculite

Novaculite artifacts are commonly translucent in thin chips, and range through shades of light to dark grey, greyish yellow, pink, and red. They are hard, dense and non-porous. Most are banded, but some are intraformational breccias. Artifacts without such structures are difficult to distinguish from quartzite without microscopy.

Twelve novaculite artifacts were sectioned and consist essentially of microcrystalline quartz, locally cut by quartz veins up to 0.5 mm thick. The interlocking quartz crystals range in diameter mainly between 0.05-0.25 mm, and two of the flakes (Nos. 74527/3, 74536/2) show palimpsests of dolomite rhombs clearly outlined by iron oxide (see Fig. 2B).

The novaculites show macroscopic and microscopic features characteristic of the Coomberdale Chert from which they were certainly derived. Novaculite artifacts are far less frequent than artifacts of fossiliferous cryptocrystalline chert at central Perth Basin sites, despite the abundance of strongly outcropping novaculite along many parts of the eastern margin of the basin. Presumably the almost perfect conchoidal fracture of the fossiliferous cryptocrystalline chert made it the more useful of the two.

Opaline and chalcedonic chert

The opaline and chalcedonic chert artifacts superficially resemble the fossiliferous cryptocrystalline chert artifacts described below, but they have a less developed conchoidal fracture and may be particoloured or mottled. The chalcedony commonly ranges from shades of light and medium grey (N8—N5) to pale yellowish brown (10 YR 6/2) and the opal ranges from white (N9) through very pale orange (10 YR 8/2) to more brownish colours where strongly stained. The minerals can be easily distinguished in some artifacts because the chalcedony is translucent whereas the opal is not.

Under the microscope (Fig. 3C) the chalcedony is generally microcrystalline, clear, and colourless whereas the opal, which has pronounced negative relief, is somewhat cracked and ranges through pale and very pale shades of brown and orange. The opal is colloform in places and commonly includes bodies of radiating-fibrous chalcedony, with quartz cores showing undulose extinction. Some of the opal is completely isotropic, but most of it has very low birefringence and fibrous structure under crossed polarisers. X-ray powder photographs of slightly birefringent opal from Esperance show several broadened α -cristobalite lines characteristic of "common" opal, i.e. the opal-CT of Jones & Segnit (1971), which is the same as Mallard's lussatite (Mallard 1890).

Palimpsests of shell fragments, and unsilicified glauconite pellets are found in some opal but are less common in the chalcedony.

Flakes of opaline and chalcedonic chert are abundant at sites in the Denmark, Albany and Esperance areas, and are mineralogically and texturally identical with nearby siliceous Plantagenet rocks. There is no doubt about the local derivation of these artifacts.

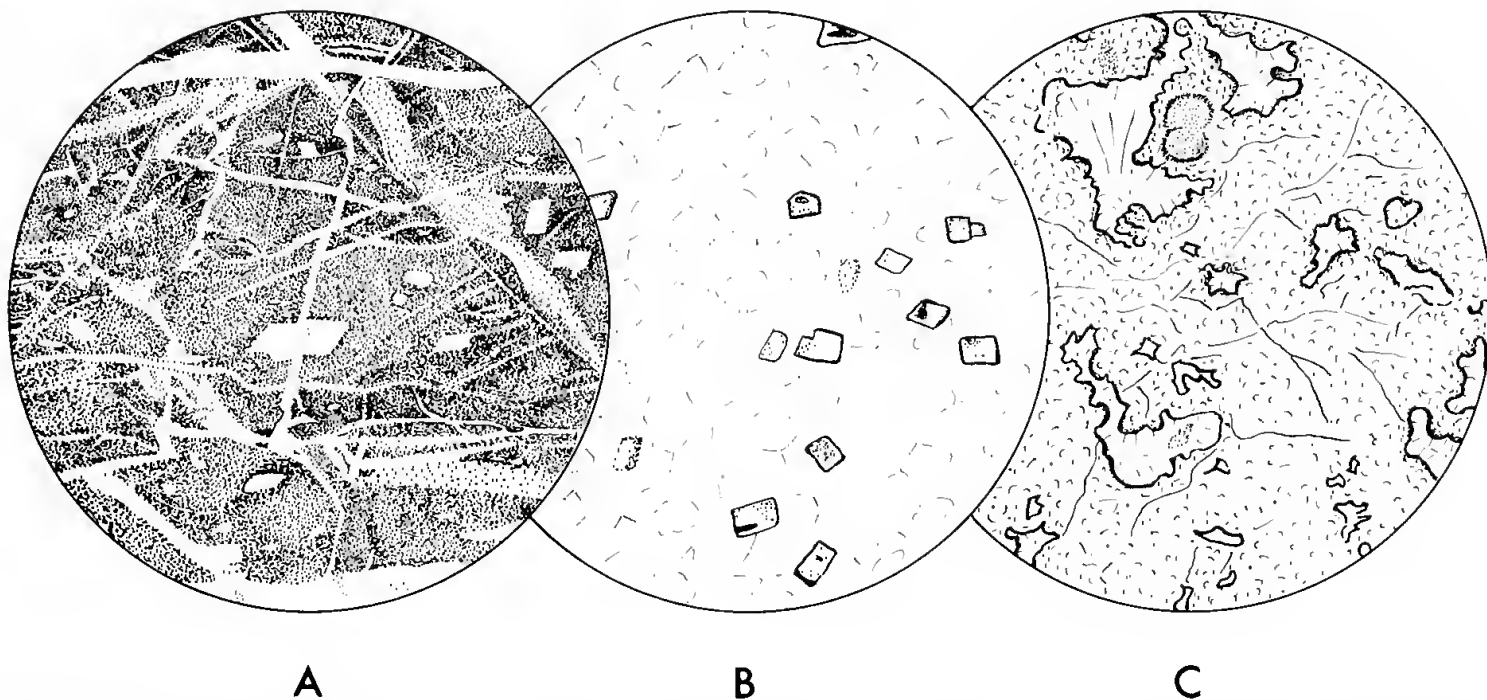


Figure 3.—Thin sections of flakes. A.—Veined epidote-bearing chert (Uni. No. 74671) from site 15, Gingin area. Veins of microcrystalline quartz cut cloudy groundmass of microcrystalline and cryptocrystalline epidote and silica. The large colourless grains consist of aggregates of interlocking microcrystalline quartz. The rock resembles in texture a meta-volcanic rock or a metamorphosed tuff, and is probably derived from Precambrian terrain. Diameter of field 3.5 mm. B.—Novaculite (Uni. No. 74536/3) from site A₇, Winchester area. Note the siliceous, rhomb-shaped palimpsests of dolomite, outlines by iron oxide, in cement of microcrystalline quartz. Probably derived from Coomberdale Chert. Diameter of field 0.26 mm. C.—Opaline and chalcedonic chert (Uni. No. 74674) from site S₄, Esperance area. The opal (stippled, with cracks) contains bodies of radiating-fibrous chalcedony. An indistinct organic remnant can be seen in the opal toward the top of the field. Derived from Plantagenet Group. Diameter of field 1.3 mm.

Farther west, in the Black Point area, siliceous amygdalae weathered out of the Neocomian Bunbury Basalt are found in artifact assemblages. The mineralogy of the amygdalae is complex and variable, but many contain only colloform common opal (opal-CT), chalcedony and quartz, and chips from these amygdalae are practically indistinguishable from palaeontologically barren chips of the Plantagenet chert. Flakes containing zeolites, celadonite or barite can be confidently ascribed volcanic origin.

Mottled ferruginous chert

Mottled ferruginous chert flakes range in colour from shades of yellowish brown to purple and are mottled with spots or patches in shades of orange and grey. Microscopic examination (Fig. 2C) shows that the mottling is caused by irregularly shaped masses of intimately associated limonite, hematite and cryptocrystalline silica separated by fringes of radiating chalcedony from aggregates and microcrystalline quartz.

Flakes of the rock are fairly numerous at site A₁ (10%) but are not normally common and seem to be confined to the northern part of the Perth Basin. Their origin is uncertain, but they may be derived from silicified portions of the Triassic Kockatea Shale.

Veined epidote-bearing chert

Veined epidote-bearing chert flakes are brown, grey and yellow, with an olive or green cast from disseminated epidote, and are cut by narrow (generally <0.5 mm) quartz veins.

Two varieties have been distinguished microscopically. One variety contains large, composite grains (up to 0.7 mm in diameter) consisting of interlocking microcrystalline quartz, and rarer large epidote grains in a cloudy groundmass of cryptocrystalline to microcrystalline silica and epidote. Some of the large composite quartz grains have remarkably straight edges, and resemble silicified phenocrysts in a metamorphosed volcanic rock or crystal fragments in a metamorphosed tuff. The rocks are microfaulted and are cut by narrow veins of microcrystalline quartz (see Fig. 3A). The second variety consists of poorly sorted, angular, strained quartz grains, microcrystalline quartz aggregates, and microcline and epidote grains in a cryptocrystalline to microcrystalline matrix of silica and epidote. These rocks are also veined and microfaulted, and resemble metamorphosed greywackes (see Fig 4A). The origin of both rock types, however, is still rather speculative¹.

Veined epidote-bearing artifacts are widely distributed throughout the Perth Basin and on its margins, but constitute only a very small proportion of material at sites examined. The parent rock almost certainly comes from shield areas.

Fossiliferous cryptocrystalline chert

Petrology: The surface colour of the fossiliferous cryptocrystalline chert flakes is generally

¹ These textures may be misleading. The flakes also resemble mylonitized Precambrian rock examined after this paper went to press.

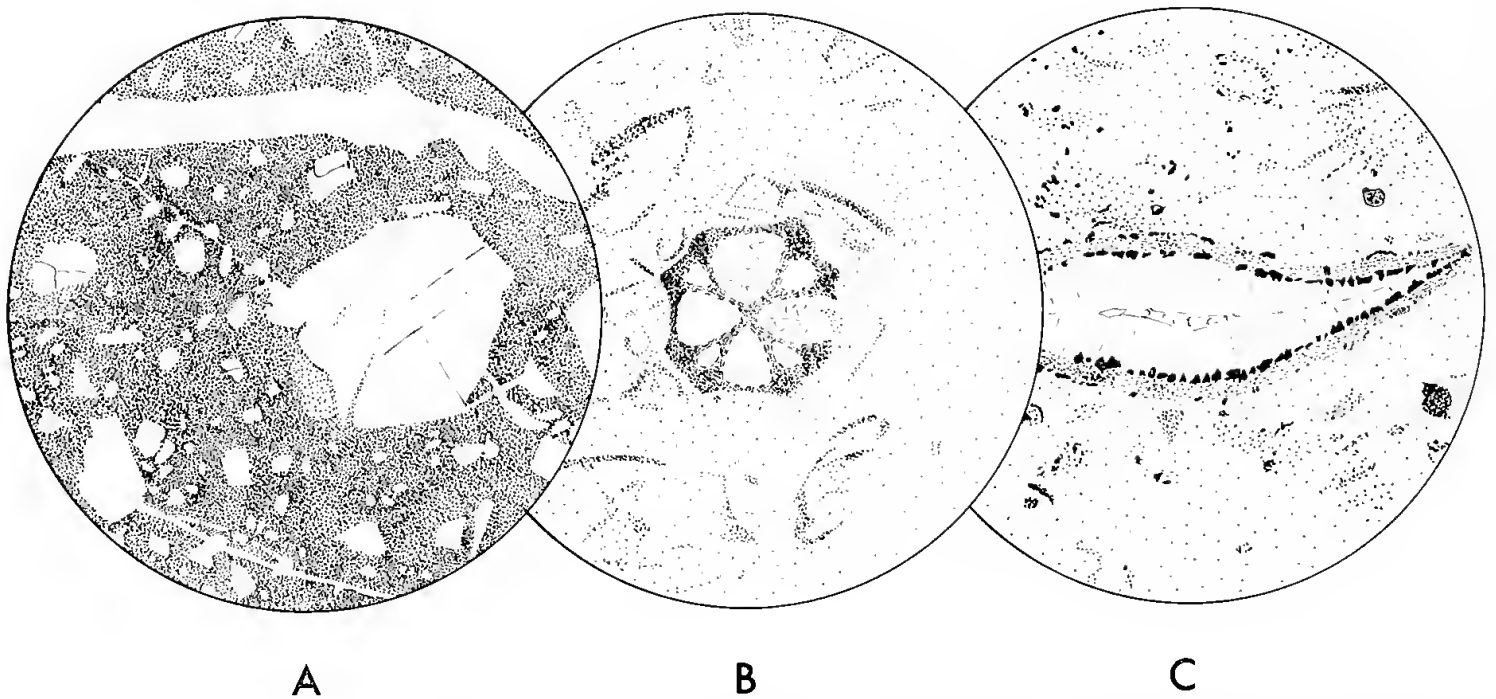


Figure 4.—Thin sections of flakes. A.—Veined epidote-bearing chert (Uni. No. 74699) from site 49, near Mundijong. Veins of microcrystalline quartz cut a cloudy matrix of microcrystalline and cryptocrystalline epidote and silica. Large grain with cleavage is microcline, other grains consist of strained quartz, or aggregates of quartz. The rock is probably derived from Precambrian terrain, and resembles meta-greywacke. Diameter of field 1.3 mm. B.—Fossiliferous cryptocrystalline chert (Uni No. 74606/1) from site 11, the Pinnacles area. Palimpsests of bryozoan and other fossils in matrix of cryptocrystalline silica. Probably silicified Eocene limestone from off-shore source. Diameter of field 1.3 mm. C.—Fossiliferous cryptocrystalline chert (Uni. No. 74606/2) from site 11, the Pinnacles area. Palimpsest of small oivalve in cryptocrystalline silica. Note drusy, opaline fringe. Probably silicified Eocene limestone from off-shore source. Diameter of field 1.3 mm.

close to the colour of the surrounding sand, and ranges mainly from white through pale shades of grey, yellow, brown and orange. Common surface colours are white (N9), pinkish grey (5 YR 8/1), greyish yellow (5 Y 8/4), pale yellowish brown (10 YR 6/2), light brown (5YR 5/6), very pale orange (10 YR 8/2) and greyish orange (10 YR 7/4). Sections through some flakes show that the outer colour is a patina that gives way to white or pinkish grey (5 YR 8/1) for up to two or three mm, and passes into a core of pale yellowish brown (10 YR 6/2) or a similar colour. Other flakes, however, particularly those taken from white sand, are white or nearly so throughout.

Thin-section examination reveals partly to completely silicified Bryozoa, Foraminifera, sponge remains, small bivalves and echinoderm fragments together with a few unsilicified glauconite pellets in an essentially cryptocrystalline matrix (Figs. 4B, 4C). A little quartz sand and silt is present in some of the chips. The epithet cryptocrystalline is justified because over 50% of the rock is composed of grains less than 0.01 mm in diameter, but it is not uncommon for about 30% of the matrix to consist of chalcedony grains between 0.01 and 0.04 mm in diameter, with somewhat coarser chalcedony filling fossil tests.

Many fossils are partly replaced by very finely divided opal, or have a drusy opaline fringe about 0.005 mm thick. In places the fringe is directed outward from the shell surface. The small size and high negative relief of the opaline bodies make them practically opaque under magnifications of less than X100, and where

finely divided opal is abundant it resembles cloudy argillaceous material. A few larger opaline bodies attain a length of 0.02 mm, and have pitted surfaces as though etched. A well-developed opaline drusy fringe is shown in Figure 4C.

Table 3.

Analysis of core and rim of a flake from the Pinnacles area.

*(from University specimen No. 74606)**

	Core	Rim
SiO ₂	97.9	98.2
TiO ₂	0.01	0.01
Al ₂ O ₃	0.13	0.19
Fe ₂ O ₃	0.17	0.17
MnO	<0.01	<0.01
MgO	0.03	0.05
CaO	0.11	0.09
K ₂ O	0.04	0.04
Na ₂ O	0.01	0.01
P ₂ O ₅	0.20	0.13
Loss on ignition	1.6	1.2
	100.2	100.1

* Analyst Supervise-Sheen Laboratories Pty. Ltd. XRF except P₂O₅ by colorimetry, SiO₂ by difference.

Most of the chert is evidently silicified fossiliferous limestone, and the texture suggests that it was originally biomicrite, according to the classification of Folk (1962). Remnants of cores commonly retain an uneven, roughly curved surface from which silicified Bryozoa project up to a millimetre or more. It appears from the general curvature and from the size of the larger cores, that the flakes were generally struck from chert nodules about the size of a man's fist. A few artifacts contain abundant spicules, indicating a spongolite precursor. A typical flake from the Pinnacles was analysed (Table 3) and shows almost complete silicification. The pale yellowish brown (10 YR 6/2) core and the white (N9) rim with its surface patina of very pale yellowish orange (10 YR 8/4) are not significantly different in composition.

The fossiliferous cryptocrystalline chert breaks fairly easily with smooth conchoidal fracture into sharp-edged flakes, which doubtless accounts for its widespread use. However, some chert fragments from sites of white sand have slightly rough surfaces, rather soft blunt edges, and are porous or even friable, apparently because of the removal of calcium carbonate, which can form up to 25% of incompletely silicified artifacts. Many flakes in white sand have probably disintegrated completely in this way.

An Eocene age is shown for the chert by the Bryozoa, and is confirmed by the presence in two chips of the Middle-Late Eocene foraminifer *Maslinella chapmani* Glaessner and Wade (Glover & Cockbain 1971).

Distribution and Source: Fossiliferous cryptocrystalline chert artifacts are found throughout the Perth Basin, and on the Northampton Block to the north and the Naturaliste Block to the south-west, a north-south distance of about 700 km. They are also found on the southern part of the Precambrian shield at a site near Tambellup. It has already been pointed out that the sites with the highest proportion of these chert artifacts are invariably near the western coast. Chert artifacts are known from sites frequented up to the ethnographic present (e.g. Lake Monger, see Fig. 1) and from strata about 12 000 to about 19 000 years old (Devils Lair, see Dortch & Merrilees 1973).

The "Middle-Late" Eocene dating of the fossiliferous cryptocrystalline chert is clearly crucial for no rocks of that age are known to outcrop in the Perth Basin (see for example Quilty 1974 *a, b*). There are several known units of requisite age elsewhere, namely Giralia Calcarenite, Merlinleigh Sandstone and Pindilya Formation in the Carnarvon Basin, Norseman Limestone on the southern Yilgarn Block, Plantagenet Group in the Albany-Esperance area, and Toolinna Limestone and Wilson Bluff Limestone in the Eucla Basin (see the correlation chart of Playford & Cope 1971).

The concentration of chert-rich sites near the western coast should be considered in the light of eustatic variation in sea level, as was well appre-

ciated by Hallam (1974, p. 80). Recent data indicate that when the oldest known Western Australian chert flakes were being manufactured (about 19 000 years BP), world sea levels were 85-90 m (i.e. about 50 fathoms) lower than now (Mörner 1971). These data may be conservative, if applied to Western Australia coasts, according to new interpretations of global isostasy (see Chappell 1974). They imply that 19 000 years ago the coast would have been about 40 km west of Perth and about 90 km west of Geraldton and Bunbury, and the Perth Basin would have had roughly twice its present exposed area. Many artifact sites were probably covered by advancing seas during deglaciation, and there are probably numerous chert-rich sites off-shore. It is reasonable to hypothesize a westerly off-shore source for the chert artifacts in silicified Late Eocene limestone. North-trending wedges of such limestone could well overlie the Late Palaeocene-Early Eocene Kings Park Formation, having survived later bevelling. Rock in these wedges could be exposed locally on the sea-floor, perhaps as windows through Pleistocene limestone. Reasons for these suppositions are set out in the three numbered paragraphs below.

(1) The ratio of chert to other rock types at artifact sites tends to increase markedly from east to west.

(2) It is unlikely that the remarkably large volume of chert at sites in the Eneabba-Mandurah belt would have been carried up to 500 or 600 km from the Carnarvon Basin or Albany-Esperance area. It is more likely to have come from western sources distant a few kilometres, or some tens of kilometres at most.

(3) Late Eocene rocks have been found in WAPET's Challenger No. 1 offshore well, about 60 kilometres west of Mandurah, between depths of 510 m and 590 m. These are the only known Late Eocene rocks in the Perth Basin, and have not been recorded from other off-shore wells. No wells have tested the rocks within 20 kilometres of the western coast opposite the Eneabba-Mandurah belt, where Late Eocene rocks, up-dip from the intersection in Challenger No. 1, could crop out on the sea floor.

Possible landward sources for the fossiliferous cryptocrystalline chert artifacts will now be considered. Of the Carnarvon Basin formations, Merlinleigh Sandstone and Pindilya Formation are lithologically unsuitable. The Giralia Calcarenite is fossiliferous, glauconitic and locally silicified but contains large Foraminifera absent from the fossiliferous chert artifacts. The low concentration of chert flakes at near-coastal sites north of Eneabba, and the increased abundance of chert to the south, farther from the Carnarvon Basin, seem at first sight to support the idea that the Giralia Calcarenite was not the source of the chert. It is not unlikely, however, that some intermediate sites rich in chert are hidden off shore. The soundest reasons for doubting that the Giralia Calcarenite is the source of the abundant chert in the central Perth Basin are the absence of large Foraminifera

fera in chert specimens examined, and the physical difficulty of transporting large volumes of chert over distances of up to 600 km¹.

The nearest possible sources of fossiliferous cryptocrystalline chert known in southern Western Australia are at least 500 km from the chert-rich artifact sites of the Eneabba-Mandurah belt. Units that should be considered are the Plantagenet Group and Norseman Limestone which patchily cover Precambrian basement rocks, the Toolinna Limestone farther east, and the Wilson Bluff Limestone exposed at Wilson Bluff near Eucla and in caves nearby. Chert artifacts from Wilson Bluff have been recorded near Eucla, and their use apparently continued into the ethnographic present. Geologically similar material has been quarried at Koonalda Cave, one hundred kilometres east of Eucla, which is shown to have been in use between 20 000 and 13 000 years ago (Polach *et al.* 1968). Chert from the Wilson Bluff Limestone closely resembles chert used for artifacts in the Eneabba-Mandurah belt, but is quite unlikely to have been carried 1 200 km to the area.

Chert flakes at sites around Esperance, Albany and Denmark are mainly composed of colloform opal and microcrystalline chalcedony, or of chalcedony alone, and are derived from local Plantagenet outcrops. No chert with colloform opal has been found in the Eneabba-Mandurah belt. Some Plantagenet chert from outcrop in the Northcliffe area kindly given to the writer by Mr. C. E. Dortch of the Western Australian Museum is composed of microcrystalline chalcedony. This resembles the Eneabba-Mandurah material more closely, but is generally coarser grained, and contains fewer microfossils.

Two cryptocrystalline chert flakes from the Tambellup area borrowed from the Museum (Museum No. B1763) have blurred textures under the microscope, but are fossiliferous and look rather like the Eneabba-Mandurah material. Two flakes from the Pemberton area (Museum No. B1038) are largely cryptocrystalline, but their unusual palimpsest texture, possibly derived from pelletal limestone, has not been precisely matched in the Eneabba-Mandurah material. The flakes from these two sites are of uncertain origin, but their most likely provenance is within a nearby area of Plantagenet rocks that are non-opaline and cryptocrystalline. It therefore seems that some Plantagenet rocks not yet examined resemble the Perth Basin flakes in lithology: if so, they could account for some of the chert flakes in the south of the basin. It is uncertain how far north such chert may have been carried, but material from the Plantagenet Group can hardly account for the distribution or volume of chert in the central part of the basin. It should be added that silicified Norseman rocks seem commonly to be

fairly opaline, and therefore appear unsuitable as a source. Silicified Toolinna Limestone, farther east, has not been examined.

