

THE SOUTH-WEST OF WESTERN AUSTRALIA



ABORIGINAL FISH TRAP—ALBANY

THE SOUTH-WEST OF WESTERN AUSTRALIA

PREFACE

Although Western Australia has an area comparable with that of India, ninety per cent of her population, which is little more than a million, live in the south-west corner of the State, in an area similar to that of the British Isles; and seventy per cent of the residents there live in metropolitan Perth. It is in the south-west, isolated by oceans and infertile, arid country, where most of the State's forests are found, where most of its intensive agriculture is practised, and where most of the population find their recreation. Here the Aboriginal inhabitants first came into extensive contact with Europeans, and here man has had his greatest impact on the environment of the State.

To mark the occasion of the 45th Congress of the Australian and New Zealand Association for the Advancement of Science, held in Perth during August 1973, the Council of the Royal Society of Western Australia decided to devote part of the Journal to a series of reviews concerning this southwestern corner. It was felt that the papers would be of interest to delegates attending the Congress, and also to residents of the State who may wish for access to information not readily obtained from more detailed papers, which are scattered through the specialist literature.

There is a further reason for believing that this is an appropriate time to review information concerning the south-west. There is a rapid increase in the rate of accumulation of knowledge about the State. Extensive exploration for minerals is in progress, and there is increasing pressure from the general public to come to terms with the environment. The number of scientists and other specialists is increasing. The Western Australian Institute of Technology has recently been established as a major tertiary institution, and in 1975, when the first students enter the new Murdoch University, the University of Western Australia will cease to be one of the world's most isolated universities, and any lingering traces of intellectual isolation will disappear.

The Society wishes to express its gratitude to the authors of the review papers; to Professor Webb (Honorary Organizing Secretary of the 45th ANZAAS Congress) for his encouragement and co-operation; and to the Government Printing Office for generous assistance in the production of the Journal.

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1.—The geology of southwestern Australia—a review

By M. H. Johnstone¹, D. C. Lowry¹ and P. G. Quilty¹

Abstract

The gneisses and granites which constitute the bulk of the Archaean Yilgarn Block give a surprisingly consistent age of $2,667 \pm 27$ m.y. However, metasedimentary belts infolded into this gneissic terrain contain boulders dated at 3,000 m.y., so the younger figure probably represents the time of stabilization of the radiogenic elements of the shield. Flanking the shield are belts of Proterozoic metamorphics which have been dated from 1300 m.y. to 670 m.y.

The first important Phanerozoic sedimentation consists of Early Permian glacially-derived rocks deposited in downwarps to the east and west of the main shield. The western trough continued to receive marine and lacustrine sediments throughout the Early Permian. In the southern Perth Basin, graben development began in the Late Permian with deposition of thick Upper Permian Coal Measures and coarse fluvial Triassic sandstone. In the north, the Upper Permian is represented by parallel to continental sandstone and the Lower Triassic by marine shale. In this northern area coarse sandstone marking the onset of graben tectonics does not appear until the Late Triassic. This tectonism and depositional style was renewed in the Late Jurassic to Early Neocomian after a period of comparative stability in the Middle Jurassic. The second tectonic phase also saw the development of a graben across the southern margin of Australia which again was filled with coarse detritus. Both of these graben were filled with detritus from the shield by an extensive river system whose relics are the chains of salt lakes seen today. In the Late Neocomian, spreading between India and Antarctica commenced and India moved away from Western Australia along the Wallaby-Perth transform. Marine shelf sedimentation then commenced on the west coast and spread into the southern graben in the Aptian when a widespread transgression occurred in the Eucla and Officer Basins. In Eocene times, the spreading between Australia and Antarctica commenced and, for the first time, warm waters from the Indian Ocean could enter the southern basins. Sedimentation in the Paleocene, Eocene and Miocene was largely carbonate but minor terrigenous material derived from the shield was deposited in the Perth Basin in the Paleocene-Early Eocene and near Albany in the Late Eocene.

Introduction

This paper is an abbreviated geological history of the southwestern portion of Australia. It highlights those phases of geological evolution which have helped to shape the landforms, soils, and the varied environments for the development of its present day unique flora and fauna.

Such a paper cannot be both all-embracing and at the same time, definitive. The later facets of the geological history of the southwestern corner of the continent which led to the isolation of this area and the development of its biological uniqueness are stressed to the detriment of the equally interesting history of the buildup of the Archaean nucleus which forms the core of the

Australian continent. The latter has been well covered in Special Publication No. 3 of the Geological Society of Australia (1971.)

A pioneer study of the Perth basin was made by Campbell (1910), who examined its northern part and made two major contributions in recognising the existence of a major fault (the Darling Fault) and also in inferring a glacial origin for the Early Permian sediments. Jutson (1934) produced a monumental work on Western Australian geomorphology and discussed in some detail the salt lake system. McWhae *et al.* (1958) produced a review of Western Australian stratigraphy and this work is still the standard reference for the Phanerozoic.

Tectonic elements

The Archaean Yilgarn Block (Fig. 1) is the major nucleus of the present Australian continent, but is one of many such nuclei of the Gondwanaland supercontinent (Fig. 2A). The dominant trend of gneissic foliation and orientation of infolded metasediments in the block is north-northwest.

Along the southern margin of the block, metamorphics of the Fraser Range and Albany-Esperance Blocks trend northeast-southwest and east-west respectively, almost at right angles to the grain of the abruptly truncated shield.

The variation of mineral association and metamorphic grade in a westerly direction in the Albany-Esperance Block is matched exactly by similar east-west trending rocks in the vicinity of the Windmill Islands in Eastern Antarctica (Oliver, 1972), providing one of the strongest pieces of evidence for the geological fit of Antarctica and Australia in the reconstruction of Gondwanaland.

Along the western margin of the Yilgarn Block, the Archaean Shield is separated from Proterozoic high grade metamorphic rocks (garnet granulites with a meridional trend) by the Darling Fault—a major crustal feature 1000 km long, trending north-south and having up to 15000 m of vertical movement since the Permian and with a history since at least the Proterozoic. To the north, the strike of the Proterozoic rocks becomes more northeast-southwest and they trend around the northern margin of the Yilgarn Block. Overlying the Archaean on the western margin of the block are several sequences of unmetamorphosed sediments which dip west into the present day Perth Basin (Billeranga and Moora Groups, Cardup Group). The Billeranga and Moora Groups (Fig. 1) may be unmetamorphosed margin facies which are age equivalents of the garnet granulites in the trough farther west.

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During the Phanerozoic, the Precambrian crystalline shield acted as a stable emergent craton and sedimentation was restricted to marginal downwarps. Along the western margin of the shield a downwarp developed early in the Palaeozoic and was reactivated in the Permo-

Carboniferous. Between the Late Triassic and the Early Cretaceous (Neocomian) a deep graben developed in the centre of this downwarp to accommodate the 15,000+ m of mainly continental sediments of the Perth Basin. Although the north-south Darling Fault forms the eastern