The source of the chert in the Perth Basin therefore remains rather enigmatic, but on balance the abundance and distribution of artifacts in the Eneabba-Mandurah belt favours the hypothesis of offshore origin for them. It also accords with Hallam's suggestion based on typology, that chert-rich sites in the Perth area were the earliest (Hallam 1972). After submergence of their source rocks the Aborigines would have been forced to use material mainly from the east, though some chert from old sites would have been re-used. The present position of sea level was probably attained by about 6 000 BP (Thom & Chappell 1975), and fresh chert would therefore have been unavailable by that time.

Conclusions

The full ethnographic significance of the artifacts will have to await further typological, stratigraphic and petrologic studies. The search for Middle-Late Eocene rocks in future off-shore wells or in dredged material is especially important. At present, the data demonstrate local derivation of material near the Northampton Block and in the Albany-Esperance area, and east-west transportation of Precambrian rocks throughout most of the Perth Basin. Superimposed on this model is a probable pattern of west-east transportation in the Eneabba-Mandurah area, of fossiliferous cryptocrystalline chert from sites now submerged. In the southern part of the Perth Basin there may be chert from both the west and Plantagenet rocks in the east. The conclusions are set out individually below.

(1) The flakes of mottled chert, and siliceous and ferruginous shale at northern sites were locally derived.

(2) The fossiliferous opaline and chalcedonic chert on the south coast was derived locally from the Plantagenet Group. Some of the non-fossiliferous material came from amygdales in the nearby Bunbury Basalt.

(3) The quartz, quartzite, dolerite, granite, schist, novaculite and veined epidote-bearing chert in the central Perth Basin came from east of the Darling Scarp. Each rock probably came from a number of localities. River boulders were a significant source of quartzite and dolerite.

(4) The fossiliferous cryptocrystalline chert found in the Eneabba-Mandurah belt probably came from an off-shore source in the west. Chert in the southern Perth Basin may have come partly from Plantagenet rocks to the east.

(5) The presence of fossiliferous cryptocrystalline chert in strata aged from about 12 000 years BP to about 19 000 years BP in the Devils Lair, and the remarkable abundance of similar material at some central Perth Basin sites, indicates extensive and persistent exploitation of the source rocks.

(6) Further petrological work on silcrete artifacts may throw additional light on the patterns of transportation.

¹ Note added in proof. Dr. P. E. Playford, Geological Survey of Western Australia, reports (pers. comm.) finding bryozoal chert artifacts (including one large core 7 x 9 x 5 cm) on Tamala Station, about 20 km south of Shark Bay. These resemble the fossiliferous cryptocrystalline chert in handspecimen. Their significance is yet to be evaluated.

(7) Fulgurite fragments are concentrated with artifacts in blowouts by deflation. There is no evidence that fulgurites were worked by the Aborigines.

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8.—The biology and taxonomy of the cardinalfish, *Sphaeramia orbicularis* (Pisces; Apogonidae)

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Abstract

A study of the biology of *Sphaeramia orbicularis* (Cuvier) at the Palau Archipelago, Western Caroline Islands was conducted from November 1971 to March 1972. In order to clarify the taxonomic position of *S. orbicularis*, a review of the genus *Sphaeramia* is included in which an additional taxon (*S. nematoptera*) is recognised. The two species differ with regards to ecology, colour pattern, and counts for the gill rakers and soft anal rays. *S. orbicularis* were usually encountered in aggregations which number from a few to about 30 individuals. They prefer shallow water, usually near the shoreline, in which shade and shelter are provided by rocks, mangrove trees, or man-made constructions. The species is a carnivore which feeds on insects and a variety of small benthic and planktonic animals. Spawning and courtship activity occurred throughout the study period. Individuals spawned at average intervals which ranged from 19 to 33 days. The males incubate the egg masses orally. The estimated number of eggs per egg mass from three incubating males ranged from 6 100 to 11 700. The eggs hatch in approximately eight days at temperatures between 27 and 30°C. The fry are presumably pelagic and make their first appearance inshore at a total length of about 10.0 mm. The average growth rate for postlarval juveniles ranged from 3.3 to 6.4 mm per month.

Introduction

The present study was conducted while the author was stationed at the Palau Archipelago, Western Caroline Islands as a biologist for the Marine Resources Division of the U.S. Trust Territory Government. The author's residence (Fig. 1) was built on stilts over the sea, situated on the edge of a tranquil lagoon, bordered by the jungle-covered slopes of Malakal Island. Realising the tremendous potential of this setting I initiated a search for a species of fish which would readily lend itself to an intensive short-term biological investigation. The perfect subject was found in *Sphaeramia orbicularis* (Cuvier), a small species of cardinalfish (family Apogonidae). There was a permanent colony of approximately 60 individuals living directly under the house. These fish are particularly interesting from a behavioural standpoint as the males exhibit the unusual habit of oral egg incubation, a trait thus far recorded in only three families of marine fishes (Apogonidae, Ariidae, and Opisthognathidae). The study period extended from November 1971 to March 1972, during which time information was gathered on taxonomy, ecology, behaviour, reproductive biology, and growth.



Figure 1.—The study area was located under the author's house at Malakal Island, Palau Archipelago (photographed at high tide).

Materials and Methods

Approximately two observation sessions per day of about $\frac{1}{2}$ hour duration each were conducted during the study period. Standard skin-diving equipment (without SCUBA) was employed. Notes were usually recorded on a plastic sheet, but on some occasions they were taken by my wife or son, who sat nearby, as I dictated the observations.

The study population was composed of 33 adults (18 males and 15 females) and usually 20 to 31 subadults and juveniles. Recognition of individual fish and the study of their growth was facilitated by clipping the basal elements of certain fin rays. These incisions, if properly executed, inhibited normal fin regeneration and could be detected throughout the study period. A combination of different clips made it possible to differentiate fish of similar size. The growth subjects were periodically recaptured, measured, and released. Juveniles and small subadults were easily collected with dipnets, but quinaldine (a chemical anaesthetic) was necessary for the capture of larger individuals. Specimens were collected for stomach content analysis with a small Hawaiian-sling multiprong spear. The stomach contents were observed with a binocular dissecting microscope. The number of eggs in the egg masses of several incubating males was estimated by teasing the eggs from the mass, then counting the number of eggs which constituted a volume of 1.0 ml. The volume of the entire egg mass was then determined and multiplied by the number of eggs per ml.

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Taxonomy

There has been some confusion concerning the synonymy of *Sphaeramia orbicularis*. For example, Weber and de Beaufort (1929), under their description of *Apogon nematopterus*, stated "this species is only a variety of *A. orbicularis* in which some rays of the soft dorsal are filamentous. The transverse band on the body is broader than in that species." Similarly, Munro (1967) suggested that *nematopterus* individuals were probably females of *orbicularis*. Fortunately, at Palau I had the opportunity to compare both forms, which were found to be clearly distinct. In order to clarify the systematic position of *S. orbicularis* a brief review of the genus *Sphaeramia* and a key to the species is presented below (see Fraser, 1972, for an analysis of generic characters).

Sphaeramia Fowler and Bean

Sphaeramia Fowler and Bean, 1930: 29 (type species, *Apogon nematoptera* Bleeker, by original designation).

KEY TO SPECIES

- 1a. Dark bar at middle of body about one scale wide; first few soft dorsal rays not produced into elongate filaments; gill rakers on first arch 24 to 27, soft anal rays 9
S. orbicularis
- 1b. Dark bar at middle of body $3\frac{1}{2}$ to 4 scales wide; first few soft dorsal rays produced into elongate filaments; gill rakers on first arch 32 to 37; soft anal rays 10
S. nematoptera

Sphaeramia orbicularis (Cuvier)

Figs. 2, 3, 5, 6, and 7

Apogon orbicularis Cuvier, 1828: 155 (type locality, Java).

Apogon nigromaculatus Hombron and Jacquinet, 1853: 32 (type locality, New Guinea).

Diagnosis.—Dorsal rays usually VI-I, $9\frac{1}{2}$ (fraction indicates last ray is bifurcate); anal rays II, 9; pectoral rays 12; lateral-line scales 26 including two scales on hypural); gill rakers on first arch 24 to 27; dark bar at middle of body about one scale wide.

Colour in alcohol: ground colour of head and body light tan; reddish-brown bar about one scale wide at level of first dorsal spine extending from dorsal fin base to abdomen; portion of head and body anterior to bar with numerous small spots especially concentrated on opercle and interorbital; posterior part of body with numerous, irregular shaped reddish-brown spots of variable size, those along the middle of the body largest and forming a broken stripe which terminates at the base of the tail; first dorsal fin pale reddish-brown with several dark spots on membranes; proximal half of pelvic fins translucent, distal half and spine dark reddish-brown; second dorsal, anal, and caudal fins generally pale, but membranes dusky; pectoral fins pale (slightly reddish) with diffuse reddish-brown spot at base.

Colour in life: ground colour of head and body pale grey with yellowish sheen; numerous small reddish-brown spots on snout, inter-orbital, and occipital; breast and abdomen slightly silvery;

reddish-brown bar at middle of body; numerous reddish-brown spots and blotches on posterior portion of body; first dorsal spine reddish-brown, except creamy yellow at tip, remainder of first dorsal fin pale yellow with reddish suffusion; second dorsal, anal, pectoral, and caudal fins generally transparent; basal half of pelvic fins pale yellow, outer half dark reddish-brown except actual fin rays and distal tip of membrane between pelvic spine and first ray which are pale yellow.



Figure 2.—*Sphaeramia orbicularis*, 55 mm SL, Palau Archipelago (photo by J. E. Randall).

Remarks.—The colour patterns of *S. orbicularis* and *S. nematoptera* are contrasted in Figs. 2 and 3. In addition, differences in counts for the anal fin and gill rakers are presented in Table 1. At Palau these two species are also ecologically separated. *S. orbicularis* generally occurs in small aggregations in extremely shallow water (0.1 to one metre) adjacent to the shoreline. It inhabits crevices and caves, and is frequently encountered among mangrove roots or in the vicinity of mangroves, breakwaters, piers, and wreckage (see section on ecology for further habitat information). *S. nematoptera*, however, is found away from the shoreline in 1.5 to six metres, usually in areas of rich coral growth. In addition, the two species appear to differ with regards to maximum size attained. The largest specimen of *S. orbicularis* which was collected at Palau was 89 mm standard length (SL), while the largest *S. nematoptera* measured 61 mm SL.

S. orbicularis has been recorded from the East African coast, Andaman Islands, Singapore, Indonesia, New Guinea, Philippine Islands, Hong Kong, Palau Archipelago, Truk, Ponape, and the Gilbert Islands.

Sphaeramia nematoptera (Bleeker)

Apogon nematoptera Bleeker, 1856: 35 (type locality, Manado, Celebes).

Amia nematophora Bleeker, 1873-76: pl. 313, fig. 1 (type locality, Celebes).

Table 1

Soft dorsal ray and gill raker counts for species of *Sphaeramia*

Species	Dorsal Rays		Gill Rakers													
	9	10	25	26	27	28	29	30	31	32	33	34	35	36	37	
<i>S. orbicularis</i>	10	...	1	1	7	1	
<i>S. nematoptera</i>	...	10	1	3	2	3	...	1	

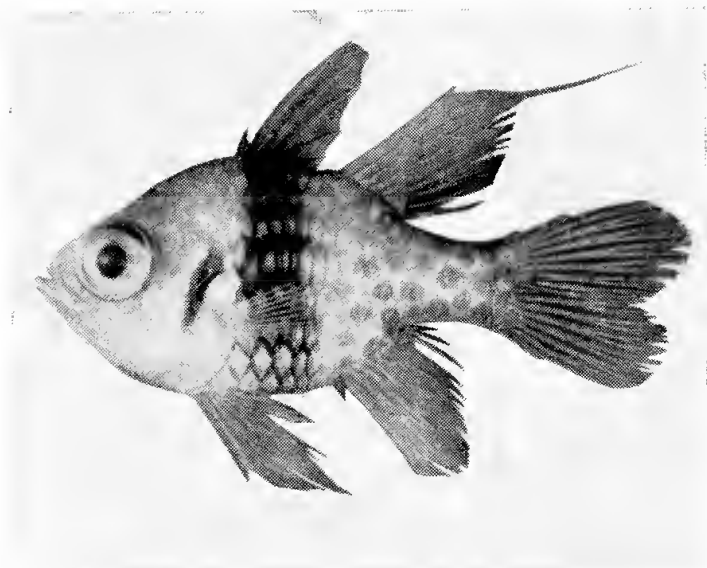


Figure 3—*Sphaeramia nematoptera*, 42 mm SL, Palau Archipelago (photo by J. E. Randall).

Diagnosis.—Dorsal rays VI-I, 9½; anal rays II, 10; pectoral rays 12; lateral-line scales 26 (including two scales on hypural); gill rakers on first arch 32 to 37; dark bar at middle of body 3½ to 4 scales wide.

Colour in alcohol: ground colour of head and body light tan to greyish; dark reddish-brown bar 3½ to 4 scales wide at level of first dorsal fin extending from dorsal fin base to abdomen; portion of head and body anterior to bar mostly pale without spots (scales may have dusky edges); interorbital, cheek, and chin brownish; yellowish patch sometimes visible on upper portion of opercle; posterior part of body with about 25 to 30 round, reddish-brown spots of nearly uniform size (slightly smaller than pupil); first dorsal and pelvic fins dark reddish-brown; second dorsal, anal, and caudal fins generally pale, but membranes dusky; pectoral fins pale (slightly reddish); pectoral base pale.

Colour in life; head and anterior portion of body with yellowish sheen, peppered with numerous minute dark spots; reddish-brown bar at middle of body; posterior portion of body whitish to pink with maroon spots; first dorsal fin mostly reddish-brown; but membranes between last two spines whitish; second dorsal, anal, pectoral, and caudal fins generally translucent; pelvic fins reddish-brown suffused with yellow (yellowish suffusion more pronounced on basal portion of fin), edge of fin with narrow whitish margin.

Remarks.—This species appears to be restricted to the region which includes Indonesia, New Guinea, Philippine Islands, and Palau Archipelago.

Ecology of *S. orbicularis* at the Palau Archipelago

Habitat.—The Palau Archipelago is situated in the southwestern corner of the north Pacific Ocean, about 960 km east of the Philippine Islands and approximately the same distance north of New Guinea. The archipelago represents the extreme western end of the Caroline Islands and extends northeastward from about 6°53'N to about 8°06'N or over 112 km at a longitude of about 134°29'E. With the exception of two oceanic atolls at the extreme north tip of the chain, the northern half of the archipelago is volcanic in origin and is dominated by the island of Babelthaup which is about 40 km long and 13 km wide. This island rises to an elevation of about 200 metres and most of the shoreline is bordered by dense mangroves. The southern portion of the archipelago is remarkably scenic, characterised by a bewildering maze of limestone ridges and conical islets which extends for approximately 48 km. The main portion of the archipelago is surrounded by a barrier reef and there is a fairly well-developed lagoon in the southwest sector.

The limestone islands and islets of the south, including Malakal Island, rise up almost vertically from the ocean floor, forming a narrow complexity of canals some with depths greater than 30 metres. The islands are deeply undercut at the high-tide line, as much as two or three metres, forming deep notches above a submarine shelf of variable width.

Sphaeramia orbicularis is usually encountered in aggregations which number from a few to about 30 individuals in shallow, sometimes brackish water. Along the coast of Babelthaup and to a lesser extent among the southern islands, it is found living among the submerged roots of mangrove trees. The preferred habitat among the limestone islands of the south appears to be the shallow submerged shelf immediately adjacent to the undercut shoreline. This area abounds with shady crevices and small caves which serve as diurnal retreats for the species. The shoreline is occasionally penetrated by relatively large caves, some of which are completely submerged. The fish are generally found around the

mouth of these or a short distance inside, but they rarely penetrate the inner depths which are perpetually dark. *S. orbicularis* is also found in the vicinity of piers, stone breakwaters, bridges, and wreckage. The substratum in these areas usually consists of mud or rock and is above the zone of live coral growth. Juveniles are sometimes found at the surface around piers, boat moorings, or floating debris. In summary, the basic habitat requirements appear to consist of shallow water, usually near the shoreline, in which shade and shelter are provided by rocks, mangrove trees, or man-made constructions. Because of the shallow depth and proximity to the land the habitat is subject to rather extreme fluctuations with regards to water depth and salinity. The daily tidal fluctuation at Palau is approximately 2.0 metres and subsequently *S. orbicularis* must make nearly constant adjustments to achieve optimum conditions of depth and shelter. Heavy rain showers are relatively frequent throughout the year. After a night of continuous heavy rain the salinity was measured with a refractometer at 21 ppt. This measurement was taken in the study area in 20 cm depth or at about the same level inhabited by the fish.

The study area proper (Fig. 1), which was located next to the boat-yard on Malakal Island, consisted of a rectangular pool-like enclosure with concrete walls on three sides. The pool had an area of approximately 24 square metres and was sometimes used for mooring small boats. It was situated directly under our residence, thus the floor of the house formed a roof which completely covered the area about 2.0 metres above the water surface at high tide. Water depth in the enclosure varied from only a few centimetres at low water to about 2.0 metres.

Food and Feeding.—The daily activity pattern of the study population can be summarised as follows: during most of the daylight hours (0900-1630) the fish were relatively inactive and remained in several aggregations directly under the house. They changed their position during the day to accommodate to changing conditions of tide and light, usually remaining in the shade, hovering at depths ranging from about 20 to 120 cm. During late afternoon the fish became more active and began to feed. It was not determined if feeding continued throughout the night, but on every occasion when nocturnal observations were made, the fish appeared to be active, ranging up to 20 metres from the house, usually in small groups of about two to 10 individuals.

S. orbicularis is a carnivore which feeds on insects and a variety of small benthic and planktonic animals. Crabs (mainly portunids and small grapsids and insects from a major portion of the ingested food items. The stomachs of 61 specimens (45 to 85 mm SL) were examined. Most of these were collected in the vicinity of the house, a short distance from the study population. Twenty-five stomachs were empty; however, seven of these were from incubating males, which do not feed during the brooding period. The results of the stomach content analysis of the 36 specimens containing food is presented in Table 2. The results are given as percentage

Table 2

Percentage volume of major groups of food organisms in stomachs of Sphaeramia orbicularis

(10 stations ; 36 specimens—45 to 82 mm SL)

Food	Volume (%)
Crabs	28.8
Insects	22.9
Copepods	12.9
<i>Sphaeramia</i> eggs	5.6
Ostracods	5.0
Polychaetes	4.7
Amphipods	3.9
Zoea	3.7
Unidentified	3.4
Sergestids (Lucifer)	3.1
Unidentified crustacean fragments	1.4
Megalops	1.2
Small fishes	1.0
Mysids	0.8
Unidentified shrimps	0.8
Stomatopod larvae	0.4
Pleagic fish eggs	0.3
Gastropod fragments	0.1

volume of the different major groups of food organisms. The percentages were estimated visually for individual fish, and the total was computed from all the stations. The stomachs which were full usually contained either one or two small crabs, a small insect, or a variety of minute planktonic organisms. Specimens collected between 1700 and 1900 hours generally contained a high percentage of grapsid crabs and insects (beetles and crickets), while individuals taken later in the evening or during the predawn hours appeared to feed predominately on plankton. Most of the specimens collected during the middle of the day (1100 to 1430) had empty stomachs. The data indicates the fish feed actively at dusk, during the early evening and predawn hours (0500-0630). Unfortunately samples were not taken from 2230 to 0500.

S. orbicularis is probably opportunistic as far as food items and time of feeding are concerned. For example, fish in the vicinity of the house actively fed on plankton which was attracted to the household lights during the evening, while a collection made at the same time about one km away in total darkness indicated that crabs were the primary food taken. Resting aggregations exhibiting a minimum of feeding activity could be readily induced to feed on plankton by switching on a 75 watt lightbulb above the study area. Similarly, inactive fish during the middle of the day will eagerly take bits of bread and assorted table scraps. As mentioned previously the fish feed actively at dusk. However, on one occasion, a collection of nine individuals made at this time of day at the edge of a landlocked (except for a narrow submarine cave to the sea) saline lake yielded only empty stomachs.

It is interesting to note that insects are a major food item. This fact is clearly understandable if the habitat is considered. With the exception of fish living in the vicinity of man-made structures the preferred habitat of the species is either adjacent to the undercut shoreline or among mangrove roots. In both localities, the vegetative canopy overhangs the habitat of the fish. In areas of undercut shoreline, the lush growth of jungle stops at the high tide mark, but because of the undercutting phenomena,

the vegetation extends a considerable distance out of the water, and at high tide the foliage is frequently adjacent to the sea surface. Thus, insects which fall from the trees or accidentally fly into the water are readily available as food.

Reproduction and early development

Courtship and spawning took place throughout the study period. Presumed courtship was observed around sunset on several occasions. During this activity pairs of *S. orbicularis* engaged in alternating patterns of chase and display. The most common display exhibited consisted of one fish confronting another in either parallel or lateral fashion while flicking the pelvic and first dorsal fin back and forth. The tips of these fins are relatively bright coloured which serves to enhance the display. Occasionally the fish chased each other for a distance of several cm and sometimes biting was observed, this activity usually being directed at either the sides or anal region. There was no evidence of sexual dimorphism except for the swollen mouth of egg brooding males (Fig. 4). Spawning was not observed and most likely takes place during the middle of the night.



Figure 4.—Male *S. orbicularis* with egg mass in oral cavity.

Spawning occurred at more or less regular intervals with individuals spawning about once or twice monthly. Daily records were kept of the number of incubating males present, which served as an index of spawning activity. The graph in Fig. 5 represents the typical pattern which was observed during the study period. There appeared to be a correlation between the time of spawning and the phase of the moon. Spawning activity was at its highest peak each month at the period between first-quarter and full moon. Also there was a lesser peak between last-quarter and new moon. It is possible that the fish spawn at these times because of the tidal levels. During both of the monthly spawning peaks the high tide occurred within 1½ to two hours of midnight. If spawning occurred during

these hours, as it suspected, there may be a requisite for high water. At low tide the fish are more or less driven temporarily away from their favoured habitat and might be reluctant to spawn.

The spawning record of several males as indicated by the presence of an egg mass in the oral cavity is indicated in Table 3. The spawning interval for these individuals ranged from 16 to 35 days with an average interval of 19 to 33 days between broods.

Table 3

Spawning Record of several male *Sphaeramia orbicularis*

Size (mm SL)	Spawning Dates			Average Interval (Days)
	First	Second	Third	
69	1/12/71	24/12/71	25/1/72	27
69	1/12/71	23/12/71	22/1/72	26
72	27/12/71	12/1/72	5/2/72	20
73	2/12/71	6/1/72	5/2/72	33
74	27/12/71	20/1/72	7/2/72	21
76	1/12/71	23/12/71	8/1/72	19
80	1/12/71	23/12/71	10/1/72	20

The spawning of this species is probably similar to that exhibited by *Apogon imberbis* (Linnaeus), which was observed by Garnaud (1950a and b). According to Breder and Rosen (1966), "Garnaud described the mating as a side-to-side affair in which the female placed her ventral under the male and he placed his anal under the female. In this position they performed the common teleost trembling movements. According to Garnaud, such behaviour did not take place when the eggs were finally extruded later. These eggs are cast in a single mass of material bound together by tendrils arising from one pole of the eggs. The male immediately takes them in in his mouth. These observations led Garnaud to postulate that this case was one of internal fertilisation." However, there is no experimental evidence to prove that internal fertilisation takes place in apogonids.

Many authors have stated that the male apogonid always incubates the eggs. However, Ebina (1932) reported that both sexes of *Apogon semilineatus* exhibit this habit. In the present study an examination of the gonads of many specimens indicated that only male *S. orbicularis* are oral incubators. Males which are incubating egg masses are easy for an observer to distinguish. The gular region is greatly enlarged which dramatically alters the lower profile of the head (Fig. 4). The incubation period lasts about eight days during which time the male periodically "juggles" or changes position of the mass in its mouth. As mentioned previously, the incubating males do not feed; however, *Sphaeramia* eggs are occasionally found in the stomachs of incubating males. Presumably, these are accidentally swallowed or, as in one case when the

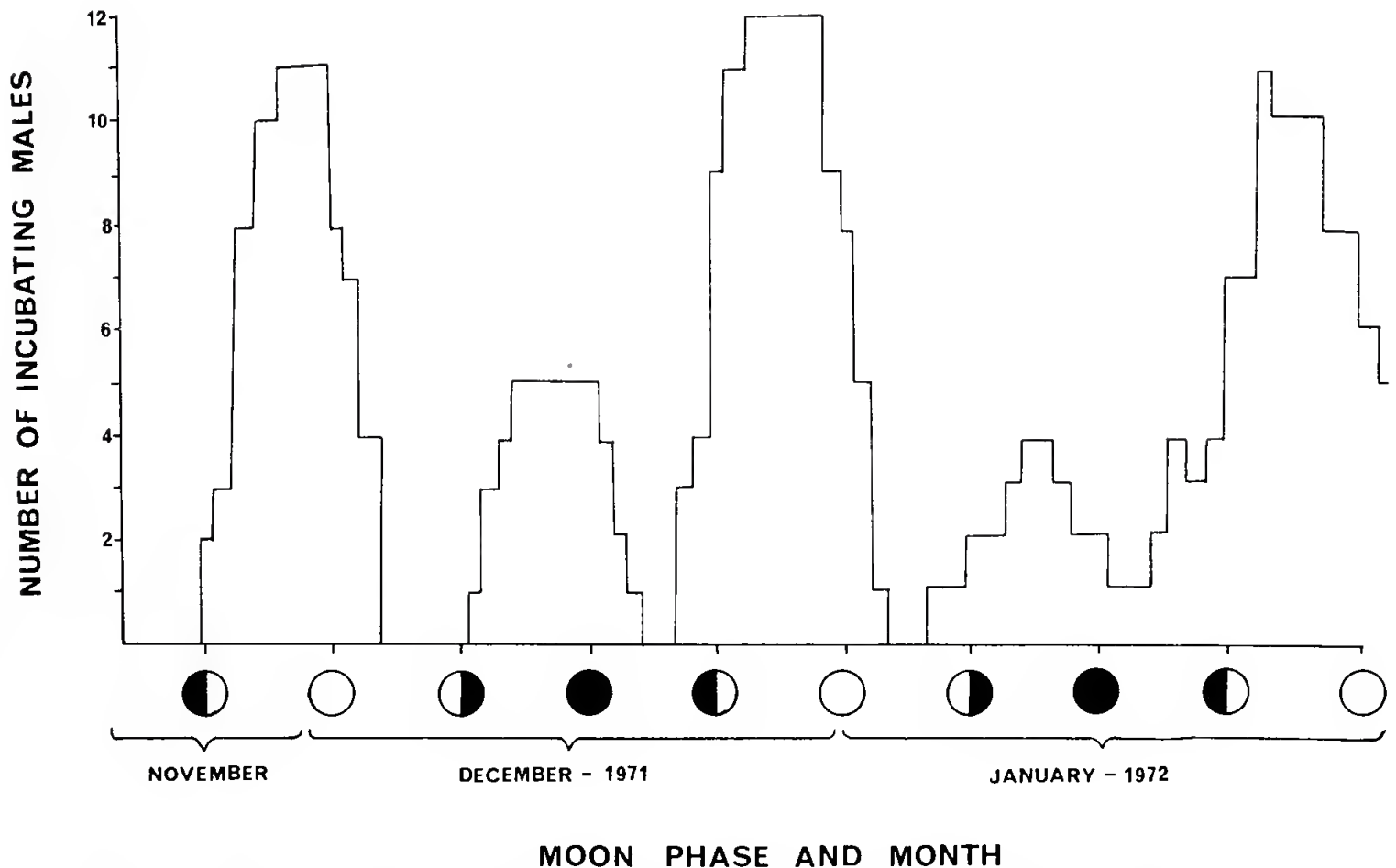


Figure 5.—Number of incubating males of *S. orbicularis* with relation to moon phase and time of month.

entire egg mass was found in the stomach, are ingested during periods of stress (specimen was captured with guinaldine). The egg masses are roughly spherical, although somewhat compressed, ranging in diameter from 14 to 20 mm. The estimated number of eggs per egg mass from three incubating males 72 to 89 mm SL, ranged from 6100 to 11700. The eggs are pinkish-orange when freshly spawned and as the embryos develop they gradually turn to purplish-brown. The smallest incubating male collected during the study was 69 mm SL; the smallest ripe female was 60 mm SL. The ovaries are elongate, compressed structures which are encapsulated in a silvery coloured sheath. One ovary of a 78 mm SL specimen was 11 mm x 26 mm and 7 mm thick.

Individual eggs are spherical and measure 0.6 to 0.7 mm in diameter. By approximately 24 hours the embryo has entered the blastula stage (Fig. 6a) and at approximately 40 hours gastrulation is in progress (Fig. 6b). Up to this point the egg is characterised by the presence of two to five large oil globules. After about 70 hours the embryo is relatively well formed (Fig. 6c). The unpigmented eyes, otic vesicles, statoliths, and somites are clearly evident. The yolk is bilobed and there is a single large oil globule present. The heart which is positioned just under the head, pulsates at a rate of 120 to 140 beats per minute.

The 110 hour embryo (Fig. 6d) is similar to the previous stage except the yolk is further reduced, the eyes exhibit pigmentation, and the median fin folds have made their appearance. By about

160 hours (Fig. 6e) the pectoral fins are evident, the eyes are well formed and pigmentation is apparent in the form of two rows of stellar-like melanophores on the ventral surface. A full term embryo is shown in Fig. 6f. Hatching occurs in approximately eight days at temperatures ranging from 27 to 30°C.

The newly hatched, transparent fry (Fig. 7a) are apparently pelagic for at least a short period. The pelagic larval stage accounts for the wide geographic distribution of the species. The smallest post-larval forms which were collected inshore measured about 10.0 mm total length

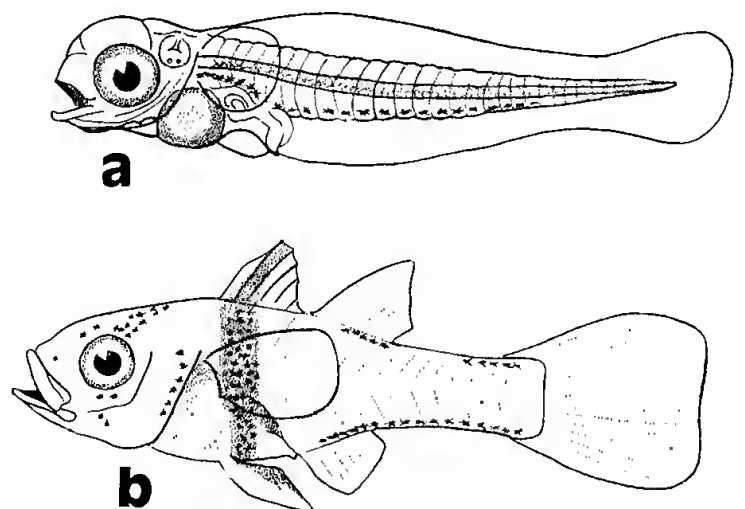


Figure 7.—Growth stages of *S. orbicularis*: a. newly hatched larva, 3.3 mm total length; b. postlarval juvenile, 10.0 mm total length.

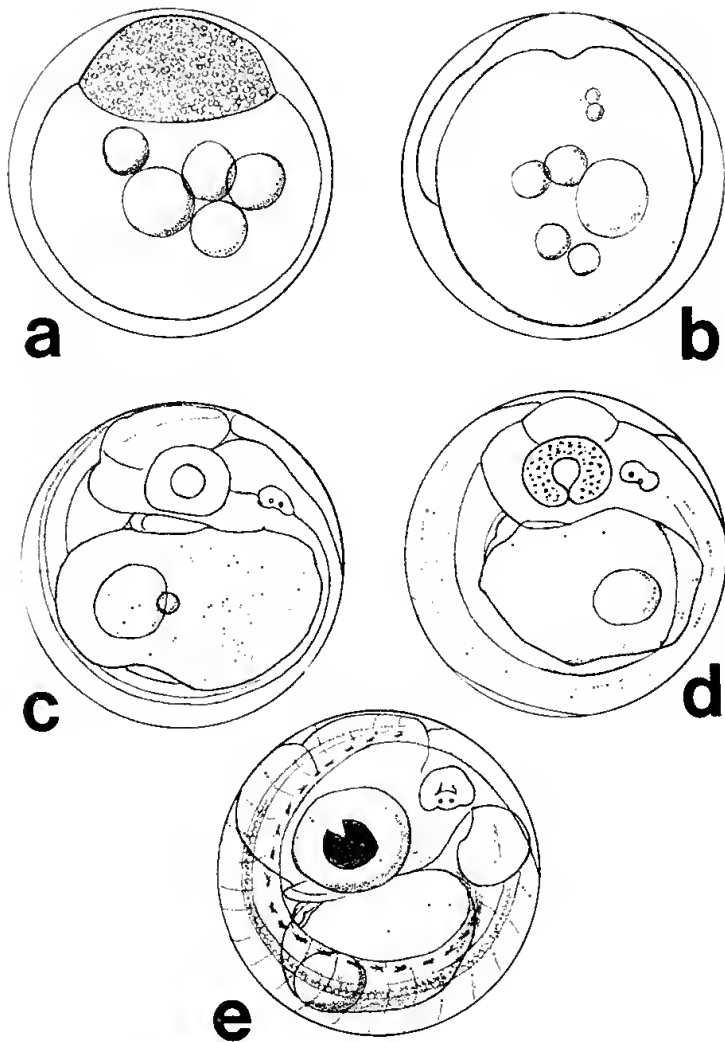


Figure 6.—Early development of *S. orbicularis*: a. 24 hours; b. 40 hours; c. 70 hours; d. 110 hours; e. 160 hours.

Table 4

Summary of growth data for juvenile *Sphaeramia orbicularis*

Initial Measurement Size	Date	Final Measurement Size	Date	Total Increase	Growth Rate per month
(mm SL)		(mm SL)		(mm)	(mm)
12.0	6/12/71	22.0	29/2/72	10.0	3.6
12.0	6/12/71	23.0	29/2/72	11.0	4.0
12.0	6/12/71	28.0	29/2/72	16.0	5.8
13.0	8/11/71	32.0	29/2/72	19.0	5.1
13.0	6/12/71	22.0	29/2/72	9.0	3.3
13.0	6/12/71	30.0	29/2/72	17.0	6.2
13.5	6/12/71	24.0	29/2/72	10.4	3.8
13.5	6/12/71	28.0	29/2/72	14.5	5.3
13.5	6/12/71	28.0	29/2/72	14.5	5.3
14.0	6/12/71	30.0	29/2/72	16.0	5.8
14.0	6/12/71	29.0	29/2/72	15.0	5.5
14.5	6/12/71	29.0	29/2/72	14.5	5.3
15.0	6/12/71	30.0	29/2/72	15.0	5.5
15.0	6/12/71	30.0	29/2/72	15.0	5.5
16.0	6/12/71	30.0	29/2/72	14.0	5.1
18.0	11/8/71	36.0	29/2/72	18.0	4.8
18.0	11/8/71	41.0	29/2/72	21.5	5.7
19.5	11/8/71	42.0	29/2/72	24.0	6.4

(Fig. 7b). These tend to form small aggregations of about five to 20 individuals. They are found in the same habitat as the adults and feed on current-borne plankton.

Growth data were collected for 18 juveniles over a four month period. These data are summarised in Table 4. The average growth rate for juveniles ranged from 3.3 to 6.4 mm per month. There was no significant growth recorded for 17 fin-clipped adults, ranging in size from 70 to 89 mm SL, during the four month study period.

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9.—*Eremophila ramiflora* (Myoporaceae), a new species from Western Australia

by B. Dell¹

Manuscript received and accepted 29 July 1975

Abstract

A new species of *Eremophila*, *E. ramiflora* is described. This species has affinities with *Eremophila fraseri* and is sympatric with *E. fraseri* in the Agnew area of the Northern Goldfields, Western Australia.

Introduction

While carrying out resin analyses on plants of *Eremophila fraseri* F. Muell. in the field the author's attention was drawn to a previously undescribed species of *Eremophila*. From a distance the plants of the two species can be readily confused. Apart from material collected by the author only two other collections have been made. Although there appears to be a need for extensive taxonomic work in the genus, publication of the description of this species is justified at this time because its boundaries appear well defined.

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Eremophila ramiflora Dell, sp. nov.

Species habitu cum *E. fraseri* optime congruens, sed differt petiolis subdecurrentibus; floribus in caulibus et novis et veteribus portatis; sepalis dorsalibus sepalis internis vix latioribus; sepalis post anthesin vix dilatatis; corolla magentea; lobo ventrali corollae longitudine tubum aequanti differt.

Compact *shrub*, 1-3 m high, vegetative parts glandular hairy, resinous; branchlets thick, rigid, with amber-coloured resin droplets, with remnants of deflexed leaf bases ca. 0.5 cm long. *Leaves* lanceolate, alternate, crowded, spreading, deflexed when mature, 1.2-2.2 cm broad, up to 7.5 cm long, slightly keeled and recurved; blades viscid, green, gradually attenuate or cuneate into the petioles which are difficult to distinguish from the lamina; petioles almost decurrent; margins entire, undulate or repand, rarely serrulate; apex acute. *Flowers* axillary, usually solitary or in small groups, borne on previous season's branchlets and on leafy young branchlets; peduncles 0.7-1.2 cm long, spreading slightly turned up under the flower; calyx segments



Figure 1.—Habit of *E. ramiflora*. Bush about 1.5 m high.

slightly imbricate when mature, oblong to spatulate, acute to obtuse, ca. 1.2 cm long when in flower, enlarging to 1.5 cm, rarely to 2.0 cm; sepals green becoming reddish and shiny after flowering, then reticulate and membranous, dorsal sepal scarcely broader than lateral sepals; corolla 2.5-3.0 cm long, glandular-hairy with some simple hairs inside towards the base; base yellowish-green; tube dark magenta with small dark spots on the outside, cylindrical, scarcely constricted above the ovary, the upper part linear-oblong, slightly curved and not much dilated; lobes unequal, the 4 upper lobes turned back and acute, dorsal lobes short, lateral lobes separated to almost 1/3 the length of the corolla,

ventral lobe long, recurved separated to the middle of the corolla, apex acute and keeled; stamens exerted, filaments glandular pubescent, anthers with magenta lateral papillae, with few glandular hairs; pistil just exerted, style sparsely hairy towards stigma, stigma red; ovary glabrous, green towards the apex, 2-chambered with one pair of ovules to each cell. *Drupe* woody, slightly compressed, shorter than the calyx, 0.6-0.8 cm broad, 0.8-1.0 cm high. Gametic chromosome number $n=18$.

Holotype.—127.5 km south of Yandal Homestead, 47 km north of Leonora on road to Melrose Station, Western Australia, 28 September 1973, Dell 1050 (PERTH).

Other Specimens.—25 km west of Carnegie Homestead, 122°45'E, 25°45'S, Chinnock 893 (AD 97347300); 127 km east of Sandstone, Dell 1029; 16, 21, 28.2, 48, 67.1 km north of Leonora on road to Wiluna, Dell 1074, 1076, 1077, 1072, 1075 (UWA); between Agnew and Leonora, Lovett (PERTH).

Discussion

Characters of *Eremophila ramiflora* which distinguish it from *E. fraseri* are the almost decurrent broad leaf bases, the flowers arising from both the old and new seasons stems, the sepals not enlarging much after flowering, the dorsal sepal scarcely broader than the internal sepals, and the magenta corolla tube with ventral lobe separated to the middle of the corolla. The resin components of the leaves and stems also differ from those of *E. fraseri*. Figures 1, 2 and 3 show details of habit, flowering shoot and floral characters respectively.

E. ramiflora occurs in the Leonora—Agnew region of the Eremean Province extending north-east as far as Lake Carnegie. There are insufficient collections to determine how far east the species extends. Both *E. fraseri* and *E. ramiflora* occur on similar red loams with many stones overlying lateritic hardpans. Near Agnew the species are sympatric, *E. fraseri* being represented as the tetraploid. The nearest diploid population of *E. fraseri* is some 400 km further north.

E. ramiflora has been seen in flower in July and September. It is likely that this species flowers after heavy rains and like *E. fraseri* blooms twice in some years.

Acknowledgements.—The author is grateful to Mr. B. G. Lay for information on the soils of the Carnegie locality, to Mr. G. J. Keighery for providing the chromosome count of the type material, and to Dr. N. H. Brittan for providing the Latin diagnosis.

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Figure 2.—Close up of stem showing flowers on new and old wood.

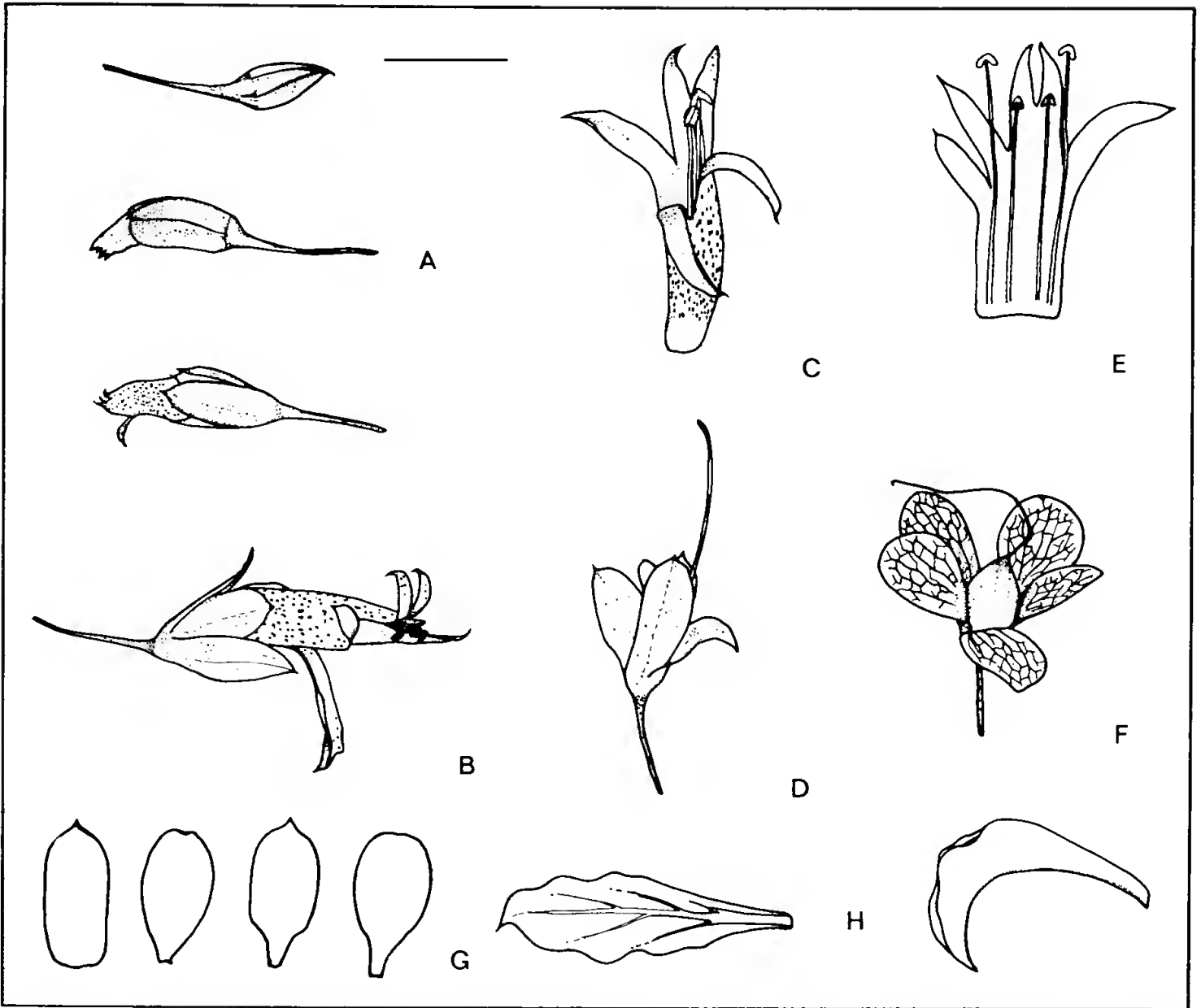


Figure 3.—Details of floral structure. (A.—developing buds, B, C.—mature flower, D.—sepals at flower fall, E.—corolla tube cut and spread, F.—fruit with strongly veined calyx segments, G.—variation in calyx segments, H.—mature leaves. All drawings to same scale; length of bar 1 cm).

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10.—Mammal remains from the upper levels of a late Pleistocene deposit in Devil's Lair, Western Australia

by A. Baynes,¹ D. Merrilees¹ and Jennifer K. Porter¹

Manuscript received 22 October 1974; accepted 29 July 1975

Abstract

This paper reports on continuing investigations of the fossil mammal fauna from the sandy deposit in Devil's Lair, a small cave in the extreme south west of Western Australia. Excavations in 1972 and 1973 produced a substantial sample of bone fragments about 12 000 to about 19 000 years old, and a much smaller sample about 19 000 to about 25 000 years old. Most of these remains appear to be of animals eaten by humans occupying the cave intermittently, perhaps in small groups.

Neither Dingo nor any of the large extinct Pleistocene marsupials is included among the 35 mammal species so far detected in the deposit. Between about 19 000 years ago and about 12 000 years ago most species are present at all levels, but at least one trend in the relative abundance of the more common species is suggested, and seems to be clearest about 12 000 years ago. An improved list of the modern mammal fauna of the district is presented and compared with the fossil fauna; there appears to have been a considerable decrease in species diversity since the Pleistocene. Species lost have mainly been those adapted to shrub formations or woodlands, whereas species adapted to forest have persisted. These changes are the culmination of the above trend in relative abundance. Two possible causes are discussed: the effects of the glacioeustatic rise in sea level acting alone by changing the extents of different habitats, or acting in conjunction with local climatic changes such as an increase in effective rainfall.

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Introduction

Excavations in Devil's Lair, a small cave in aeolian calcarenite in the extreme south west of Western Australia, were begun in 1955 by E. L. Lundelius with the object of learning something of the prehistoric mammal fauna of the region. After various unsystematic extensions of these initial excavations, and after realisation that the deposit included an archaeological component, the Western Australian Museum began a series of systematic excavations, to be spread over a number of years. In preparation for this series, a reserve including the cave has been vested in the Museum, and a steel mesh fence erected across the cave mouth. Thus it seems justifiable to leave excavations open from field season to field season and to extend them as opportunity offers.