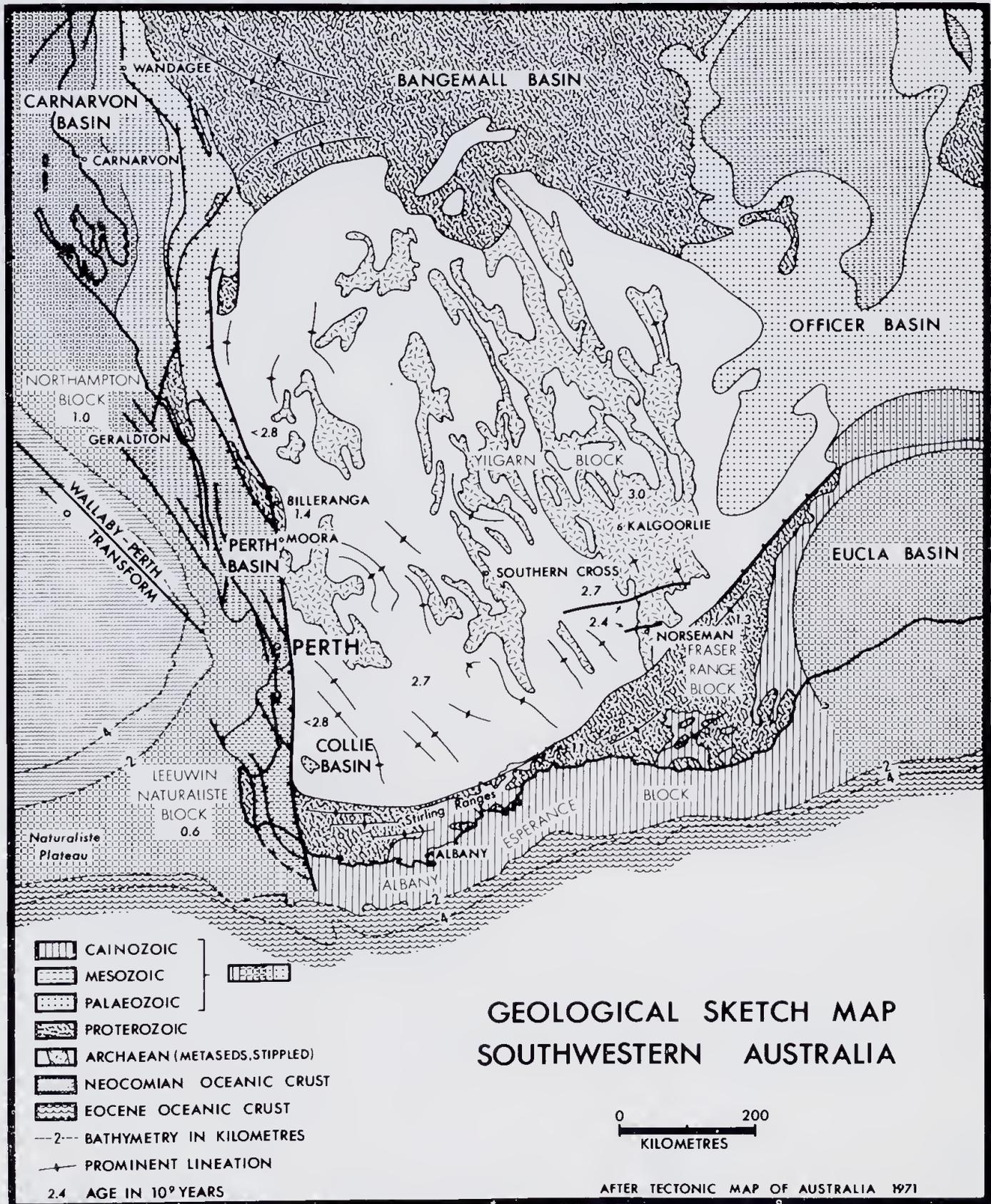


Figure 1.—Geological sketch map of southwestern Australia.

boundary between this graben and the shield (Jones and Pearson, 1972), an equally prominent fault alignment in the graben is NNW, paralleling the grain of the Archaean Shield and that of a prominent transform fault in the Indian Ocean postulated by Falvey (1972).

Along the southern margin of the shield, a graben paralleling the lineation of the Albany-Esperance Block is inferred to have developed at least as early as the Late Jurassic but possibly even contemporaneously with the earlier Triassic formation of the Perth Basin. Little is known of the early history of this graben, since no remnant of it has yet been discovered off the southern coast of Western Australia, and much of its history is inferred from the Elliston Trough and the Robe-Penola Trough in South Australia. The whole of the western portion of this graben probably now lies on the Antarctic plate. A marginal marine Eocene sequence laps the southern coast and, probably, a thin veneer of Miocene limestones occurs offshore, overlying the crystalline basement beneath the southern shelf.

The eastern margin of the Yilgarn Block has never been downfaulted. Gentle epirogenic warping formed the Eucla and Officer Basins where several relatively thin, flatlying sequences of sediments were deposited. In the latter, Ordovician, Permian, and Early Cretaceous sediments were laid down and the later Eucla Basin contains Cretaceous and Tertiary sequences.