The deposit yields vertebrate remains in abundance as well as substantial numbers of artifacts, so that a few excavators working for some days produce material requiring many months of preparation and study. The intention is to report progress at intervals, leading to a summary in due course. Present indications are that several more years' work must precede any such summary.

This paper presents an analysis of animal remains recovered from excavations made in February 1972, and March 1973. A general report on the first of the series of systematic excavations, made in December 1970, has been issued by Dortch and Merrilees (1972), and a report dealing mainly with the archaeological component from the 1972 excavations has been issued by Dortch and Merrilees (1973). Dortch (1974) has discussed archaeological aspects of the 1973 excavations, and Glover (1974) has discussed geological aspects of the material of some of the artifacts recovered. Davies (1968, and Appendix to Dortch and Merrilees, 1973) has described human incisor teeth. Other specialist reports are in preparation.

We follow the mammal species concepts and names of Ride (1970).

Devil's Lair lies about 5 km from the sea on the eastern side of a ridge. The vegetation of the region has been described by Smith (1973). The western slope of the ridge, which is exposed to the prevailing westerly winds off the southern Indian Ocean, is covered by an open heath in which *Acacia decipiens* is the principal species. Near the sea *Olearia axillaris* and *Scaevola* spp. are also important components. Where some shelter exists on the top of the ridge open scrub,

low woodland, or low open forest may occur. Peppermint (*Agonis flexuosa*) or Jarrah (*Eucalyptus marginata*) are usually the principal species in these formations. On the eastern slopes of the higher parts of the ridge open forest quickly gives way to high open forest in which Karri (*E. diversicolor*) grows in fairly pure stands. Devil's Lair lies in the middle of one such belt of Karri forest which stretches for some 20 km from Calgardup Brook in the north to Turner Brook in the south. On the inland (eastern) side of the Karri is an extensive open forest of Jarrah and Marri (*E. calophylla*) continuing in to the valley of the Blackwood River some 10 km to the east, and for a much greater distance to the north east. Only about 3 km to the east of Devil's Lair is McLeod Creek along which dense shrub vegetation grows.

The 1972 and 1973 Excavations

Several trenches were opened in Devil's Lair during the 1972 and 1973 field seasons, for reasons given by Dortch and Merrilees (1973), who show the positions of these trenches in the cave and briefly describe the geological setting. Very few animal remains were recovered from Trenches 3 and 4. This paper is based almost entirely on specimens recovered from Trench 6 and from a complex of trenches, Nos 2, 5, 7 and 8 (7 and 8 with subdivisions) of our field and laboratory records.

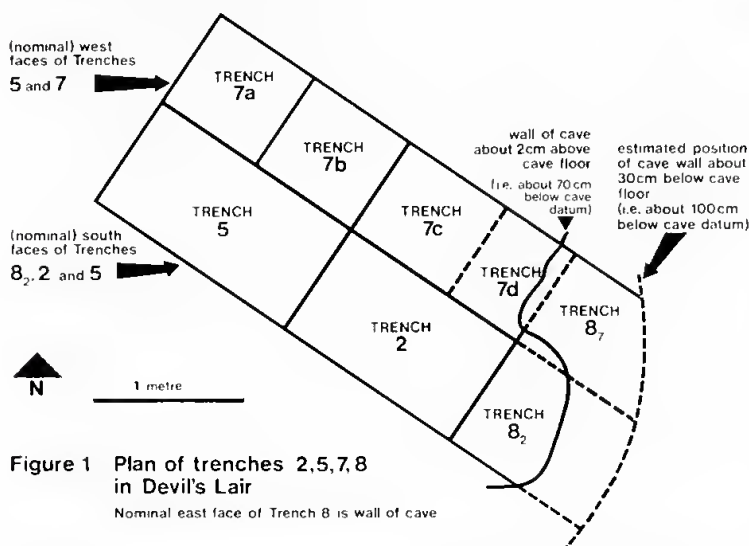


Figure 1 Plan of trenches 2, 5, 7, 8 in Devil's Lair
Nominal east face of Trench 8 is wall of cave

The relations of Trenches 2, 5, 7 and 8 to one another and their dimensions are shown in Figure 1. Trench 6, oriented similarly to Trench 5 but $1\frac{1}{2}$ m long by 1 m wide, was close to the cave wall about 3 m south west and slightly down slope from Trench 5. All depths have been recorded below the same arbitrary datum mark on the wall of the cave, and thus may be compared directly.

The various trenches have been excavated to different depths, which are recorded in the tables in Appendix 1. Trenches 7 and 8 have been excavated only to shallow depths as yet, Trenches 5 and 6 to intermediate depths, while Trench 2 is deepest, but no trench has yet reached the bottom of the deposit, and steel rods driven down from the bottoms of Trenches

6 and 2 show at least a metre thickness of deposit below each.

Nature and age of the deposit

Much of the Devil's Lair deposit is made up of grains of quartz to some extent coated and lightly cemented by calcite. As a result excavation is usually easy, yet vertical excavation walls remain stable for years. The colour of the deposit varies. The sandy portions show various shades of orange and brown, but there are paler coloured bands and irregular masses which have been more or less strongly lithified by calcareous cement, while the uppermost layer is black. Flowstones, stalagmites and other almost entirely calcareous materials, crystalline at the macroscopic level, are interbedded with the sandy material. Calcareous solutions drip from the roof of the cave and permeate the deposit during the wetter months of the year at present, and presumably always or usually have done so, and have been responsible for patches and zones of lithification.

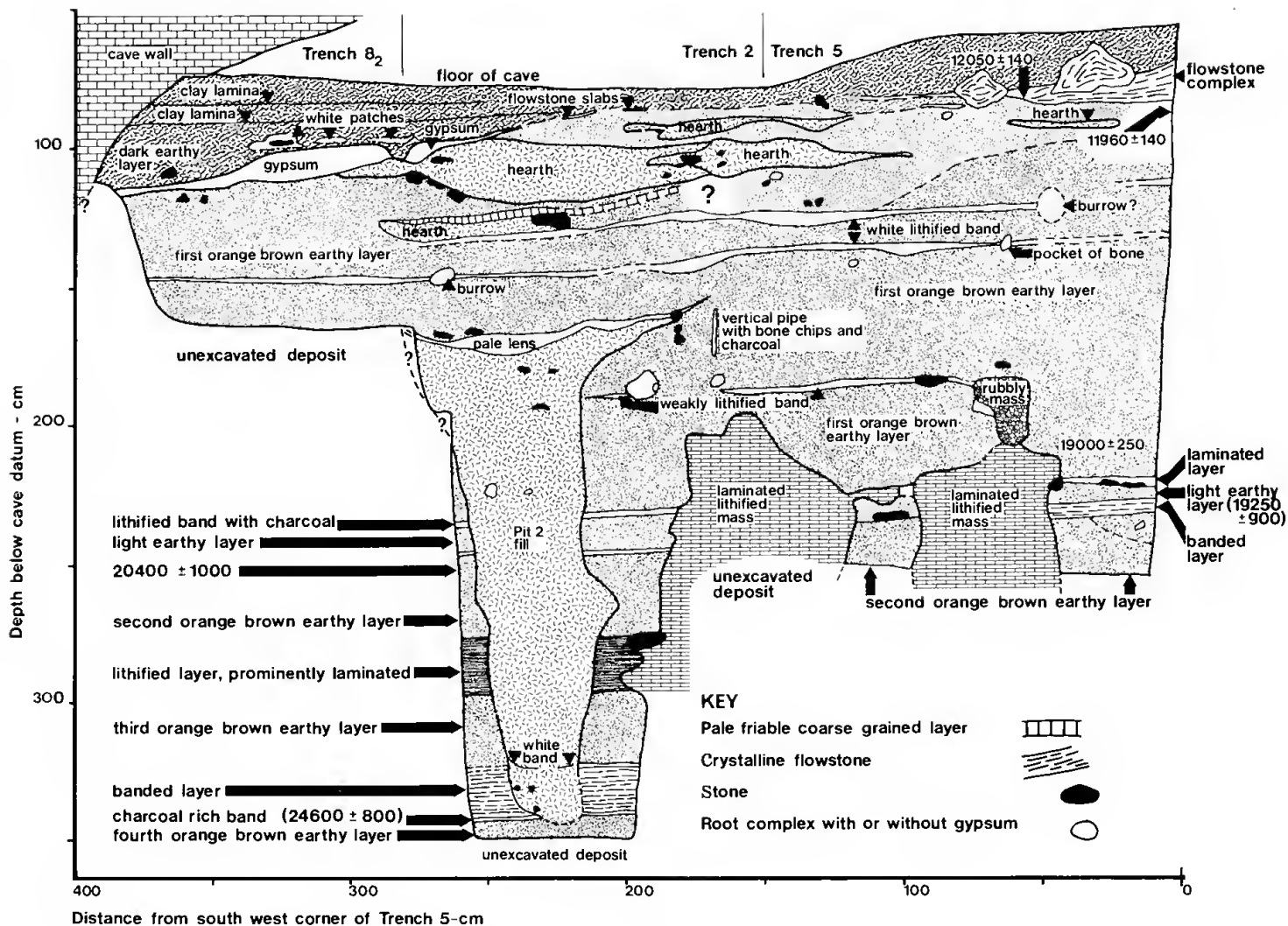
During the drier months of the year, the sandy portions of the deposit become sufficiently dry to pass easily through our screens, but enough moisture is present at some times of the year to support the growth of tree roots. These appear to be associated in some way not at present understood with bands and pockets made up entirely or partly of gypsum.

There are lenticular inclusions of ashy appearance, which we have interpreted as hearths, particularly near the top of the deposit. Charcoal is widely dispersed, usually in small pieces not exceeding a few millimetres across. Fragmented bone is also widely dispersed through the deposit, and there is a small but significant proportion of rock fragments foreign to the cave. Large and small rock fragments, mainly of calcareous material, much or all of which could be derived within the cave, are abundant in places, and broken stalactites also occur.

Detailed analysis of the sediments is in progress, and will be reported in due course by M. L. Shackley.

In order to avoid prejudice to later determinations of stratigraphic equivalences throughout the cave, we have used field designations for the "natural" stratigraphic divisions or arbitrary depth determined units of excavation ("spits") differing from trench to trench or field season to season. These field designations are recorded not only in our field notes but also on specimen labels and in the Museum catalogues, and to some extent are reproduced in the Appendix 1 tables.

However, we have attempted to group and analyse our data in terms of the major stratigraphic divisions recognised by Dortch and Merrilees (1973), and comparison of their stratigraphic sections and names with ours may be made readily even though we have modified the names slightly in some cases. A stratigraphic section revealed in the southwestern walls of the adjacent Trenches 5, 2 and 8₂ is represented in



DEVIL'S LAIR: (NOMINAL) SOUTH FACES, TRENCHES 8₂ 2 5

Figure 2.—Section revealed by excavations to 1973, south faces of adjacent Trenches 8₂, 2 and 5.

Figure 2; for convenience this has been called the "south" face, though its trend is actually N 123°. Dortch (1974) illustrates the shallow north face of Trench 7, opposite that shown here in Figure 2.

Radiocarbon dates on charcoal samples from various parts of the deposit have been reported by Dortch and Merrilees (1973). These dates have been included in Figures 2, 4, 5 and in the Appendix 1 tables in their relative stratigraphic positions. They show that the uppermost major stratigraphic unit ("dark earthy layer") is less than 12 000 years old by an amount not at present known, and that the other major stratigraphic units so far excavated extend back in age from about 12 000 to about 25 000 years before the present. This is the period covered in the present report. Dortch and Merrilees (1973) suggest that the bottom of the deposit represents a time more than 30 000 years B.P.

Procedures

Excavation was made by trowel and brush, the excavated material being sieved with "coarse" and "fine" screens (5 mm and 3 mm square openings respectively), with random samples passed additionally through screens of 1½ mm

square openings (our "finest" screens). The material remaining on the screens was examined at the site, in the cave in 1972 and in full daylight in 1973, and bone and artifacts removed. The residue was thrown away after two screeners were satisfied that sorting was complete. Some material may have been overlooked in sorting, especially in 1972 when artificial light was used. Checks on randomly selected samples of material passing through the fine screens suggest that little macroscopically identifiable material was lost.

Samples for pollen analysis, radiocarbon dating, and sediment analysis were taken as described by Dortch and Merrilees (1973).

The bone recovered was well preserved, with details such as muscle scars, foramina or tooth cusps sharply defined, though concealed by calcareous coatings in some cases, and showing brown coloration in most. Calcareous coatings were often easily removable with brushes or steel dental probes, though in some cases the coatings were well cemented and required considerable pressure to flake them off. Even so, the tooth and bone beneath generally suffered little damage and very little acid preparation of specimens was necessary.



Figure 3.—Typical bone fragments from Devil's Lair, excavated from unit O in upper middle subdivision of first orange brown earthy layer in Trench 8₂, 136-149 cm below cave datum. This is not the whole sample. *Left*: fragments which for practical purposes are not identifiable. *Centre*: identified and catalogued fragments typical of those on which this paper is based. *Right*: fragments which could be, but which for lack of time have not been identified.

A conspicuous feature of the bone samples recovered from Devil's Lair, unlike those from some other caves nearby, was fragmentation, as illustrated in Figure 3. Bone fragmented to about the same degree was abundant at most stratigraphic levels, so much so that for practical reasons a selection had to be made of what was to be identified and studied. All fragments bearing teeth or with tooth sockets, and all isolated teeth were included, and all clearly recognisable fragments of calcaneum, femur, pelvis, humerus and scapula of mammals, and vertebra and femur of lizards. Any of the highly characteristic fragments (such as the tibiotarsus in the case of birds or vertebra in the case of snakes) representing the lower vertebrates also were included. Other material was excluded from our analysis, even in cases such as the tibia in macropods, which is readily identifiable, in order to keep the findings comparable from taxonomic group to group, especially among the mammals.

From the material identified, estimates were made of the minimum number of individuals of each taxon represented in each stratigraphic subdivision or arbitrary spit excavated from each trench. At least one fragment representing each such individual was given a catalogue number and appropriate catalogue entry, but it was not feasible so to catalogue every fragment recovered. Identified but uncatalogued fragments

all have been stored with their catalogued counterparts, and the remaining unidentified fragments from each subdivision or spit have been stored with some catalogued specimen from that subdivision. Thus any specimen retrieved from the screens, whether or not formally catalogued, is available for further study.

Except for bone artifacts (stored in the archaeological collection) and human skeletal remains (so far only two isolated incisor teeth, stored in the anthropological collection) all bone and other biotic material from the Devil's Lair excavations is stored in the Western Australian Museum palaeontological collection. Catalogue numbers for vertebrate material from the 1972 and 1973 excavations are as follows: 73.7.148-1006, 73.8.1-998, 73.9.1-1156, 73.10.1-1452, 73.11.1-1059, 73.12.1-512, 74.5.32. Thus 6 037 specimens have been catalogued. We have not counted identified uncatalogued specimens, but they probably amount to several thousands while unidentified fragments amount to tens of thousands. Dortch and Merrilees (1972) reported upon 1 486 catalogued vertebrate specimens.

In making the estimates of minimum numbers of individual animals shown in Appendix 1 tables, we regard each "natural" stratigraphic unit or arbitrary subdivision or spit excavated in each trench as an entity separate from every other such entity. In fact, many of these units were merely portions of a continuum. Even in

some cases where clear cut lithological differences appeared to mark breaks in the continuum, these differences may have arisen in various secondary ways within a continuous sediment. In other cases, bone fragments left lying on a surface marking a significant pause in sedimentation may have been mixed with bone fragments from the stratigraphic unit below them by trampling, digging or other processes both natural and artificial. Furthermore, it is likely that the bones of any individual would be scattered over an appreciable lateral area, whatever agent was bringing the bones into the cave, and that frequently this lateral scattering would be beyond the confines of our trenches.

Thus it is to be expected that different parts of the same skeleton would turn up in different stratigraphic units and different trenches, and would not normally be recognised as parts of the same animal. Thousands of individuals were represented in most of our major trenches, so that averaging effects probably were operating, but even so, the excavating and counting procedures we adopted may have led us to overestimate the minimum numbers of animals represented in the deposit.

We estimated minimum numbers of individuals in each stratigraphic unit by first assigning each identifiable fragment to a species and then determining for each species sample which anatomical element was most numerous. We then considered each other anatomical element from the point of view of whether it could represent an individual additional to those previously counted. An example is given in Appendix 3 for *Sminthopsis murina*, and other authors (e.g. Bökönyi 1970, Chaplin 1971) have given other examples of this method.

Criticisms of such methods of attempting to quantify animal bone samples have been made by Uerpmann (1973), Perkins (in Matolcsi 1973) and others. Uerpmann advocates weighing all the bones of each species in order to estimate the meat they represent, but it would not be feasible for us to separate all the fragments found into species. Perkins suggests that each bone found should be taken to represent a separate individual unless the time range of the sample is known, there was a high rate of preservation of bone and there was virtually complete recovery from the excavation. All these conditions are met by our sample, and we would probably greatly overestimate the animals actually contributing to the sample if we accepted even each identifiable fragment as representing a different individual, ignoring unidentifiable fragments.

Thus we have adhered to the usual "minimum number" estimate, recognising that this is only a comparative figure, possibly differing quite substantially from the number of animals actually contributing to the sample. In order to gauge the degree of overestimation we made the investigations reported in Appendix 3. We conclude that our methods may lead to overestimation which becomes more likely with increasing size of the animal concerned and decreasing thickness of the excavation unit sampled.

Stratigraphic reliability of the sample

We have suggested that the estimates given in the Appendix 1 tables of minimum numbers of individuals involved in our sample must be used with caution on statistical grounds. There are in addition some stratigraphic considerations which suggest caution in the use of these estimates.

We are not yet able to quantify the effects of deliberate digging by human beings on vertical mixing of the sample nor of digging or reworking by other agencies. But it is clear that there was much digging in the deposit by the human occupants of the cave.

The digging in prehistoric time of the large, steep sided Pit 2 must have resulted in a substantial number of bone fragments being brought up from depths of as much as 3 m and distributed over the floor from which Pit 2 was dug. See Figure 2. Dortch and Merrilees (1973) reported the finding of the lower part of Pit 2, but were unable to trace the upper part of this pit. Subsequent examination has revealed the top and upper western wall of the pit. The "pale lens" shown in Figure 2 at a depth of about 170 cm in Trench 2 is interpreted by us as occupying the slightly slumped top that might be expected to result from the filling of an open hole by sediment and occupational *débris*. The stratigraphic implications of this interpretation are (a) that Pit 2 was dug from a floor (not so far recognised in our excavations) at a depth of about 150 cm, i.e. at an intermediate depth in first orange brown earthy layer and (b) that Pit 2 fill is stratigraphically equivalent to an intermediate depth in undisturbed first orange brown earthy layer. However, it is possible that the pit was refilled with the original material by the people who dug it because otherwise it would have been a hazard in an unlit cave.

There is probably confusion in our sample from some intermediate depth in what has been labelled "first orange brown earthy layer" in Trenches 2 and 5, and possibly also in Trenches 7 and 8, of old bone fragments brought up from Pit 2 with the bone fragments representing the then current human occupation of the cave. It is even possible that this contamination by older *débris* extends as far as Trench 6, about 3 m south of the known boundary of Pit 2 in Trench 2.

During the 1972 excavations, it took some time to appreciate the full extent of hearth and pit digging illustrated here in Figure 2, and Dortch and Merrilees (1973) draw attention to the resulting stratigraphic confusion of samples from the large Hearth 1 in Trench 6 and the underlying brownish earthy layer into the top of which Hearth 1 was dug. In our appendix tables, this confusion is noted. There must be some similar confusion in the upper parts of Trench 5 which has gone unremarked in our appendix tables because it was not recognised in the field and its extent was not recorded. In these cases the mixing is not likely to involve bone fragments of very different ages.

We believe that specimens 73.9.1066 (recorded as coming from Pit 2 fill), 73.9.1004, 1005 (recorded as coming from banded layer) and 73.9.1039, 1040, 1048, 1049 (recorded as coming from fourth orange brown earthy layer), from the lower parts of Trench 2 represent the same animal. It is possible to match broken edges in two specimens, the various parts look alike in texture and colour, all fragments represent an extremely young animal, and some bones are unbroken and clearly associated with one another, a very unusual occurrence in Devil's Lair. The animal concerned was a young individual of *Bettongia lesueur* (not *Pseudocheirus peregrinus* as recorded by Dortch and Merrilees 1973 p.99). The stratigraphic implication is that the exact boundaries of Pit 2 were uncertain, as suggested by dotted lines in the section drawings, Figure 2 herein and Figure 5 of Dortch and Merrilees (1973).

It is possible that other material from the bottom of Pit 2, contemporaneous with an intermediate level in first orange brown earthy layer, has been confused with older material from banded layer or from fourth orange brown earthy layer, and we do not know the extent of any such confusion. However, because the charcoal rich band from which a charcoal sample was taken for dating is very well defined and clearly is not present in Pit 2 fill, we consider that the date recorded ($24\ 600 \pm 800$ yr B.P., SUA-31) reliably represents undisturbed material. We believe that four quartz and some probable calcrete artifacts catalogued as B1545 and B1546 from below this charcoal rich band also came from undisturbed material.

Two detached lumps of flowstone (now in the geological collection of the Western Australian Museum under catalogue numbers 13324, 13325) were found near the western face of Trench 7a in its uppermost part, resting on thick macrocrystalline flowstone obviously in its undisturbed position (flowstone D, illustrated in Figure 3 of Dortch 1974). These lumps were upside down. The stratigraphic implication is that they and possibly some or all of the bone fragments and other material from the uppermost western part of Trench 7a are disturbed and of unknown age. We suspect that they represent spoil from the unsystematic excavation of the upper part of Trench 2 (shown by Dortch and Merrilees 1972, Figure 1, as "Small Excavation"), which was made before the present systematic series began in 1970, or that they are spoil from ancient digging.

From the presence of an unbroken thin lithified band (labelled B in our field records) in the uppermost eastern part of Trench 7a and extending into Trench 7b and 7c, we are satisfied that most of the dark earthy layer in Trench 7 is undisturbed, as illustrated in Figure 3 of Dortch (1974). Nevertheless, some (probably most) of the animals recorded for dark earthy layer in Trench 7 in Appendix 1 tables represent disturbed material of unknown stratigraphic origin. This disturbance probably affected dark earthy layer in Trench 5 but was not detected during excavation. Therefore we make no inferences from the fauna recorded from dark earthy layer.

Source of the bone sample

Dortch and Merrilees (1973) and Dortch (1974) show that humans occupied Devil's Lair at times, and it is possible that much of the bone sample here discussed represents discarded remnants of human meals. A small proportion of the bone fragments recovered are charred, possibly in the process of cooking carcasses, or possibly from being discarded into camp fires, as mentioned by Hammond (1933) for modern Aborigines. Charring has been noted affecting the following taxa in Devil's Lair; the catalogue number in brackets represents one example:—*Dasyurus* (73.8.294), *Isoodon* (73.8.359), *Perameles* (73.8.448), *Potorous* (73.12.173), *Bettongia penicillata* (73.10.1264), *B ? lesueur* (73.12.154), *Petrogale* (73.9.1151), *Macropus fuliginosus* (73.9.783), *Setonix* (73.12.182), *Rattus fuscipes* (73.11.60), lizard (73.8.821), snake (74.5.32).

Presumably marrow would have been eaten by ancient Aborigines, as by other people (e.g. modern American Indians—Neumann and DiSalvo 1958). Also it is possible that small bones were attractive as food items to a people accustomed to using their teeth as vigorously as described by Campbell (1939) for modern Aborigines and by Neumann and DiSalvo (1958). But it is difficult to account for the extreme fragmentation of practically all bones in the sample (see Figure 3) unless food preparation methods then in use included systematic pounding of the carcasses before or after cooking, as described by Gould (1968a) for modern inland Aborigines. Tedford (in Gould 1968b) comments on fragmentation and charring of bones from an inland archaeological site, suggesting that pounding of food animals is a long standing practice of these inland peoples. Brain (1970) suggests that extreme fragmentation of bone in a deposit, and Gorman (1971) that fragmentation with some charring, is a hallmark of human contribution.

Lundelius (1966) believed that fragmentation of bone, presence of predator remains, and bone bearing coprolites together indicated that a bone deposit had been accumulated by that predator, in this case *Sarcophilus*. Indeed, the name "Devil's Lair" was conferred on the site because of his belief. Much of the bone from our excavations is reminiscent of that recovered from the modern *Sarcophilus* leavings described by Douglas, Kendrick and Merrilees (1966).

It is possible that while primary fragmentation of our bone sample was the work of Aborigines, secondary fragmentation resulted from devils working over the leavings of human beings after (or perhaps even during) human occupation of the cave. Devils now live successfully in close contact with human activities in parts of Tasmania (Guiler 1970). They may long have done so, and indeed may have occupied the place later held by dogs in Aboriginal camps. If dogs had been living in Devil's Lair it seems very probable that some remains would have been detected.

Thus we cannot be sure of how much of the bone in our sample represents human meals, but from the charring of some of it and the form of bias demonstrated below in the remains of

Macropus fuliginosus, we are confident that some of it does. Adult *M. fuliginosus* are too large to be killed by devils; however, some remains of this species may have been brought into the cave as carrion. The presence of shell fragments of mussel and the eggs of emus (Dortch 1974) marine shell (Dortch and Merrilees 1972) and the single fish vertebra (73.11.177) which is the basis for the fish entry in Trench 8, in the appendix tables, also point to man as a contributing predator. No other single predator species is likely to have sampled the wide range of habitats suggested by the mammals in the deposit.

Possibly other predators, such as *Dasyurus* or owls contributed to the bone sample, but Devil's Lair does not show an overwhelming preponderance of small (mouse or rat sized) mammals as do some other deposits (e.g. those described by Archer and Baynes 1972) interpreted as accumulated by owls or *Dasyurus*.

Our provisional belief is that the bone sample in the main represents the leavings of human beings, but that other predators may have contributed remains of their own prey or modified the human refuse.

Bias in the sample

The bone recovered from Devil's Lair is generally well preserved, yet there is marked imbalance in the frequency of occurrence of different parts of the skeleton within most species.

For example, we examined *Macropus fuliginosus* specimens from Trench 6, assembling all bones attributable to this species, not only those cranial and post cranial elements admitted to our faunal analysis, but also vertebrae, ribs and other elements not so admitted. There were large discrepancies between the numbers of bones and teeth of all kinds actually present and the numbers which would have been present if all teeth and bones of all *M. fuliginosus* individuals represented in our sample had been left lying within the confines of Trench 6. Discrepancies in numbers of teeth, of bones of the hands and feet, and of vertebrae, are set out in Table 1.

There appeared to be similarly large discrepancies between numbers actually present and expected numbers of long limb bones, pelvis, and so on for all parts of the skeleton, but because these were all fragmented, the discrepancies are not easily quantified and tabulated. For example in the "top" subdivision of brownish earthy layer, at least 7 individuals of *M. fuliginosus* were represented. But there were only 2 distal and no proximal fragments of humerus, only 1 fragment of radius, only 2 proximal and no distal fragments of femur and so on.

Perhaps the most striking discrepancy was in the distinctive large lower incisor teeth. Only 1 of these (73.8.977, from a young animal) was recovered from the whole 2.27 cubic metres of deposit excavated from Trench 6. Yet, as shown in Appendix 3 at least 17 individuals of *M. fuliginosus* must have contributed to the sample, and it is very likely that 24 or even more individuals actually contributed.

If most of the animals represented were taken into the cave as whole carcasses, cooked and eaten on the spot, and the bones discarded, one would expect considerable lateral scattering of the bones of any individual. But if most parts of the cave were used, there should be considerable overlap of the discarded scattered bones of several individuals of any of the more common species on any occupation floor. In an excavation sampling these old occupation floors, one would expect mixtures of individuals to be represented, but if distribution were random any particular anatomical element, such as the first lumbar vertebra, would be about as well represented as any other element, such as the fourth metatarsal of the right foot.

Our examination of *M. fuliginosus* from Trench 6 suggests that one or more selective processes have operated.

Many writers, especially under the stimulus of the "osteodontokeratic" concept of Dart (1957), have discussed such selective processes. Butchering of large carcasses at the kill site followed by removal of some but not all the bones back to the campsite in dismembered joints (including the "schlepp effect") is often cited as biasing

Table 1

Macropus fuliginosus in Trench 6

Stratigraphic subdivision	Minimum number of individuals (juveniles in brackets)	Tooth most abundantly represented, and number present	Teeth		Bones of hand and foot		Vertebrae	
			Total present	Expected number	Total present	Expected number	Total present	Expected number
Dark earthy layer	1 (2)	0	0	20	0	104	0	50
Pale band	1 (2)	0	0	20	1	104	0	50
Flecked lens	1 (1)	0	0	24	2	104	1	50
Second dark earthy layer	2 (1)	2 x RI ²	10	44	1	208	0	100
Cave pearl and bone layer	2 (1)	(1 each of several)	8	44	7	208	4	100
Top, brownish earthy layer	7 (5)	7 x LI ¹	30	160	26	728	15	350
Upper middle, brownish earthy layer	2 (1)	2 x LI ¹	7	44	1	208	3	100
Lower middle, brownish earthy layer	8 (6)	7 x LI ¹	43	184	107	832	52	400
Bottom, brownish earthy layer	2 (2)	2 x RI ¹	8	48	20	208	11	100

bone samples, for example by White (1952, 1953a, b, 1955), Innskeep and Hendy (1966), Perkins and Daly (1968), Daly (1969), or Perkins (1969). Dart (1954, 1957), Kitching (1963), Wolberg (1970), and others have stressed selection of some bones for use as tools. Brain (1967a, b, c, 1970), Isaac (1967), Schaller and Lowther (1969) and others stress carnivores acting alone, or carnivores acting on accumulations of bone left by human beings. White (1953c, 1956) describes personal or group habits and customs biasing bone samples.

In the case of Devil's Lair it seems unlikely that the discrepancy between bones present and bones expected has anything to do with off site butchering methods because most of the animals eaten were small and even a large kangaroo carcase can be carried by a man. But selection of bones for making tools can be inferred. For example it seems likely that the dearth of kangaroo lower incisors, mentioned above, was due to the removal of these teeth, or even of whole jaws containing them, for use as tools. Dortch and Merrilees (1972) illustrate a wallaby lower incisor with transverse incisions which may have been used to bind it to a stick, or may have resulted from such binding. Kangaroo lower incisors may well have been used similarly. The one kangaroo lower incisor found in Trench 6 had a very open root, such as one finds in very young animals, and hence may have been too fragile to serve as a tool. Other bone implements from the deposit are described by Dortch and Merrilees (1973) and Dortch (1974).

It is probable also that much bone was eaten by man or by devils and reduced to fragments small enough to pass through our screens. Douglas, Kendrick and Merrilees (1966) report observations on living devils and their effects upon bone, and the specimens concerned, still preserved in the Western Australian Museum, include a good deal of finely comminuted bone recovered from the faeces of the devils observed. Not only devils, but also human beings accustomed to using their teeth more vigorously than do most modern people, might fragment and ingest appreciable quantities of bone.

Many of the bone fragments in our sample show rounding and smoothing of what initially must have been jagged fracture edges. Many tooth bearing fragments (e.g. *Bettongia penicillata* specimens 73.8.719, 73.9.51, 73.12.379) show this rounding, and also many small fragments of post cranial bones of many kinds. At present we are uncertain about the smoothing process involved. It might be from human handling and use, for example to flesh animal skins or smooth wooden spear shafts. It might be from the trampling of fragments into a sandy floor, as described by Brain (1967b, c), or from passage through and corrosion in the gut of devils or human beings. Whatever the rounding process, it is reasonable to suggest it converts some proportion of the original bone sample into particles below the limit of our recovery methods.

The bone sample as an index of human use of the cave.

By assuming that all the bone recovered in our excavations came from animals eaten in the cave by humans, and by making the other assumptions set out below about the bone sample, we arrive at a very rough estimate of the extent to which the cave might have been used from about 19 000 yr B.P. to about 12 000 yr B.P. To do this, we have combined data from first orange brown earthy layer in Trench 5 and brownish earthy layer in Trench 6.

For the purpose of comparing estimates of minimum numbers of individuals of a particular species in one stratigraphic unit with the same species in another, we have made no attempt to correct any overestimation shown in the Appendix 1 tables. However, for the purpose of interpreting our bone sample in terms of the meat it represented, we must compare estimates for different species, and therefore have applied correction factors to the numbers obtained from the appendix tables. These correction factors are based on our study of the degree of overestimation in *Sminthopsis*, *Pseudocheirus* and *Macropus fuliginosus* reported in Appendix 3. We multiply the numbers shown in the appendix tables for *Macropus fuliginosus*, the only large animal present by $\frac{1}{2}$, and for the animals of intermediate body size (*Dasyurus*, *Sarcophilus*, *Thylacinus*, *Isoodon*, *Perameles*, *Trichosurus*, *Pseudocheirus*, *Potorous*, and species of *Bettongia*, *Petrogale*, *Macropus eugenii*, *M. irma* and *Setonix*) by $\frac{2}{3}$. We leave unchanged the numbers shown for all other vertebrate taxa which are of small size. Thus corrected, the numbers of individuals for first orange brown earthy layer in Trench 5 and brownish earthy layer in Trench 6 together are:

large kangaroos	27
animals of intermediate size	653
small vertebrate animals	566

To translate these findings into numbers of human meals, we assume that about 1 kg live weight of any animal would constitute one meal of meat for one person (cf. McArthur in Mountford 1960; Gould 1967). Each large kangaroo might then represent 20 meals, each animal of intermediate size 2 meals, while 5 small animals might be required for one meal. On these assumptions, at least 2 000 meals of meat are represented by the bone sample under consideration. It is unlikely that the human occupants of the cave lived entirely on vertebrate prey animals. If we assume that half their diet was plant food, remains of which have dissipated or have not been recognised in our excavations, and invertebrate animals, then at least 4 000 meals are represented by our bone sample.

The area excavated in Trenches 5 and 6 is probably not more than 1% of the area of cave floor below which a thick deposit might exist. If we assume that the 19 000 to 12 000 yr B.P. section of the deposit is typified in Trenches 5 and 6, then the bone sample from these trenches represents only about 1% of what could be re-

covered from the cave. Thus at least $4\ 000 \times 100 = 400\ 000$ meals were eaten in the cave over a period of about 7 000 years. This is an average of about 60 meals per year.

A family group of 5 people spending 6 consecutive days in the cave and eating 2 meals (one of meat) each day in the cave would account for 60 meals. Thus one visit to the cave each year by such a family group would be enough to account for the minimum number of individual prey animals represented by our bone sample.

However it is likely that our estimates of minimum numbers of individuals greatly underestimate the actual number of animals eaten in the cave (cf. Perkins in Matolcsi 1973). Also the tables of Appendix 1 suggest that the rate of occupancy of the cave was far from uniform. It is reasonable to suggest alternatives to this concept of a small family group staying in the cave for a few days at a time once a year. Such a group might have stayed there for longer periods less often and the digging and presumably use of the large Pit 2 (described by Dortch and Merrilees 1973) reinforces this suggestion. Or the cave may have served as a meeting place for a larger number of people for a few days even less often.

At present we are unable to choose between these or other possible alternatives. Indeed, there are so many unexamined and in some cases unexaminable assumptions underlying our calculations that we conclude merely that our sample indicates intermittent rather than continuous human occupation of the cave between 19 000 and 12 000 years ago.

The fossil mammal fauna of Devil's Lair

We have recognised 35 species of mammals among material recovered from the 1970, 1972 and 1973 excavations in Devil's Lair, and these are listed in Table 2. Descriptions of the animals concerned, together with vernacular names, authors of systematic names, and a selected list of scientific studies are given by Ride (1970).

Table 2

Mammal species recorded from the 1970, 1972 and 1973 excavations in Devil's Lair

Carnivorous marsupials

Dasyurus geoffroii
Phascogale tapoataja
Antechinus flavipes
Sminthopsis murina
Sarcophilus harrisi
Thylacinus cynocephalus

Bandicoots

Isodon obesulus
Perameles—species not so far identified

Possums

Trichosurus vulpecula
Pseudocheirus peregrinus
Cercartetus concinnus

Rat-kangaroos

Potorous tridactylus
Bettongia penicillata
Bettongia lesueur

Wallabies and kangaroos

Petrogale—species not so far identified
Lagorchestes—species not so far identified
Macropus eugenii
Macropus irma
Macropus fuliginosus
Setonix brachyurus

Native rats and mice

Hydromys chrysogaster
Pseudomys albocinereus
Pseudomys occidentalis
Pseudomys shortridgei
Pseudomys praeconis
Notomys—species not so far identified
Rattus (probably all *R. fuscipes*)

Bats

Macroderma gigas
Nyctophilus timoriensis
Nyctophilus geoffroyi
Eptesicus pumilus
Chalinolobus gouldii
Chalinolobus morio
Pipistrellus tasmaniensis
Tadarida australis

Our estimates of minimum numbers of each mammal species from the 1972 and 1973 excavations, and also of other vertebrate taxa, arranged stratigraphically, are tabulated in Appendix 1. Dortch and Merrilees (1972) similarly tabulate such estimates for the 1970 excavation.

Some species are represented by a few individuals only, others by many individuals. We have attempted to show in Figures 4 and 5 the changes in relative proportions of the species more abundantly represented from about 19 000 to about 12 000 years ago in the 1972 and 1973 excavations. Our sample from about 25 000 to about 19 000 years ago, as shown in Appendix 1, is so small that we have not attempted to show relative proportions of the various species involved.

The modern mammal fauna of the Devil's Lair district

As with most other localities in Australia, the mammal fauna now living in the Devil's Lair district is not the same as that present just before the arrival of European man. Drastic changes to habitats, efforts to exterminate native "pests", and introduction of exotic species have all had profound effects on the mammal populations. Therefore we use the term "modern mammal fauna" to mean that occurring in immediately pre-European times. This fauna is the only one meaningful for comparison with the fossil fauna, since it represents the end product of the prehistory of the area.

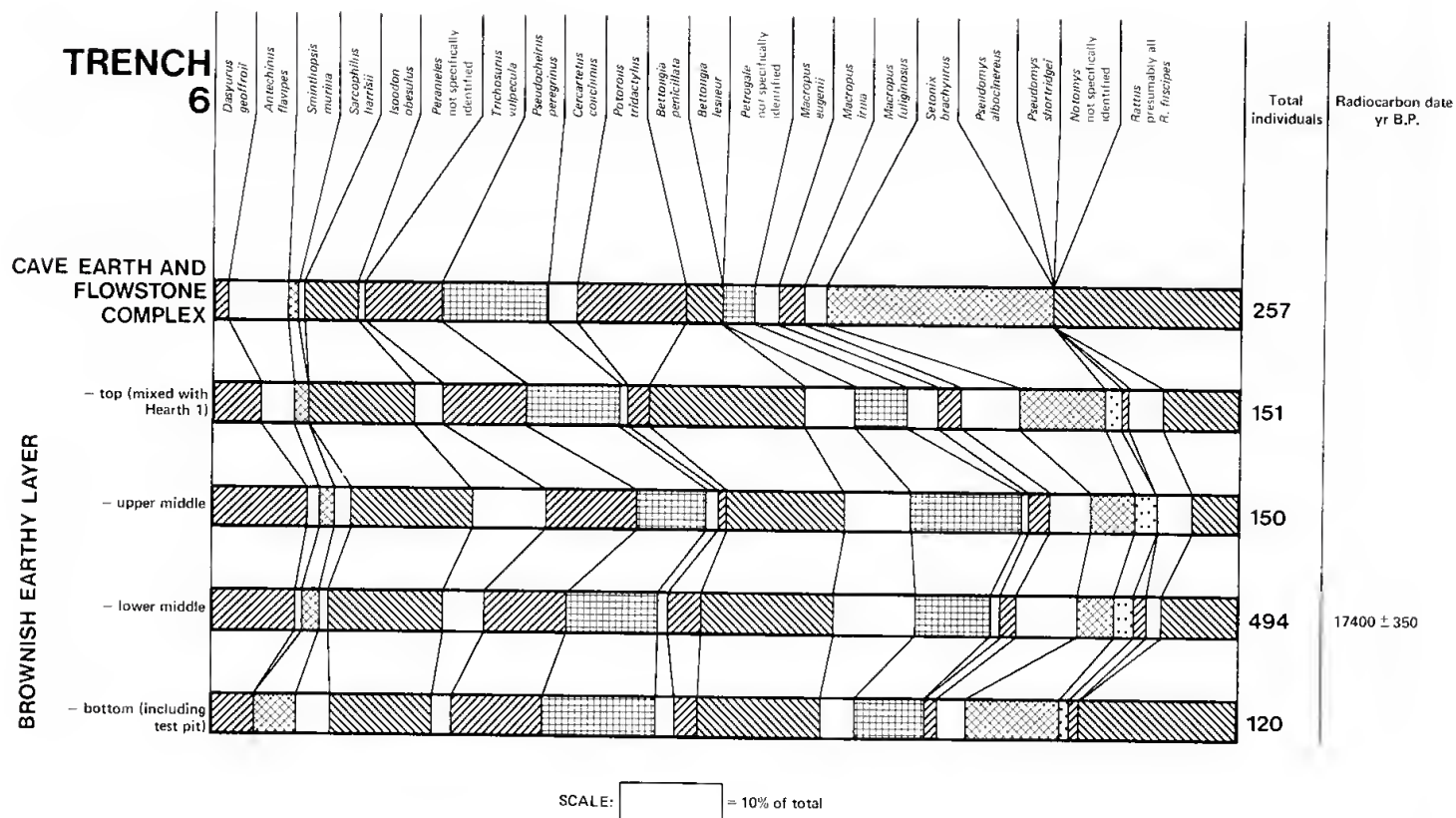


Figure 4.—Relative proportions of the well represented mammal species in two major stratigraphic divisions in Trench 6, Devil's Lair.

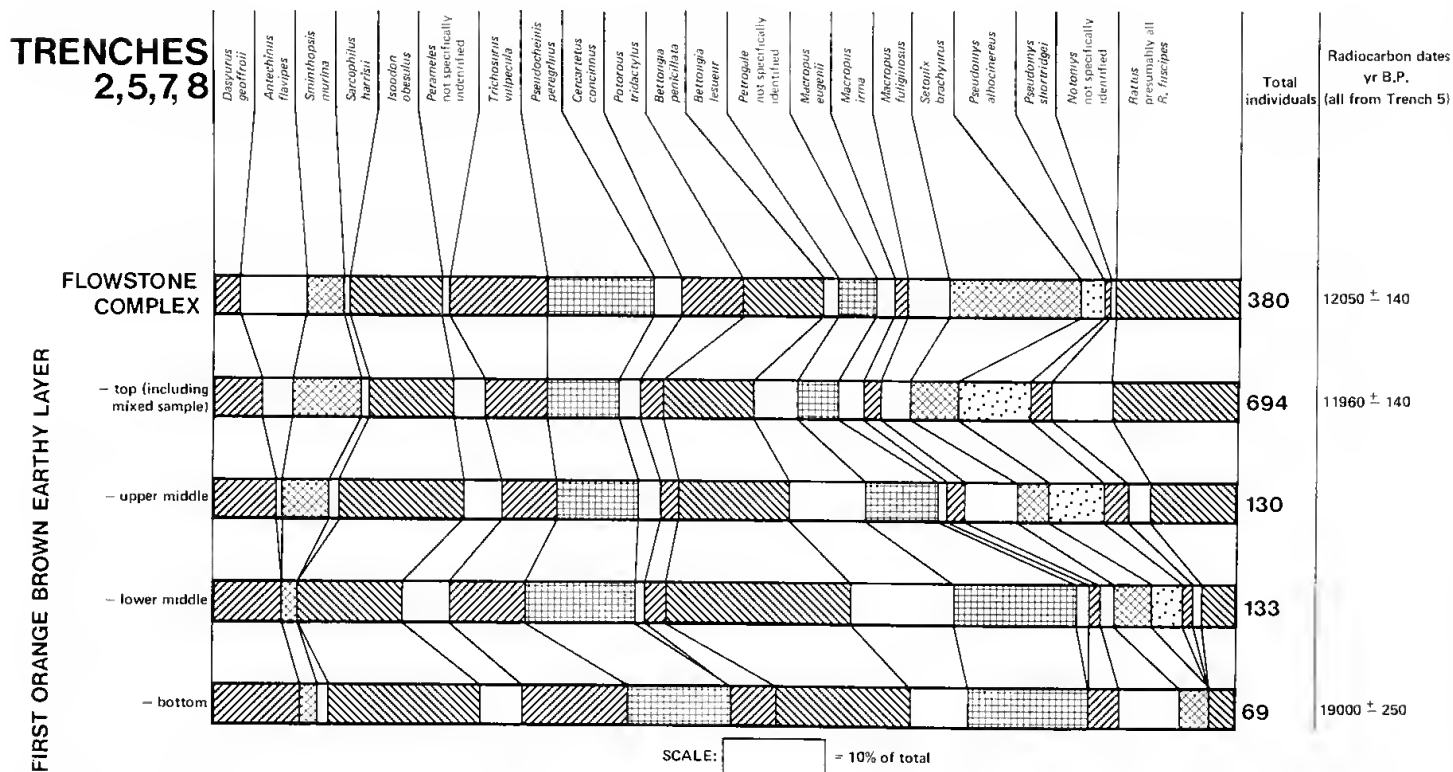


Figure 5.—Relative proportions of the well represented mammal species in two major stratigraphic divisions in Trenches 2, 5, 7 and 8 combined, Devil's Lair.

Appendix 2 gives details of museum and other records forming the basis of our reconstruction of the modern mammal fauna of the Devil's Lair district. These enable us to refine previous attempts (e.g., Merrilees 1968, Archer and Baynes 1972). We have taken into account the likely ranges from Devil's Lair covered by predators bringing prey back to the cave; and by "Devil's Lair district" we mean this predator determined area.