The Precambrian crystalline shield and associated sediments

The dominant geological element in southwestern Australia is the Archaean Yilgarn Block which forms the nucleus of the Western Australian Shield. This extends from near the south coast for 900 km to the north and has an east-west width of 700 km. Around this nucleus, belts of younger Precambrian rocks have accreted and its western margin is now marked by the deep Mesozoic graben of the Perth Basin. The eastern and southern margins of the shield have been overlapped by Cretaceous and Tertiary sediments.

Apart from the dissected western margin, the Yilgarn Block has an ancient, subdued land surface, and most of the older rocks are obscured by the widespread cover of laterite and its associated soil horizons which form extensive sandplains. The shield is composed mainly of gneisses and granites, with minor infolded belts of metasediments with a general north-northwest strike. These metasediments reveal different grades of regional metamorphism. The westernmost belt—the Jimperding belt (Prider, 1944), which has undergone the deepest dissection—consists of sillimanite-zone and kyanite-zone rocks. The other major belts, notably those of Southern Cross and Kalgoorlie, show degrees of metamorphic grade which lessen in an easterly direction (Fig. 1). The Jimperding and Southern Cross belts contain thin bedded, shallow water sediments whereas those of the Kalgoorlie region contain a thick eugeosynclinal sequence containing pillow basalts. The sedimentary and volcanic rock suites and the chemical composition and areal distribution of

the various volcanic and hypabyssal rocks of the Eastern Goldfields are similar to those of present day island arcs and subduction zones. Possibly these Archaean greenstone belts represent the earliest zones of thick sedimentation when the "continental" crust was little more than a basaltic differentiate from the mantle (White *et al.*, 1971).

The original crust on which these ancient sediments were laid down has not yet been positively identified or dated radiometrically. The belts of metasediments are folded into the gneissic complex of the shield which probably represents a granitization of some of the earlier crustal differentiate. Alternatively, the greenstone belts became closed to the loss of radiogenic daughter elements earlier than the gneissic terrain of the catazonal basement rocks. Thus the geologically older gneisses may give younger radiometric ages (Windley and Bridgwater, 1971). The age of granitization is remarkably uniform over the Yilgarn Block, giving a Rb/Sr age of $2,667 \pm 27$ m.y. Granitic boulders within conglomerates in the Kalgoorlie greenstone belt have given an age of 3,000 m.y. which is consistent with the above theory (Compston and Arriens, 1968). It is interesting to note that the age of a prominent metasomatic event in the Kalgoorlie area ($2,670 \pm 30$ m.y.) agrees closely with the widespread age of the gneissic parts of the shield (Arriens, 1971).

A final major event in the history of the Archaean shield was the emplacement of large east-west trending basic dykes near Norseman, of which the Jimberlana Dyke is the best known (Campbell *et al.*, 1970; and McCall and Leishman, 1971). These, and the associated gold mineralization at Kalgoorlie, are dated at $2,400 \pm 40$ m.y. (Fig. 1).

To the southeast of the Yilgarn Block, and striking approximately at right angles to the north-northwest trend of the main shield is a zone of augen gneisses with associated amphibolites and granulites which were welded onto its southern margin approximately 1,300 m.y. These rocks appear to merge into the east-west trending gneisses, granites, and metasediments of the Albany-Esperance Block which are dated at $1,150 \pm 40$ m.y. (Compston and Arriens, 1968) and which form the entire southern boundary of the shield.

Movement on the Darling Fault formed the Perth Basin—a graben with as much as 15,000 m of Late Palaeozoic and Mesozoic sediments. The Precambrian high grade metamorphics which floor this graben are much younger than the adjacent shield. To the north of Geraldton, the outcropping garnet granulites of the Northampton Block (Fig. 1) have been dated at $1,040 \pm 50$ m.y. whereas similar rocks from the Leeuwin-Naturaliste Block in the southwestern corner of the State give an isochron dating of 670 ± 25 m.y. (Compston and Arriens, 1968). The age of the younger granulites is also registered in overprinted micas and pegmatites along the western margin of the Yilgarn Block.

Also along the western margin of the Yilgarn Block, two sequences of relatively unaltered sediments rest unconformably on the Archaean.