Table 3

Mammal species we are confident were present in the modern fauna of the Devil's Lair district

Carnivorous marsupials

Dasyurus geoffroii
Phascogale tapoatafa
Sminthopsis murina

Possoms

Tarsipes spencerae
Trichosurus vulpecula
Pseudocheirus peregrinus
Cercartetus concinnus

Rat-kangaroos

Bettongia penicillata

Wallabies and kangaroos

Macropus fuliginosus
Setonix brachyurus

Native rats and mice

Hydromys chrysogaster
Rattus fuscipes

Table 4

Mammal species probably in the modern fauna of the Devil's Lair district

Carnivorous marsupials

Antechinus flavipes

Bandicoots

Isodon obesulus

Rat-kangaroos

Potorous tridactylus

Wallabies and kangaroos

Macropus irma

Native rats and mice

Pseudomys shortridgei
Pseudomys praeconis
Rattus tunneyi

Bats

Nyctophilus timoriensis
Nyctophilus geoffroyi
Eptesicus pumilus
Chalinolobus morio
Pipistrellus tasmaniensis

Carnivorous eutherians

Canis familiaris

Table 5

Mammal species possibly forming part of the modern fauna of the Devil's Lair district

Wallabies and kangaroos

Macropus eugenii

Bats

Chalinolobus gouldii
Tadarida australis

We are confident that the species listed in Table 3 were part of the modern fauna, and we think it probable that the species listed in Table 4 were too. Table 5 lists mammals recorded within 75 km of Devil's Lair in modern time, but whose inclusion in the modern fauna of the Devil's Lair district is doubtful for reasons discussed in Appendix 2.

Comparison of modern and fossil mammal faunas from Devil's Lair

By combining the species listed in Tables 3 and 4, we suggest that the mammal fauna of the district just before it was affected by European man probably included 25 species, and it may have included the 3 additional species listed in Table 5. Of this total of 28 species, only *Tarsipes spencerae*, *Rattus tunneyi* and *Canis familiaris* are not so far recorded in the fossil fauna from Devil's Lair.

The fossil fauna listed in Appendix 1 includes 33 species, and 2 additional species were recovered from the 1970 excavation, namely *Lagorchestes* sp. and *Chalinolobus morio*, discussed below. Of these 35 fossil species (see Table 2), the 10 species listed in Table 6 appear not to have formed part of the modern fauna of the Devil's Lair district.

Small, frail remains of *Tarsipes spencerae* may have escaped detection. Although the species is known to live at present in heaths in many localities between Yanchep and Dongara, only one fossil specimen (Archer 1973) has been recognized from any of the numerous caves in this region, many of them containing large accumulations of bone from owl pellet deposits. But we suggest that the absence of *Rattus tunneyi* and *Canis familiaris* from the fossil fauna so far recognized represents a real absence of these two species from the Devil's Lair district in ancient times.

Dortch and Merrilees (1972) suggested that a single canine tooth (70.12.202) found by them in 1970 might have represented a Dingo, but this tooth has been examined subsequently by Professor N. W. G. Macintosh and colleagues, and is considered by them (Macintosh, personal communication) in fact to represent *Sarcophilus*. No specimen representing *Canis* was found in the 1972 and 1973 excavations. However, the carnivorous marsupial of size comparable with *Canis* namely *Thylacinus*, is represented only by two isolated teeth. The possibility remains that both the marsupial and the

eutherian carnivores were present, but were difficult to catch or distasteful to eat, and therefore are not well represented, or not represented at all, in the litter left lying in the cave. However, the Dingo is generally believed to have been introduced into Australia by Aborigines migrating in Recent time (Jones 1970), and our evidence is consistent with this view.

Archer and Baynes (1972) postulate that *Rattus tunneyi* extended its range along the western coastal plain into the extreme south west of Western Australia, including Devil's Lair district, only in Recent time. This is supported by unpublished studies by one of us (J.K.P.) of a stratified deposit in a cave near Augusta, in which *Rattus tunneyi* occurs only in the top layers of the deposit, dated on charcoal as 2900 ± 80 radiocarbon years B.P. (date SUA-227) or later.

Dortch and Merrilees (1972) report the presence of a single specimen (70.12.1132) tentatively ascribed to *Lagorchestes* sp. Unless the specimen is aberrant, we concur in this identification. Among the specimens simply listed as "bats" by Dortch and Merrilees (1972), we have recognized three as *Chalinolobus morio*. The three specimens (70.12.776, 70.12.911 and 71.1.223) come from three different levels in Trench A1. Neither *Lagorchestes* sp. nor *Chalinolobus morio* was recognized in the material excavated in 1972 and 1973.

Even though some species of mammals present as fossils were not present in the modern fauna of the Devil's Lair district, all are present in the modern fauna of Australia as a whole (including Tasmania), and only two of these species seem to have disappeared from the Australian mainland. These are *Thylacinus cynocephalus* and *Sarcophilus harrisii*, both of which are known to have survived on the mainland until late Recent time (Partridge 1967, Archer and Baynes 1972).

Table 6

Mammal species not forming part of the modern fauna of the Devil's Lair district, but recorded from the 1970, 1972 and 1973 excavations in Devil's Lair

Carnivorous marsupials
<i>Sarcophilus harrisii</i>
<i>Thylacinus cynocephalus</i>
Bandicoots
<i>Perameles</i> sp.
Rat-kangaroos
<i>Bettongia lesueur</i>
Wallabies and kangaroos
<i>Petrogale</i> sp.
<i>Lagorchestes</i> sp.
Native rats and mice
<i>Pseudomys albocinereus</i>
<i>Pseudomys occidentalis</i>
<i>Notomys</i> sp.
Bats
<i>Macroderma gigas</i>

Thus it seems that 2 or possibly 3 mammal species have arrived in the Devil's Lair district, and at least 10 species have disappeared (see Table 6) since the fossiliferous parts of the deposit were sealed by thick flowstone about 12 000 years ago.

Modern distribution patterns and habitat adaptations of mammal species

On the basis of general patterns revealed by unpublished studies of modern mammal distributions in south western Australia made by one of us (A.B.), we have divided the species listed in Table 2 into two categories. These are "forest mammals" and "non-forest mammals". The forest mammals, listed in Table 7, are defined as those species whose modern distributions include the "forest block", which is the area mapped by Gardner (1944, Plate X) as sclerophyllous forest and mesophytic forest. It includes the formations mapped by Smith (1973) in the Busselton-Augusta region as high open forest and open forest. *Sarcophilus harrisii* and *Thylacinus cynocephalus* are regarded as forest mammals on the basis of their modern Tasmanian distributions, even though they apparently did not persist in Western Australia into modern times. The non-forest mammals, listed in Table 8, are defined as those species recorded from Devil's Lair whose distributions do not include the forest block. The distribution studies suggest that the natural eastern margin of the forest block, where it merged into woodland or shrub formations (before most of the area was cleared for agriculture), represents an important demarcation of modern faunas. The ranges of most forest mammals extended beyond this line, but it appears to have represented a barrier to non-forest mammals in immediately pre-European times.

No thorough investigation has been made of differences between the mammal faunas of the Karri high open forest and the Jarrah-Marri open forest. It is possible that fewer mammal species occur naturally in the Karri forest, but in the absence of data we assume that all the forest mammals occurred in both.

Species which are restricted in range of distribution or habitat are the most useful indicators of environmental conditions. The forest mammal with the most restricted distribution is *Potorous tridactylus*. In Western Australia, where it may now be extinct, *P. tridactylus* appears to have been limited to the area of the extreme south west in which some rainfall occurs throughout the summer. There it probably inhabited densely vegetated watercourses and wet heaths. *Setonix brachyurus* also finds densely vegetated forest gullies an optimum habitat; but it has a wider distributional range, from Gingin Brook in the north (Roe 1971) to the Hunter River east of Bremer Bay. The latter locality represents an eastward extension of the previously known range. It is based upon a dentary (M10519), considered to represent a modern animal, which was picked up in 1970 by W. H. Butler. The distribution of

Setonix brachyurus within the northern part of the forest block appears to have been restricted to the western areas; its range probably did not reach the eastern margin.

The distribution of *Rattus fuscipes* in Western Australia is unlike that of any other mammal. It occurs in the southern part of the forest block, principally along river systems, and also in coastal dune systems and heaths from Jurien Bay round to Israelite Bay. There appears to be no reliable evidence for its occurrence in the northern areas of the forest block. Both of the specimens from that area cited by Taylor and Horner (1973), Western Australian Museum M5815 and C.S.I.R.O. CM859, have been examined by one of us (A.B.) and are considered to be *Rattus rattus*. Near Devil's Lair *Rattus fuscipes* has been collected live both in regenerating Peppermint open scrub and Karri high open forest.

It is possible that the ranges of the three forest mammals *Macropus eugenii*, *Chalinolobus gouldii*, and *Tadarida australis*, listed in Table 3, did not cover the extreme south west of the forest block. In addition little is known of the habitat requirements or full ranges of the other bat species included in Table 7. Some uncertainty also exists in the cases of *Sarcophilus harrisii* and *Thylacinus cynocephalus*.

Table 7

Forest mammals recorded from the Devil's Lair deposit

Carnivorous marsupials
* <i>Dasyurus geoffroyi</i>
<i>Phascogale tapoatafa</i>
* <i>Antechinus flavipes</i>
* <i>Sminthopsis murina</i>
* <i>Sarcophilus harrisii</i>
<i>Thylacinus cynocephalus</i>
Bandicoots
* <i>Isoodon obesulus</i>
Possums
* <i>Trichosurus vulpecula</i>
* <i>Pseudocheirus peregrinus</i>
* <i>Cercartetus concinnus</i>
Rat-kangaroos
* <i>Potorous tridactylus</i>
* <i>Bettongia penicillata</i>
Wallabies and kangaroos
* <i>Macropus eugenii</i>
* <i>M. irma</i>
* <i>M. fuliginosus</i>
* <i>Setonix brachyurus</i>
Native rats and mice
<i>Hydromys chrysogaster</i>
* <i>Rattus fuscipes</i>
Bats
<i>Nyctophilus timoriensis</i>
<i>N. geoffroyi</i>
<i>Eptesicus pumilus</i>
<i>Chalinolobus gouldii</i>
<i>C. morio</i>
<i>Pipistrellus tasmaniensis</i>
<i>Tadarida australis</i>
*Well represented through the deposit and included in Figures 4 and 5.

Records indicate that the other 13 forest mammals, not discussed above, occurred right through the forest block. Of these *Phascogale tapoatafa*, *Antechinus flavipes*, and *Pseudocheirus peregrinus* also occurred in the high rainfall woodlands. *Hydromys chrysogaster*, the Water Rat, is a specialized species normally only found in or adjacent to bodies of water. The remainder have been recorded from a broad spectrum of habitat types, and some range far into the dry inland of Australia: e.g., *Dasyurus geoffroyi* and *Trichosurus vulpecula* both formerly occurred widely in desert areas.

Table 8

Non-forest mammals recorded from the Devil's Lair deposit

Bandicoots
* <i>Perameles</i> sp.
Rat-kangaroos
* <i>Bettongia lesueur</i>
Wallabies and kangaroos
* <i>Petrogale</i> sp.
<i>Lagorchestes</i> sp.
Native rats and mice
* <i>Pseudomys albocinereus</i>
<i>P. occidentalis</i>
* <i>P. shortridgei</i>
<i>P. praeconis</i>
* <i>Notomys</i> sp.
Bats
<i>Macroderma gigas</i>
* Well represented through the deposit and included in Figures 4 and 5.

Since we are unable to identify some of the non-forest mammals listed in Table 8 beyond generic level, we here discuss the species most likely on biogeographical grounds to be represented in Devil's Lair—*Perameles bougainville*, *Petrogale penicillata*, *Lagorchestes hirsutus* and *Notomys mitchellii*.

Six non-forest mammals share a common distributional characteristic, that is they have been recorded along the inland side of the forest block. These are *Perameles bougainville*, *Bettongia lesueur*, *Pseudomys albocinereus*, *P. occidentalis*, *P. shortridgei* and *Notomys mitchellii*. Of the other four species, *Petrogale penicillata* and *Lagorchestes hirsutus* are recorded from just north east of the forest block, *Macroderma gigas* from the coastal plain north west of the forest block, and *Pseudomys praeconis* from just north of the forest block. The modern distributions of all five species of native rats and mice, and possibly *Bettongia lesueur*, also included the northern part of the western coastal plain.

Although only two of the non-forest mammals (*P. shortridgei* and *P. praeconis*) extended south on this plain along the western side of the forest block in modern time, we suggest below that all

our non-forest mammals occupied the southern part of the western coastal plain at some time during the accumulation of the Devil's Lair deposit.

The south western populations of *Petrogale*, restricted in modern time to rocky hills inland from the forest block, are probably conspecific with other populations occurring in arid localities such as the Macdonnell Ranges (Ride 1970), but we are not sure that any is conspecific with the Devil's Lair population. Most *Petrogale* species now seem to inhabit rock outcrops which shield them from extremes of temperature.

Macroderma gigas ranged over much of desert and tropical Western Australia (Douglas 1967), but its remains, presumably of Recent age, are widespread in caves between Yanchep and Dongara. In one deposit it was present throughout the Recent (unpublished data from Hastings Cave, A.B.) associated with a mammal fauna characteristic of heath habitats (Lundelius 1960, with the qualifications of Archer and Baynes 1972).

Sand appears to be a substrate requirement of *Pseudomys albocinereus* and most species of *Notomys*. While *P. albocinereus* occurs mainly in coastal sand plains carrying open heath, *Notomys mitchellii* occurs not only in such habitats but also on inland sand plains carrying open heath and other shrub formations. *Perameles bougainville* probably also occurred in sand plains in south western Australia (Ride 1970).

Although *Pseudomys occidentalis* remains are known from the surface in caves in the coastal sand plains, modern specimens have mainly been collected in areas which have a loam or gravelly sand substrate.

Insufficient information is available to determine the habitats occupied by *Bettongia lesueur*, *Largorchestes hirsutus*, *Pseudomys shortridgei* and *P. praeconis* in the south west of Australia.

Changes in the mammal fauna around Devil's Lair, and interpretation

We have attempted to quantify information on the mammals from our excavations, but have shown that the results must be viewed with

caution. We have not applied statistical tests. In order to assess changes in the mammal fauna, we distinguish between the small sample available for the period 25 000 to 19 000 years ago and the larger sample available for the period 19 000 to 12 000 years ago, and between species which are represented only in small numbers widely spaced in the deposit, and those which are present at most levels (even if only in small numbers).

The relative abundances of the well represented species for the later period in Trench 6 and in the Trench 2, 5, 7 and 8 complex are shown as bar diagrams in Figures 4 and 5 respectively. The stratigraphic groupings shown in these figures seem to us broad enough to minimize stratigraphic uncertainties in our sampling procedures and to allow comparisons to be made between Trench 6 and Trenches 2, 5, 7 and 8.

We infer real changes in relative abundance where species show similar trends from level to level in Trench 6 and in Trenches 2, 5, 7 and 8. We make no such inferences where trends are dissimilar.

We have compared the change in relative abundance of each species from one stratigraphic level to the next higher level in Trench 6 with the corresponding change in Trenches 2, 5, 7 and 8. The numbers of species synchronously increasing, decreasing and changing in opposite ways are set out in Table 9. There is no case of a species remaining unchanged. Our comparisons were made using Figures 4 and 5.

The substantial proportion of species changing in opposite ways at all levels (right hand column of Table 9) suggests that much of the observed change is random. However, there appears to be some decrease in randomness towards the top of the deposit. This is explained by the trend shown in the central column of Table 9. More species decline in the upper levels of the deposit.

Figures 4 and 5 show that, between the top subdivision of brownish/first orange brown earthy layer and (cave earth and) flowstone complex, 5 non-forest mammals (*Perameles* sp., *Bettongia lesueur*, *Pseudomys albocinereus*, *P. shortridgei*, and *Notomys* sp.) and 4 forest mam-

Table 9

Numbers of species changing in relative abundance in the same way in Trench 6 and in Trenches 2, 5, 7 and 8 from stratigraphic level to next higher stratigraphic level—data of Figures 4 and 5, dealing with 21 species well represented through the deposit.

Stratigraphic level	No. of species increasing in relative abundance	No. of species decreasing in relative abundance	No. of species showing opposing trends, or changes in one trench but not in the other
(Cave earth and) flowstone complex			
Brownish/first orange brown earthy layer			
-top	5	9	7
-upper middle	5	6	10
-lower middle	7	5	9
-bottom	7	2	12

mals (*Dasyurus geoffroi*, *Sminthopsis murina*, *Bettongia penicillata* and *Macropus eugenii*) decline. These forest mammals are all species recorded from a broad spectrum of habitats. At the same time, the 2 species (*Potorous tridactylus* and *Setonix brachyurus*) most restricted within forest show their greatest increase.

Of the 21 species shown in Figures 4 and 5, 15 species (* in Table 7) are forest and 6 species (* in Table 8) are non-forest mammals.

We next analyse the forest and non-forest mammals which change in relative abundance from level to level in the same way in Trench 6 as in Trenches 2, 5, 7 and 8. The results (in Table 10) suggest that these forest mammals show no discernible trend from about 19 000 years ago (the time of deposition of the bottom subdivision of brownish/first orange brown earthy layer) to about 12 000 years ago (the time of deposition of cave earth and flowstone complex). On the other hand, the non-forest mammals analysed at first increase and then decrease in relative abundance during this period.

We have no data from Devil's Lair on trends in relative abundance of mammal species between about 12 000 years ago and modern time, but we have shown above that 10 species (Table 6) which were present about 12 000 years ago were not present in modern time, whereas only 2 (or at most 3) species which were present in modern time were not present in the Devil's Lair deposit. This net impoverishment of the mammal fauna of the district is mainly of the non-forest mammal component. The disappearance of the 2 forest mammals (*Sarcophilus harrisii* and *Thylacinus cynocephalus*) may be causally related to the appearance of *Canis familiaris*.

Thus we suggest that most of the non-forest mammals began to decline in terminal Pleistocene time, that the decline was marked by about 12 000 years ago, and that it continued subsequently until at some time not at present known, these species became extinct locally. On the other hand, the forest mammals appear to have fluctuated in relative abundance, but to have persisted into modern time.

At present forest habitats predominate over non-forest habitats in the Devil's Lair district. As described in the Introduction, Devil's Lair is now surrounded by Karri forest which gives way within 2 km to the east to very extensive Jarrah-Marri forest, and within 2 km to the west to low tree and shrub formations. For our purposes we divide the vegetation into a "forest zone" occupied by the forest mammals and a "non-forest zone" to which the non-forest mammals are restricted. Our forest zone comprises the Karri high open forest and Jarrah-Marri open forest mapped by Smith (1973). The main formation in our non-forest zone is Smith's Acacia open heath, but it includes small areas of Peppermint open scrub, Banksia open woodland, Peppermint low woodland, Jarrah low open forest, and Peppermint low open forest. The boundary between Karri high open forest (Figure 6) and Acacia open heath (Figure 7) is now very sharply demarcated near Devil's Lair by a crest which shelters the Karri forest from the prevailing winds. We include two low tree formations in our non-forest zone because the same plant communities at times pass from shrub formations to these low tree formations as they approach climax, and they probably continue to harbour non-forest mammals. This applies particularly to communities in which Peppermint is an important component. On the other hand, the high open and open forest which we include in our forest zone are tree formations from very early stages of their cycles.

The faunal changes described above suggest there was a diminution or contraction away from Devil's Lair of the non-forest zone which began to affect the fauna in terminal Pleistocene time and continued into the Recent. It is tempting to suggest climatic change as the main cause of this inferred vegetational change, but glaciostatic rise in sea level must also be considered as a contributing or indeed even as the main cause.

There seems to have been a lag between maximum glaciation and maximum glaciostatic fall in sea level, and the extent of both lag and fall have been variously estimated, even for the last glaciation (Milliman and Emery 1968, Guil-

Table 10

Comparison of numbers of species of forest with non-forest mammals which show the same trends in relative abundance in Trench 6 and Trenches 2, 5, 7 and 8 from one stratigraphic level to the next higher level—data from Figures 4 and 5.

Stratigraphic level		Species showing same trend in Trench 6 as in Trenches 2, 5, 7, 8. (see Table 9)	Forest mammals increasing in relative abundance	Forest mammals decreasing in relative abundance	Non-forest mammals increasing in relative abundance	Non-forest mammals decreasing in relative abundance
(Cave earth and) flowstone complex Brownish/first orange brown earthy layer	-top	14	5	4	0	5
	-upper middle	11	5	3	0	3
	-lower middle	12	5	4	2	1
	-bottom	9	2	2	5	0



Figure 6.—Karri growing on the eastern side of the ridge, near Devil's Lair. The density has been reduced by felling.

cher 1969, Jongsma 1970, Richards 1970, Mörner 1971, Gill 1971, Walcott 1972, Andrews 1973, Hopkins 1973 and many others). The subject is controversial and we here assume that at some time after 19 000 yr B.P. the sea west of Devil's Lair fell to 100 m or more below its present level, and then began to rise, reaching about 40 m below its present level by 12 000 yr B.P., and reaching its present level at some time in the Recent. We assume also that soundings in Hamelin Bay (Archdeacon 1878) reveal a topography which has not changed markedly since 19 000 yr B.P., whether submerged or not. On these assumptions, the sea coast would have lain more than 20 km west of its present position soon after 19 000 yr B.P., and more than 6 km west about 12 000 yr B.P., but has been close to its present position for several thousand years.

The boundary between forest and non-forest zones may have occupied more or less its present position near Devil's Lair at the time of lowest sea level, perhaps 16 000 years ago. This would have resulted in a non-forest zone some 30 km wide between it and the coast rather than the 3 km of the present day.

In this case, human hunters or other predators operating from Devil's Lair within a radius of about 10 km and hunting mammals impartially in forest and non-forest zones would have obtained forest and non-forest mammals in comparable proportions about 16 000 years ago. As

sea level rose from 16 000 yr. B.P. to, say, 13 000 yr. B.P., the non-forest zone may have been narrowed, but may still have exceeded the hunting range of predators operating from Devil's Lair, so that the proportions of mammals obtained by them from different zones would remain unchanged.



Figure 7.—Acacia open heath on the seaward slope of the ridge west of Devil's Lair.

But by about 12 000 yr. B.P. the encroaching sea may have reduced the non-forest zone to less than 10 km width. Then the Devil's Lair hunters would have brought back to the cave a smaller proportion of non-forest than of forest mammals. Subsequently with continued encroachment of the sea, the proportion of non-forest mammals would have fallen further. On this view, the critical time at which the extent of the non-forest zone available to hunters fell below their hunting range would have coincided with the end of accumulation of first orange brown earthy layer in Trench 5, for example. By the time that flowstone complex accumulated, forest mammals would have formed a larger proportion of the hunters' prey. This may have been a time of very rapid rise in sea level (Cullen 1967).

Such a view fits our data, but it may seem unlikely that the boundary between forest and non-forest zones would have been stable. This boundary probably results from dynamic balance of a number of determinants such as amount and distribution of rainfall, windiness, etc., which would have been subject to considerable fluctuation between 19 000 and 12 000 years ago. Churchill (1968) in his study of Karri, Jarrah and Marri extending back over much of Recent time has shown that rainfall characteristics rather than temperature determine the distribution of these species. Another determinant (Smith 1973), probably not subject to fluctuation, is topographic—shelter from the prevailing winds.

By analogy with other parts of the world, it would appear likely that temperature, quantity of rainfall, distribution of rainfall, windiness, evaporation rates and other climatic determi-

nants of plant growth varied from 19 000 to 12 000 years ago, even for a middle latitude site with strong maritime influence like Devil's Lair. From consideration of the studies of Van Andel, Heath, Moore and McGeary 1967, Galloway 1967, Damuth and Fairbridge 1970, Howard and Hope 1970, Derbyshire 1971, Adam 1971, Bowler and Hamada 1971, Quinn 1971, Bowler, Thorne and Polach 1972, Colinvaux 1972, Costin 1972, Klein 1972, Löffler 1972, Mercer 1972, Van der Hammen 1972, Webster and Streten in Walker 1972, Bonatti and Gartner 1973, Goudie, Allchin and Hegde 1973, Kershaw 1973, Martin 1973, Van Geel and Van der Hammen 1973, and others, we suggest that temperature and quantity of rainfall may have increased, windiness decreased, and evaporation rates changed little from about 19 000 to about 12 000 years ago in the Devil's Lair district. In such circumstances, the forest boundary might have lain more or less in its present position, and our model outlined above (of human or other hunters based on Devil's Lair finding the proportion of non-forest zone available to the decreasing relative to forest) might be tenable.

The model above requires postulation of minimum environmental difference between late Pleistocene and present day conditions around Devil's Lair. But our data are also consistent with more substantial differences. For example it is possible that there was no Karri and all the forest mammals lived in open forests, or even that the non-forest zone surrounded Devil's Lair.

However, we are able to suggest that a forest barrier separated Devil's Lair from the wide variety of vegetation formations on the inland side of the forest block. While our forest mammals include all the species recorded in modern time from the forest block, except *Myrmecobius fasciatus* and *Tachyglossus aculeatus*, our non-forest mammals appear to be a biased sample. There are about 46 species of mammals recorded from habitats near the forest block. Of these, 22 species inhabit both forest and non-forest habitats and are included in our "forest mammals". Of the remaining 24 species, only 10 are recorded from Devil's Lair and hence included in our "non-forest mammals".

We suggest that this reflects the types of habitats through which our non-forest mammal species had to pass to invade the Devil's Lair district. There appears to be a predominance of species characteristic of open heath habitats in our non-forest mammals. Such a bias would be consistent with species spreading south along a wider western coastal plain carrying predominantly shrub formations, round persistent forest acting as a barrier to inland populations.

Our sparse data on poorly represented species, and on the fauna of the period 25 000 to 19 000 years ago do not permit us to make many inferences. The minimum number of vertebrate individuals available to represent the period from about 25 000 to about 19 000 years ago is only 217 and the number of mammal species included is 21. (See Appendix 1 tables for

Trench 2 and the lowest part of Trench 5.) These 21 species represent both forest and non-forest zones, and we can infer therefore that both zones lay within reach of hunters based on Devil's Lair. Hence they could procure the same kinds of mammal prey as their successors, but it remains to be seen whether the proportions differed greatly.

Two *Pseudomys occidentalis* individuals were recovered from this small sample from the lowest levels in our excavations, whereas only a single tooth represents this species in the upper levels. This tooth, although it was found in Trench 6, could have come from old material dug out of Pit 2 in ancient times and distributed about what was then the cave floor. *P. occidentalis* may have disappeared early from the Devil's Lair district. However, little should be inferred from absence of any of the sparsely represented species. Archer and Baynes (1972) commented on the presence of *Hydromys chrysogaster* and *Nyctophilus timoriensis* in their deposit at Turner Brook (south of Devil's Lair) and the absence of these two species from the 1970 and previous excavations in Devil's Lair. They suggested that these two species might be found as excavation proceeded in Devil's Lair, and so it has proved. The virtual absence of *Pseudomys occidentalis* from the abundant remains so far recovered from upper levels in the Devil's Lair deposit may be just such another sampling accident.

Bats are only sparsely present in the Devil's Lair deposit. None occasions any surprise with the exception of *Macroderma gigas*, previously recorded by Cook (1960) and now confirmed by us. Douglas (1967) discusses possible reasons for major contraction in the former range of *M. gigas*, among them that it might find difficulty in exploiting even abundant prey in a forested area. Its presence in Devil's Lair may provide further evidence of a more extensive non-forest zone than now, or the few animals represented might be storm blown vagrants which sheltered in the cave but perished from cold or hunger without establishing a viable local colony.

Between the time of sealing with thick flowstone of the richly fossiliferous parts of the Devil's Lair deposit and modern time, various non-forest mammals disappeared. We have at present little understanding of the reasons for these disappearances, and little knowledge of their timing. Perhaps it is a simple matter of further shrinkage of the non-forest zone and expansion of the forest zone in Recent time as sea level continued to rise and/or annual or summer rainfall increased.

It is possible that non-forest mammals might have been able to maintain viable populations in the Devil's Lair district while a broad coastal corridor permitted contact with the main populations further north. When this link became attenuated as the corridor contracted towards its present dimensions, they may have been broken into isolated colonies which dwindled and eventually disappeared. The late arrival of *Rattus tunneyi* (see above) by a narrow coastal corridor may not be inconsistent with

this concept. *R. tunneyi* is probably preadapted to success in this situation because it can maintain large populations in pockets of vegetation among mobile sand dunes at beach edges (e.g. specimens M8750-60 collected in 1970 at False Entrance, Shark Bay, by A.B.).

Conclusions

Our scanty data on the period 25 000 to 19 000 years ago, and our fuller data on the period 19 000 to 12 000 years ago, suggest that the mammal fauna in the Devil's Lair district remained approximately stable in the sense of neither gaining nor losing many species. Despite the growth of glaciers and ice sheets to a maximum and their subsequent decline in higher latitudes than that of Devil's Lair, despite any causative or consequent changes in climate on a world wide scale which might have had repercussions at Devil's Lair, and despite the corresponding changes in sea level, a sufficient variety of habitats was present to support a more diverse mammal fauna than that present just before the arrival of European man. A similar degree of stability is reported by Flood (1973) for an inland site in eastern Victoria from before 18 000 to about 8 000 years ago. In the case of our coastal site, stability may have begun to break down about 12 000 years ago.

Within this framework of late Pleistocene stability in species composition of the mammal fauna around Devil's Lair, fluctuations in relative proportions of the species probably occurred. Our stratigraphic control, understanding of the processes by which the deposit accumulated, and framework of radiometric dates are not yet sufficiently precise to define such fluctuations in detail. However our data do suggest a decline in mammals not known to inhabit forest. This trend appears to have been well established about 12 000 years ago and may have continued into the Recent. At all events, most of this group of mammals were locally extinct before European man arrived.

To account for the changes we have observed it is not necessary to postulate any major difference between the observable present and inferred past vegetational boundaries near Devil's Lair, and hence any marked climatic difference between late Pleistocene and modern time. But equally our data are consistent with climatic changes of some kinds, such as increase in total rainfall or in summer rainfall, in which case our findings would match in trend those reviewed by Fairbridge (1972). We are unable at present to separate climatic and non-climatic effects. As Calaby (in Mulvaney and Golson 1971), Freeman (1973) and others have pointed out, it is not easy to make palaeoenvironmental inferences from mammal remains. Lower vertebrates, land snails, pollen or other biota more stringently controlled by climate may be more useful. Our climatic model is based on analogy with distant regions and like other such models may be misleading (Ver-

stappen 1970, Galloway in Mulvaney and Golson 1971). All we can claim is that our climatic and sea level model is consistent with our data.

The first lists of mammal species present in the Devil's Lair deposit (Lundelius 1960, 1966; Cook 1960) were improved and extended by Dortch and Merrilees (1972), and we have been able to add to the list, perhaps most notably by the inclusion of *Pseudomys occidentalis*. Despite these additions to the faunal list from Devil's Lair, there are some notable absences: *Canis familiaris* on one hand, and species of *Sthenurus*, *Protemnodon*, and other large extinct marsupials on the other. We suggest that the Dingo did not arrive in the district until after flowstones sealed the richly fossiliferous deposit about 12 000 years ago, and perhaps *Sthenurus*, *Protemnodon* and other such taxa had become locally extinct before 25 000 years ago.

Since we know that a considerable depth of deposit remains to be excavated, we think it possible that these extinct taxa may yet be found. If the assessment of Jones (1973) is sound and there was a major episode of extinction "a geologically short time before 30 000 B.P.", this possibility seems more likely. On the other hand, if Aboriginal occupation of south western Australia is an ancient one, and if the arrival of the Aborigines is causally related to the extinction of *Sthenurus*, *Protemnodon* and the like (Merrilees 1968, 1973), then Jones' "geologically short time" might be tens or even hundreds of thousands of years. It remains to be seen whether the Devil's Lair deposit is deep enough to contain such extinct taxa.

We suggest that human occupation of the cave was sporadic and, if groups larger than single families were involved, very infrequent. Peterson (in Mulvaney and Golson 1971), Taylor 1972, and others have commented on the archaeological consequences of such situations, and in the case of Devil's Lair, with its low average rate of sedimentation, we cannot expect often to find the record of a single visit by a family group, which usually is "below the threshold of archaeological visibility". We may have to be content with the mixed traces of several or many visits unless we can refine our stratigraphic understanding very greatly. Thus it may be difficult to detect any seasonal rhythm in the use of the cave unless this was very regular and of long standing, and it may be difficult even to fit Devil's Lair into any such pattern as that mentioned by Wright (1971—following Hale and Flannery); we have as yet made no attempt to examine our data from these points of view.

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TRENCH 6

Stratigraphic divisions and subdivisions
with radiocarbon date - yr B.P.

Depth below cave datum in line of section
NW corner of trench, cm

Dasyurus geoffroyi
Phascogale tapoatafa
Antechinus flavipes
Smintropsis murina
Sarcophilus harrisii
Thylacinus cynocephalus
Isodon obesulus
Peromyscus not specifically identified
Trichosurus vulpecula
Pseudacricetus peregrinus
Cercartetus concinnus
Potorous tridactylus
Bettongia penicillata
Bettongia lesueur

		54															
Floor of cave		54- 77															
First dark earthy layer		(Levels 1,2)	54- 77					1					1				
Cave earth and flowstone complex	- Pale band	(Level 3)	77- 87			1					1	2	2	1	1		
	- Flecked lens	(Levels 4,5)	87-c. 97	1+1?		4				3	1	4	2	2	3	3	1?
	- Mixture including parts of subdivisions above and below					2				1		2	2	1	1		
	- Second dark earthy layer	(Level 6)	97-c. 107	1		1				6		8	9	1	9	3	1?
	- Mixture including parts of subdivisions above and below					3						1	1	1	1	2?	
- Cave pearl and bone layer interfingering with flowstone	(Levels 7,8)	107-c. 109	2		4	2	1		4		4	11		12	3		
Total			4+1?		15	2	1		14	1	20	27	7	27	10+2?	2?	
- top (including Hearth 1)		c.109- 131	2	1	3	2		1	8	2	8	9		2	16	3	
		131- 141	5		2+1?				8	2	4	5	1	1	7	4	
Total			7		5+1?	2		1	16	4	12	14	1	3	23	7	
- upper middle		141- 151	5		2+1?		1	1?	7	4	5	4	1		6	5	
		151- 161	3						5	3	3	3			5	3	
		161- 171	6		1?	2	1		6+1?	4	5	3	1	1	6	2	
Total			14		2+2?	2	2	1?	18+1?	11	13	10	2	1	17	10	
- lower middle		171- 181	5			2			7	2	3	5	1?	1	4	4+1?	
		181- 191	4						5	1	3	3			3	4	
		191- 201	4+1?			2			7	4	6	4	1	3	9	5+1?	
		201- 211	4	1			1		5	3	4	2	1?	2	6	3+1?	
		211- 221	5		1	2			7	2	5	7	1+1?	2	7	4+1?	
		221- 231	3	1		1	2		4	2	4+1?	3		1	7	8	
		231- 241	5			1			8	3	7	8		5	12	6	
		241- 251	5		2+1?	1			7	2	4	8		3	7+1?	2+2?	
		251- 261	5		1	1			6	1+1?	3+1?	5	2		7	3	
Total			40+1?	2	1	11+1?	5		56	20+1?	39+2?	44	4+2?	17	62+1?	39+6?	
- bottom (including small test pit in SE corner of trench)		261- 271	3			3	1		5	1	5	6	2	1	9	2	
		271-c. 290	2			1	3		7	1	6	7		2	5	2	
Total			5			4	4		12	2	11	13	2	3	14	4	
(Bottom of excavation, but possibly not of Brownish earthy layer, Level 9)		c. 290															
Unexcavated deposit		at least 400															

TRENCH 5

Stratigraphic divisions and subdivisions with radiocarbon dates - yr B.P.		Depth below cave datum in line of section, NW corner of trench, cm	<i>Dasyurus geoffroii</i>	<i>Phascogale tapoatafa</i>	<i>Antechinus flavipes</i>	<i>Sminthopsis murina</i>	<i>Sarcophilus harrisii</i>	<i>Thylacinus cynocephalus</i>	<i>Isaodon obesus</i>	Perameles not specifically identified	<i>Trichosurus vulpecula</i>	<i>Pseudocheilus peregrinus</i>	<i>Cercartetus concinnus</i>	<i>Potoraus tridactylus</i>	<i>Bettongia penicillata</i>	<i>Bettongia lesueur</i>
Floor of cave		56														
Dark earthy layer		56-67	1	1	1	2			1		1	2	1	1?	3	
Flowstone complex	12050 ± 140	67-78	1		3	3	1		4		5	9	1	4	5	
Mixture including parts of divisions above and below			2	1				1	3		1	3		1	2+1?	1?
- top	11960 ± 140	78-95	3		2	3			3	1	3	4	1	3	5	2
		95-101	2	1					3	1	3	3			2	2
Total			5	1	2	3			6	2	6	7	1	3	7	4
- upper middle		101-111	1						2		1	2		1?	5	1
		111-121	2						3	1	1	1			2	2
Total			3						5	1	2	3		1?	7	3
- lower middle		121-141	5+1?			2			8	4	5	6		1	8	6
		141-161	2						4		1	3		1	6	2+1?
		161-171	1						1	1	3	2	1		8	3
		171-181	1						1	1	1	3		1	2	2
Total			9+1?			2			14	6	10	14	1	3	24	13+1?
- bottom	19000 ± 250	181-201	2				1		3		2	1		1	2	1
		201-c.212	1						1	1	1	3		1	1	1
Total			3				1		4	1	3	4		2	3	2
Laminated layer		c.212														
Light earthy layer	19250 ± 900	212-220							1		1	1		1	1	
		220-c.231							2		1	1		1	1	1?
Total									3		2	2		1	2	1?
Banded layer		c.231														
Second orange brown earthy layer		231-245	1						3		1	1		1	2	1
(Bottom of excavation, but not of Second orange brown earthy layer)		245														
TRENCH 2																
(Upper part of deposit removed prior to 1972)																
(Pit 2 fill, lower part only)																
- bottom		184-199	1			1			3	1	1	1			2	1
		199-209	1			1?			2	1	1	1		1	1	1
		209-219	1						1		1	1			2	
		219-c.223									1				2	
Total			3			1+1?			6	2	4	3		1	6	2
Lithified band with charcoal		c.223														
Light earthy layer		223-237	1						1		1	1			1	
Second orange brown earthy layer	20400 ± 1000	237-c.267	1	1					2	2	1	2		1	1	
Lithified layer, prominently laminated		c.267-296	1			2			1		1	2	2		1	
Third orange brown earthy layer		296-316				1										
Banded layer		316-c.339	1			3			2	2		2	1			1
Charcoal rich band	24600 ± 800	c.339														
Fourth orange brown earthy layer		340-346	1			1?			1			1				2
(Bottom of excavation, but possibly not of Fourth orange brown earthy layer)		346														
Unexcavated deposit		at least 460														

recovered from excavations made in Devil's Lair in 1972 and 1973

TRENCH 5

<u>Petrogale</u> not specifically identified	<u>Macropus eugenii</u>	<u>Macropus irma</u>	<u>Macropus fuliginosus</u>	<u>Setonix brachyurus</u>	<u>Hydromys chrysogaster</u>	<u>Pseudomys albocinctus</u>	<u>Pseudomys occidentalis</u>	<u>Pseudomys shorridgei</u>	<u>Pseudomys preonensis</u>	<u>Notomys</u> not specifically identified	<u>Rattus fuscipes</u>	<u>Rattus</u> not specifically identified	Muridae total	<u>Macroderma gigas</u>	<u>Nyctophilus timoriensis</u>	<u>Nyctophilus geoffroyi</u>	<u>Eptesicus pumilus</u>	<u>Chalinolobus gouldii</u>	<u>Pipistrellus tosoni</u>	<u>Todorrho australis</u>	bird	lizard	snake	frog	fish	Total vertebrate individuals	Volume of major stratigraphic division excavated, cu. m	Incidence of vertebrate animals, individuals per cu. m	Depth below cave datum in line of section, NW corner of trench, cm		
	1?	1		1						1	2	1	3								3	5				29	0.17	170	56- 67		
	1	1+?	2	6		2					5	4	7								8	4	p			67	0.18	370	67- 78		
2	1		1	3								1	1								2	2	p								
1	3	1	1	5			1?			1	1	1	3								1	6	p							78- 95	
2			1	1								1	1								1	3	p							95- 101	
3	3	1	2	6			1?			1	1	1	4								2	9	2			79	0.28	355			
2	1		2	1							1	1	1									7								101- 111	
2			1	1						1	1	1	2									4								111- 121	
4	1		3	2						1	2		3									11				49	0.24	205			
6	1		1	4		3	1+?			1	2	4	11								3	13	p							121- 141	
4+1?	1		1	1								1	1								3	5	p							141- 161	
2																					1	3	p							161- 171	
4		1	1			1						1	2								1	2	p							171- 181	
16+1?	2	1	2	5		4	1+?			1	2	5	14								8	23	4			174	0.66	265			
3		1	1									1	1									3								181- 201	
1			1									1	1								1	1								201- c. 212	
4		1	2									2	2								1	4				37	0.30	120			
			1									1	1																	212- 220	
1			1	1		1							2								1									220- c. 231	
1			2	1		1						1	3								1					19	0.15	130			
1			1+?							1			2								1	2				18	0.11	160	231- 245		

TRENCH 2

1			1							1			2								1	1	p			14	0.02	700			
1			1	1									1									1									184- 199
1		1	1	1									1								1	2	p							199- 209	
1						1?							1								1	1	p							209- 219	
1													1								1	1								219- c. 223	
4		1	2	2		1?							2								1	5	2			48	0.25	190			
													1																		
			1									1	1									2	p			10	0.07	140	223- 237		
2			1	1		1?							2								2	2		1		22	0.15	150	237- c. 267		
			1	1		1	1			3	9	11									1	1				25	0.13	190	c. 267- 296		
1?		1	1	1		1				1	1	2	4									1				9	0.09	100	296- 316		
	1	1	1	1		5	1	3		2	6	5	17								2	2				36	0.10	360	316- c. 339		
			1	1		2	1				2	2	5								2	1				16	0.03	530	340- 346		

TRENCH 7

Stratigraphic divisions and subdivisions		Depth below cave datum in line of section, cm	<u>Dasyurus geoffroi</u>	<u>Phascogale taparitofo</u>	<u>Antechinus flavipes</u>	<u>Sminthopsis murina</u>	<u>Sarcophilus harrisi</u>	<u>Thylacinus cynocephalus</u>	<u>Isaodon abesulus</u>	Perameles not specifically identified	<u>Trichasurus vulpectus</u>	<u>Pseudocheirus peregrinus</u>	<u>Cercartetus concinnus</u>	<u>Potorous tridactylus</u>	<u>Bettongia penicillata</u>	<u>Bettongia lesueur</u>
		(NW corner of Trench 7c)														
Floor of cave		69														
Dark earthy layer (A,B,C, A under C,E, A under E)		69-c. 79	5		7+1?	4	1		9	1	6+1?	7+1?	4	6+1?	6	4
Mixture including parts of divisions above and below					2				1		2			1		
Flowstone complex	- D	79- 87	1+2?						3		3	1		3	3	1
	- G,H,I	87-c. 90	2		4				7		10	8+1?		5	7	1
	- J								6	1	6	11	2	3	5+3?	1+2?
	- K (including Occupation Floor 1, Dortch 1974)	c. 90	2		4	6			6		1	1			1	
	- L	c. 91				1			1		1	1				
- Mixture including parts of subdivisions above			2	1?	5	3			9		7	5+1?	3	5+1?	3+2?	1+1?
Total			7+2?	1?	13	10	1?		25	1	27	25+2?	5	16+1?	19+5?	4+3?
Mixture including parts of divisions above and below			1		1				2		3	3		1?	3	
First orange brown earthy layer	- top															
	- Hearth 2	92- 93	2		2	7	1		3		3	5	2	5	3	2+1?
	- M (including orange and brown mottled portions)	93- 110	9	2	1	11	1+1?		23	8	16	16	2	4+1?	26	9+1?
	- Hearth z		2						3		2			1	1	1?
	- HP					1?			1		1	1			1	
	- "below HP"		1						1		1	1				1?
	- MM (pale friable coarse grained layer)	110-c. 115	3			2+2?	2		4	2	3	4			5	4
- Hearth y		1			1?			1	1	1	1	1	1	2	1	
- Sub MM		2			2	1?		2	2	1	1	1	1	2	1	
Total			20	2	3	22+4?	4+2?		38	13	25	31	6	12+1?	40+1?	17+3?
(Bottom of excavation but not of First orange brown earthy layer)		c. 115														

TRENCH 8

Stratigraphic divisions and subdivisions		Depth below cave datum in line of section, cm	<u>Dasyurus geoffroi</u>	<u>Phascogale taparitofo</u>	<u>Antechinus flavipes</u>	<u>Sminthopsis murina</u>	<u>Sarcophilus harrisi</u>	<u>Thylacinus cynocephalus</u>	<u>Isaodon abesulus</u>	Perameles not specifically identified	<u>Trichasurus vulpectus</u>	<u>Pseudocheirus peregrinus</u>	<u>Cercartetus concinnus</u>	<u>Potorous tridactylus</u>	<u>Bettongia penicillata</u>	<u>Bettongia lesueur</u>
		(NW corner of Trench 8 ₁)														
Floor of cave		79														
Dark earthy layer (A,C, A under C,E, A under E)		79-c. 109			2				1	1	2					1
Mixture including parts of divisions above and below			3		7+2?	5	1		6	1	5+1?	5	4	5	4	1+1?
Flowstone complex	- F (gypsum)	c. 109- 110	1						1		1	1		1	1	
	- K (including Occupation Floor 1, Dortch 1974)	110- ?	1		8	2			4	2	4	3	3	3	4	2
Total			2		8	2			5	2	5	4	3	4	5	2
- top																
		(NW corner of Trench 8 ₂)														
First orange brown earthy layer	- M	116- 122	1		7	5	1		3	2	2	2	1	1	2	1
	- MM (pale friable coarse grained layer)	122- 128				3			1	1	1		1			1
	- Hearth y	128- 129	2		4	2			2	1	2	1	4		3	1
	- Mixture including parts of subdivisions above				1	3			1	1	1	1	1?		1	1
	- Hearth y plus Sub MM		1						1	1	1	1			1	1
	- Sub MM	129-c. 136	1			1			2	1	1	2		1?	1	1
Total			7		18	19+2?	1		13	7	12	10	6+1?	3+1?	12	9
- Mixture of subdivisions above and below						1?			1			1			1?	
- upper middle																
		(NW corner of Trench 8 ₃)														
	- N	c. 136														
	- O	136- 149	1	1	1	3			5	1	2	3		1	3	3
	- P	149- 151	2			1			3	1	1	1	2		1	1
	- Q	151- 161	2			2	1		3	2	2	2	1	1	3	3
Total			5	1	1	6	1		11	4	5	6	3	2	7	7
(Bottom of excavation but not of First orange brown earthy layer)		161														

recovered from excavations made in Devil's Lair in 1972 and 1973

TRENCH 7

<u>Petrogale</u> not specifically identified	<u>Macropus eugenii</u>	<u>Macropus irma</u>	<u>Macropus fuliginosus</u>	<u>Setonix brochurus</u>	<u>Hydromys chrysogaster</u>	<u>Pseudomys albocarinatus</u>	<u>Pseudomys occidentalis</u>	<u>Pseudomys sharpidgei</u>	<u>Pseudomys proecons</u>	Notomys not specifically identified	<u>Rattus fuscipes</u>	<u>Rattus</u> not specifically identified	Muridae total	<u>Macrotermes gigas</u>	<u>Nyctophilus timoriensis</u>	<u>Nyctophilus geoffroyi</u>	<u>Eptesicus pumilus</u>	<u>Chalinolobus gouldii</u>	<u>Pipistrellus tosoni</u>	<u>Todorida australis</u>	bird	lizard	snake	frog	fish	Total vertebrate individuals	Volume of major stratigraphic division excavated, cu. m.	Incidence of vertebrate animals, individuals per cu. m.	Depth below core datum in line of section, cm.				
6	1	1	3	8	5	3	1+1?	16	12	29						1		1+1?	11	7+1?	p				135	0.19	710	69- c. 79					
1				1								1	2									2	2	p									
2	1	1?	1	4								2	3									2	2	p						79- c. 87			
4		1+1?	4	14	1						6	10	14	1	1?							6	6	p	1?					87- c. 90			
1	2	1	3	7+1?	4						4	5	13						1?			11	7	p						c. 90			
3	2	2?	3	7						1?	9	8	16							1		10	8	p						c. 91			
10	5	2+4?	11	32+1?	5					1?	19	25	46	1	1?					1?	1	29	24	4	1?	351	0.37	950					
1	2		1	2	1						1	3	4									4	2	p									
1	1	1+1?	2	4	4					2	6	6	14	1	1?		1	1	1?			9	3	p						92- c. 93			
10	8+1?	2+1?	8	9	12	3+1?	11+1?	22	22	54	22	22	54			1		1				19	36	p						93- c. 110			
1			1	1								1	1										2										
1			1							1?			1									2	4	p									
2	1	1	1	3	4			3	6	8	16					1						2	19								110- c. 115		
1	1	1			3			3	1	7												1	7										
1+1?	1	1		1	4			3	4	2	12											2	11										
18+1?	12+1?	6+2?	13	18	27	3+1?	22+2?	39	40	105	1	1?	2	1	2	1?					35	83	3			549	0.58	950			c. 115		
TRENCH 8																																	
(NW corner of Trench 8 ₂)																																	
		1?		1						3	5	5										5	2			21	0.31	70	79- c. 109				
3+2?	3	1+1?	2	8	5	1	2+1?	19	25	34	1					1	1				9	5	p										
2		1	1	3			1	1?		3	4	6										2	1	p								c. 109- c. 110	
1	1	2	2	6	2	1	1			7	14	18			1?		1+2?	1			7	4	p	1	1						110- ?		
3	1	3	3	9	2	2	1?	1	10	18	24				1?		1+2?	1			9	5	2	1	1	108	0.05	2000					
2	1	1	2	3	3	3	3	3	7	15	24								3		6	9	p										
(NW corner of Trench 8 ₂)																																	
1		1	1	2	4	1	4	8	9	18									1	2		6	4	p	1						116- c. 122		
1		1	1	2	6	1	6	5	13	26									1			1	4	p	1						122- c. 128		
1	1	1	1	2	3	2	1?	2	4	11				1								4	8	p	1						128- c. 129		
1			1		1	1	1		1	4												2	5	p									
1			1?		3			1	1	4												2	3									129- c. 136	
8	2	4	5+1?	8	24	9	1?	19	26	46	98			1		1	6				22	36	4	2		319	0.29	1100					
					1					2																							
3		1	2	1	2	1	1	3	2	7												1	36	p								c. 136	
1		1	1?	1	3	1	1?	2	4	10												1	44	p								136- c. 149	
1		1?	1	1	2	1	1	2	2	6												4	24	p								149- c. 161	
5		2+1?	4	2+1?	1	7	3	1?	2	7	8	23										6	104	3		210	0.18	1200					

Appendix 2

Records forming the basis for the modern mammal fauna of the Devil's Lair district

by A. Baynes

The evidence presented here depends upon unpublished research on the distributions of most south western mammal species. Some have not yet been fully covered, and their status is correspondingly less certain.

Unless otherwise stated all specimens referred to are in the collections of the Western Australian Museum. Those in the modern mammal collection are distinguished by a simple number, usually with the prefix M; vertebrate palaeontological collection specimens quoted have numbers divided by two fullstops, and no letter prefix.

Mammals listed in Table 3, confidently included in the modern fauna

Dasyurus geoffroi. Three specimens (M1839, M1852, M1861) in the modern mammal collection of the W.A. Museum were obtained in 1934 from Forest Grove 8 km N.E. of Devil's Lair. Two specimens (M1824, M1825) sent in from Forest Grove in the same year, and another (M1717) from Karridale 7 km south in the previous year were all discarded after registration.

Phascogale tapoatafa. The closest specimen was obtained from Forest Grove in 1933. Other single records from within 20 km of Devil's Lair are M2032 from Forest Grove in 1936 (discarded), M2270 from Witchcliffe in 1938, M2711 from East Witchcliffe in 1946 (discarded), M5090 from Kudardup in 1962, and M7944 from Augusta in 1967. In addition eight *P. tapoatafa* have been recorded from Margaret River; those for which the accession number as well as the year is in brackets were discarded: M1588 (1931), (M2707, 1946), (M2911, 1952), M4028 (c. 1960), M4293 (c. 1960), M4534 (c. 1960), M4569 (1961), M6901 (1966).

Sminthopsis murina. A specimen (M206) was obtained in the "Caves District" in 1915, and three others (M1171, M1642, and M2059) were sent in from Forest Grove in 1929, 1932 and 1936 respectively.

Tarsipes spencerae. A specimen (M1250) was sent in to the W.A. Museum in 1930 from Group 75 which is probably east of Forest Grove rather than near its postal address at that time, which was Karridale. Either way the specimen probably originated within 10 km of Devil's Lair. Another specimen (M2397) obtained from Karridale in 1940 was not kept.

Trichosurus vulpecula. A specimen (M112) from near Mammoth Cave was registered in 1914 but discarded; another (M6583) was collected at the same locality in 1965. A specimen (M224) was obtained from Margaret River in 1915.

Pseudocheirus peregrinus. Only a single modern specimen (M5835) has been found near Devil's Lair. It consists of a jaw picked up on the surface from near Lake Cave, about 8 km N. of Devil's Lair, in 1963. Shortridge (1910) reported that the species was fairly plentiful near Margaret River at the time of the Balston Expedition of 1904-1907. He collected several at Burnside. Remains of *P. peregrinus* are also moderately common on the surface in other caves near Devil's Lair.

Cercartetus concinnus. This species is represented as a modern mammal in the immediate area by a single record, M1715 from Forest Grove, sent to the Western Australian Museum in 1933 but subsequently lost. Another (M2217) was obtained from Margaret River in 1937. Its remains are found on the surface of cave deposits in the region. Also it was represented in a small cave deposit at Turner Brook, 14 km S. of Devil's Lair which was radiocarbon dated at 430 ± 160 years B.P. (Archer and Baynes 1972).

Bettongia penicillata. A series of specimens (M17-M23) were obtained near Mammoth Cave in 1912. Of these M17 and M20 are still represented by specimens in the W.A. Museum. Two (M1084, M1086) were obtained from Karridale in 1928, and another two (M1340, M1351) were sent in from Karridale in 1930. M1351 was discarded.

Macropus fuliginosus. A modern skull (M2364) was obtained from Calgardup Brook in 1939 and another (M2389) sent in to the W.A. Museum in the same year from Witchcliffe. Remains of the species are common on the floors of many other caves in the area around Devil's Lair. Kangaroos of this species were seen frequently during field work at Devil's Lair in 1973.

Setonix brachyurus. Modern specimens were sent in from Karridale as follows: M1121, M1125 (1929), M1402 (1931), and M1765 (1933). The catalogue indicates that another (M115) merely labelled as from the Margaret River district, was collected near Mammoth Cave in 1914. Specimen 8924 originated from Margaret River in 1907. Surface specimens of the species are common in caves throughout the Cape Leeuwin-Cape Naturaliste region. *Setonix brachyurus* was collected at Augusta by John Gilbert (Thomas 1888).

Hydromys chrysogaster. A specimen (M1685) sent in from Forest Grove in 1933 was discarded, but three others (M6576, M6580-1) were collected alive in Mammoth Cave in 1965. Specimen M7 was sent in from the Margaret River district in 1912, and M221 was obtained from the same area in 1915 but discarded.

Rattus fuscipes. This species is today common in the immediate vicinity of Devil's Lair, e.g. M8166. There is a modern specimen (44.2.15.36) from Augusta registered in the British Museum (Natural History) in 1844 (Taylor and Horner 1973): this was probably collected by John Gilbert.

Mammals listed in Table 4, probably part of the modern fauna

Eight of the twelve species in this group are represented by specimens collected alive in the general area.

Antechinus flavipes. A specimen (M2037) was obtained in 1936 from Rosa Brook about 22 km N.N.E. of Devil's Lair. Also species is abundant in the fossil fauna from the small deposit at Turner Brook (Archer and Baynes 1972). *A. flavipes* remains are present on the surface in several caves near Devil's Lair.

Isoodon obesulus. Five specimens have reached the W.A. Museum from the Margaret River district at various times: M226 (1915), M4522 (1959), M4466 (1960) M7580 (1966), M7626 (1967). The species was also collected near Margaret River by Shortridge (1910). Its remains are abundant on the surface in a number of caves near Devil's Lair, and it was present in the small deposit at Turner Brook (Archer and Baynes 1972).

Potorous tridactylus. Although this species has not been collected as a live animal near Devil's Lair its remains are very common on the surface in caves in the area. It seems likely that it was present as a member of the modern fauna around Devil's Lair. Information obtained by Shortridge (1910) from Aborigines also suggests that it was present in the Margaret River district during the last century.

Macropus irma. In some ways this species represents the greatest problem of interpretation because specimens collected alive in the region may falsely suggest the species to have been a member of the modern fauna around Devil's Lair. A specimen (M458) was obtained from Augusta in 1920, and another (M8335) along the Brockman Highway between Augusta and Margaret River in 1968. Perry (1971) includes *M. irma* in a list of species frequently seen along the lower Blackwood River in 1919. Against this evidence is the fact that although remains of the species are known from caves near Devil's Lair the specimens have all undergone some chemical alteration, suggesting age. Most originate from caves known to contain material of considerable antiquity. It is possible that *M. irma* reinvaded the area near Devil's Lair after the first felling of the forests last century.

The three rodent species in Table 4 were all present in the deposit at Turner Brook (Archer and Baynes 1972). Both *Pseudomys shortridgei* and *Rattus tunneyi* were abundant in the deposit; *Pseudomys praeconis* was only represented by 3 specimens in a total of about 650. However, this low relative abundance of *P. praeconis* in a cave deposit fauna is typical of this species in the southern part of its range (A. Baynes, unpublished observations).

Nyctophilus timoriensis. The modern specimens collected nearest to Devil's Lair were obtained about 60 km away: M36 from Nannup in 1913, and M1247 and M1248 from Wonerup in 1929. However, the

total number of modern specimens in the collection is quite small. The species is included in Table 4 on the record of its presence in the deposit at Turner Brook (Archer and Baynes 1972).

Many bat species are among the mammals not yet fully covered in the survey of distributions, but the modern mammal collection of the Western Australian Museum includes specimens of four species collected near Devil's Lair. One specimen with its year of capture is quoted for each: *Nyctophilus geoffroyi* M6584 near Strongs Cave just to the west of Devil's Lair in 1965, *Eptesicus pumilus* M4183 Boranup about 1/2 km east of Devil's Lair in 1961, *Chalinolobus morio* M3788 in Mammoth Cave 10 km north of Devil's Lair in 1959, and *Pipistrellus tasmaniensis* M4182 from Boranup in 1961.

Canis familiaris. Shortridge (1936) collected five specimens of Dingo from Margaret River during the Balston Expeditions of 1904-07 and Perry (1971) includes it in the list of species frequently seen on the Lower Blackwood River in 1919. The W.A. Museum has only a single modern specimen from the Margaret River district, M4204 collected in 1958. However, the locality of even this one is suspect. The species is abundantly represented by remains on the surface of deposits in caves near Devil's Lair. One cave has been named Dingo Cave because so many skulls have been recovered from it.

Mammals listed in Table 5, possibly forming part of the modern fauna

Macropus eugenii. This species is placed here mainly because of a lack of fossil specimens of young appearance from caves near Devil's Lair. All those known originate from caves which include material of considerable antiquity. They are generally encrusted or appear to have undergone chemical alteration. The closest record to Devil's Lair of *Macropus eugenii* taken alive is the specimens collected by Shortridge (1910) at Ellensbrook about 30 km to the north. W. D. L. Ride possesses copies of the data on the labels of five of these specimens which are in the British Museum (Natural History). The label attached to the skin of No. 6.9.1.32 bears the following note "*Macropus eugenii* does not seem to occur to the south of Margaret River on the coast (according to natives)", Ride (pers. comm.). The author of the note was probably Shortridge. There are other specimens from this general area in the W.A. Museum modern mammal collection. One from Cape Naturaliste about 65 km north of Devil's Lair consists of only a skin to which is attached a Tunney collecting label bearing the number 06 and the locality, but no date. It was probably collected between 1900 and 1910. Three other specimens (12860-2) were collected at Lake Muir about 140 km E. of Devil's Lair in 1912.

Chalinolobus gouldii. The nearest records of modern specimens are from 55 km from Devil's Lair: M8391 at Busselton in 1969 and M10935 from Darradup in 1973.

Tadarida australis. The nearest record is M5420 collected in 1963 at Donnelly River Mill, about 75 km E. of Devil's Lair.

Mammals listed in Table 6, not present in the modern fauna of the Devil's Lair district but recorded in the fossil fauna.

It is necessary to consider the records of one of the species included in Table 6.

Petrogale sp. It is unlikely that any species of *Petrogale* was present in the modern fauna of the Devil's Lair district. Fossil specimens are known from a number of caves near Devil's Lair, but all originate from deposits which are known to include specimens of considerable age, and most appear to have undergone some chemical alteration. In addition there is one specimen which must be discussed in detail. It is a skull of *Petrogale* sp., at present in the vertebrate palaeontological collection (69.6.62), but formerly in the modern mammal collection (M114). The catalogue indicates that M114 is a skull of *Setonix brachyurus* from "Mammoth Cave, Margaret River" collected by L. Glauert in April 1914. Specimen M115 is a skin and skull of *Setonix brachyurus* with the same locality data as M114. Skull 69.6.62, still bearing the number M114, retains the remains of dried flesh (e.g. the left eardrum) it also shows starred fractures of the cranium behind the left orbit. On this evidence it seems likely that the specimen was collected as a live animal, probably with a shot gun, and that it is not a fossil. The nearest locality from

which living specimens of a *Petrogale* sp. have been recorded is Dale River near Beverley (Shortridge 1910). This is about 240 km N.N.E. of Mammoth Cave. When this gap is considered in conjunction with the absence of young fossil material from caves near Devil's Lair, it appears likely that specimen 69.6.62 is the result of misassociation of specimen and data during preparation or storage.

Appendix 3

Investigation of degree of overestimation inherent in our methods of obtaining "minimum numbers" of individuals

The entries in Appendix 1 represent our estimated "minimum number" of individuals for each taxon for each stratigraphic unit specified. In the case of Trench 6, however, excavation was made by 2 cm spits from 109 cm to 271 cm, but for convenience in tabulation, we show the data grouped into 10 cm intervals. Grouping was made by adding the 2 cm spit records for each taxon.

In order to investigate the maximum degree of overestimation of "minimum numbers" of individuals inherent in our methods, we chose the 211 cm to 271 cm interval in Trench 6 because it both contained sufficient numbers of specimens of very large and very small animals, and appeared to be a stratigraphic continuum. This interval was excavated in horizontal spits 2 cm thick in what we later judged from the sections and from our observations as excavation progressed to be a continuum of gently dipping sediments. Not only were our spits very small but they transgressed the dipping bedding planes, so that different beds might be represented in the same spit.

We assembled all the bone material of three species, catalogued or otherwise, which was admitted to our analysis from this 211 to 271 cm interval in Trench 6. The first of these species was one of the smallest sized mammals represented, *Sminthopsis murina*, the second was a species of intermediate body size, *Pseudocheirus peregrinus* and the third was the largest species (with the possible exception of man) so far recorded in the deposit, *Macropus fuliginosus*. In each case, the number of individuals was estimated without regard to depth, as though complete vertical mixing had occurred. This was in contrast to the assumption on which the appendix tables were prepared, namely that no vertical mixing had occurred between 2 cm spits. It is to be expected that the true number of individuals represented in the deposit would lie between these two extremes. The degree of overestimation in the appendix tables would be expected to be least for *Sminthopsis*, intermediate for *Pseudocheirus* and greatest for *M. fuliginosus* because a small thickness of sediment would completely cover all *Sminthopsis* bones, most *Pseudocheirus* bones, but few *Macropus fuliginosus* bones. Vertical mixing would be greatest for this last named species because larger bones would be more likely to be dislodged by scuffling human or other feet, whereas small bones would be more likely to be trodden in.

The number of individuals of *Sminthopsis murina* recorded in the Appendix 1 tables between 211 and 271 cm in Trench 6 is 10. When we considered the specimens as a single sample

irrespective of depth, there proved to be 5 left dentaries, 6 right dentaries, 2 left maxillae and 2 femora. Some of these were incomplete, but no two tooth bearing fragments from the same quarter could have represented the same animal. So on these grounds at least 6 individuals were represented. Appreciable tooth wear was discernible on 3 of the left dentaries but not on any of the 6 right dentaries, so that at least 3 aged animals and 6 young animals must have contributed to the sample, making 9.

Of the 29 spits involved, only two pairs of adjacent spits contained *S. murina*. These pairs and the other 6 spits containing *S. murina* were separated from one another by at least 2 cm and up to 8 cm. On depth grounds alone at least 8 individuals might be expected.

Thus it would appear that our methods did not result in great overestimation of the numbers of individuals of *S. murina*. By extrapolation to other depth ranges and other very small species, we suggest that the numbers in the appendix tables are not greatly overestimated.

The specimens of *S. murina* involved in this test were 73.8.638, 746, 802, 892, 927, 958, 969; 73.9.24, 41, 37; 73.12.309, 310.

The number of individuals of *Pseudocheirus peregrinus* recorded in the Appendix 1 tables between 211 and 271 cm in Trench 6 is 37. By assembling the specimens irrespective of depth, we could demonstrate the presence of only 21 individuals, the key anatomical structure in this case being left dentary fragments with third molars or their alveoli. Thus our methods may overestimate the numbers of individuals of this, and presumably other animals of intermediate size, to an appreciable extent. In this case we had no guide from depth considerations because all but one of the 29 spits contained *P. peregrinus*.

The specimens involved were 73.8.584, 585, 602, 625, 653, 654, 671, 713, 732, 751, 781, 782, 808, 809, 826, 855, 856, 876, 877, 895, 909, 910, 930, 931, 948, 962, 972, 988; 73.9.18, 28, 47, 48, 67, 75, 89; 73.12.332, 339, 343.

The number of individuals of *Macropus fuliginosus* recorded in the Appendix 1 tables between 211 and 271 cm in Trench 6 is 17. From the specimens assembled as one sample, irrespective of depth, we could demonstrate the presence of only 6 individuals, the key anatomical structure in this case proving to be left upper first incisor teeth.

In order to judge the possible effect of excavating by 10 cm instead of 2 cm spits, we then assembled the *M. fuliginosus* specimens from the 211 to 271 cm interval in Trench 6 in groups from 211 to 221 cm, 221 to 231 cm, and so on. If we had in fact excavated Trench 6 in these 10 cm spits, we would have recorded only 9 individuals of *M. fuliginosus*, thus probably overestimating, but much less seriously than by excavating as we did in 2 cm spits.

The *M. fuliginosus* specimens involved were 73.8.591, 608, 644, 738, 763, 793, 815, 836, 863, 883, 900, 901, 917, 935, 977; 73.12.308, 333, 335, 372.

As a further check on the degree of overestimation of *M. fuliginosus*, we considered specimens from spits of about 10 cm thickness excavated from Trench 5, between 78 cm and 212 cm. We believe these range through the same

major stratigraphic division as the interval from Trench 6 previously considered, though the Trench 5 sample probably represents a larger proportion of this stratigraphic division. There were 9 individuals of *M. fuliginosus* recorded for the 78 to 212 cm depth interval in Trench 5. When we assembled the specimens as a sample irrespective of depth, we could demonstrate the presence of only 4 separate individuals, with anterior molariform teeth providing the best guide to numbers in this particular sample. The specimens concerned were 73.9.354, 381, 409, 429, 430, 460, 532, 677, 703, 783; 73.12.499.

As a final check on overestimation of *M. fuliginosus*, we assembled all the material from Trench 6, not only of the categories used to assemble the data for the appendix tables but also any other post cranial material attributable to *M. fuliginosus* by reason of its size or form. Ignoring all consideration of depth or stratigraphy, we could demonstrate the presence of only 17 individuals of *M. fuliginosus*, compared with 50 estimated by adding the entries for the various stratigraphic subdivisions, as in Appendix 1.

By considering separately the major stratigraphic subdivisions of Trench 6, but using the full sample of *M. fuliginosus* rather than the partial sample on which Appendix 1 is based, and omitting stratigraphically mixed samples, we reached the following estimates of minimum numbers:—

First dark earthy layer	1 (not included in Appendix 1 tables because based on post cranial elements not admitted to our analysis)
Pale band	1 (ditto)
Flecked . . . lens	1 (ditto)
Second dark earthy layer	2 (cf. 1 in Appendix 1 tables)
Cave pearl and bone layer	2 (cf. 3 in Appendix 1 tables)
Brownish earthy layer—top	7 (cf. 8 in Appendix 1 tables)
Brownish earthy layer—upper middle	2 (cf. 6 in Appendix 1 tables)
Brownish earthy layer—lower middle	8 (cf. 28 in Appendix 1 tables)
Brownish earthy layer—bottom	2 (cf. 3 in Appendix 1 tables)

The lower middle subdivision of brownish earthy layer, for example, was excavated in 43 two centimetre spits and 1 four centimetre spit, and minimum numbers for each species estimated for each spit. The 28 *M. fuliginosus* individuals recorded in Appendix 1 for this subdivision represent the sum of the numbers recorded for each spit; this is in marked contrast with only 8 individuals estimated by treating the subdivision as though it were a discrete stratigraphic entity. (There may be some connection between the high degree of overestimation in this stratigraphic subdivision and the low degree of bias imposed by the collecting agency, implied in Table 1, but if so, we have made no study of any such connection.)

We conclude that our methods may lead to overestimation, which becomes more likely with increasing size of the animal concerned and decreasing thickness of the excavation unit sampled.

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