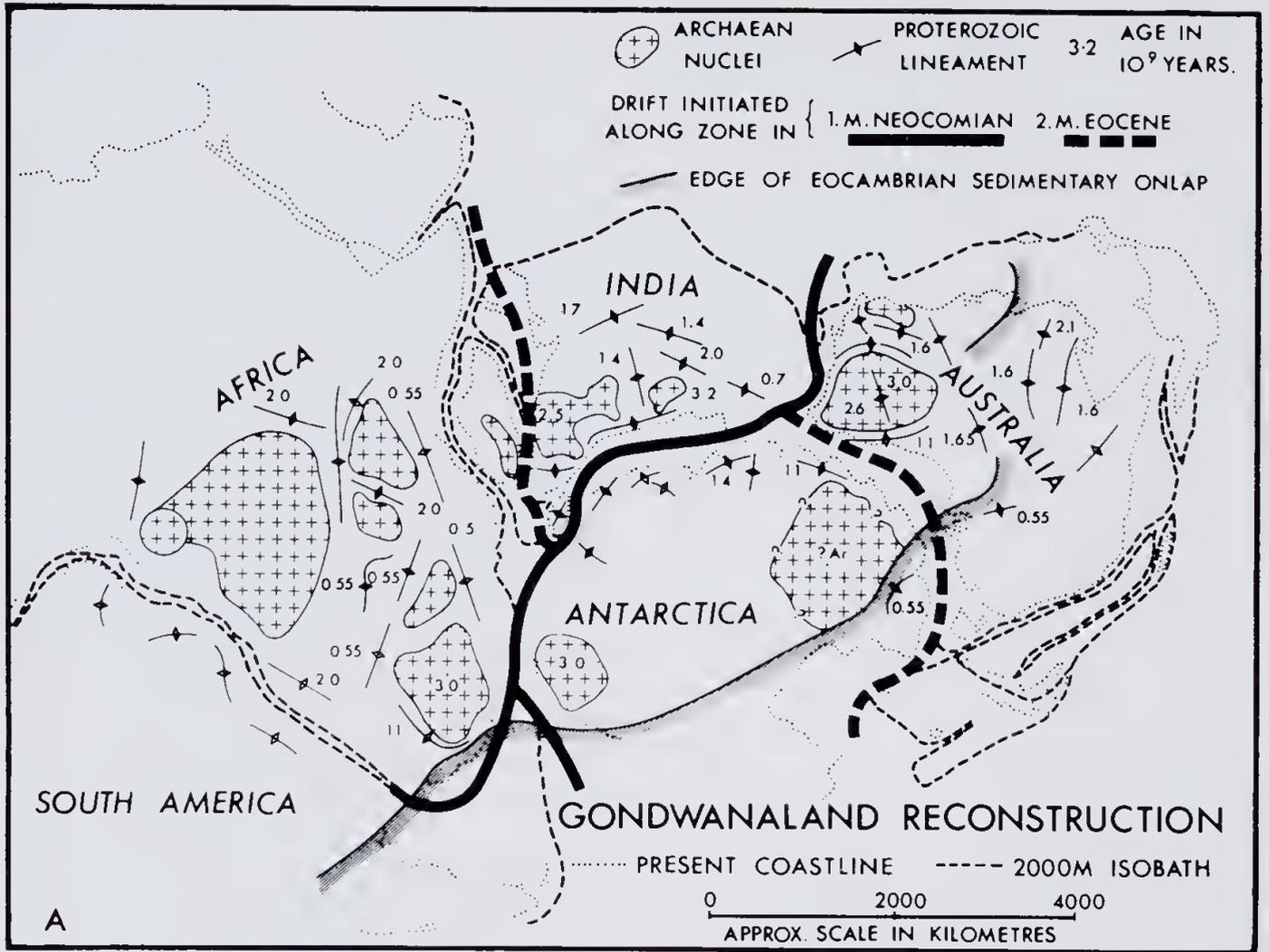


Figure 2A.—Reconstruction of the Gondwanaland continents (after several authors) showing major Precambrian cratonic elements and later Precambrian lineaments. Radiometric ages are shown in 10^9 years. Note that the prominent "Pan-African Event" of 0.55×10^9 years is primarily an overprint of a later tectonic event on earlier Proterozoic belts. The zones along which Gondwanaland broke in the Neocomian and in the Eocene are shown.

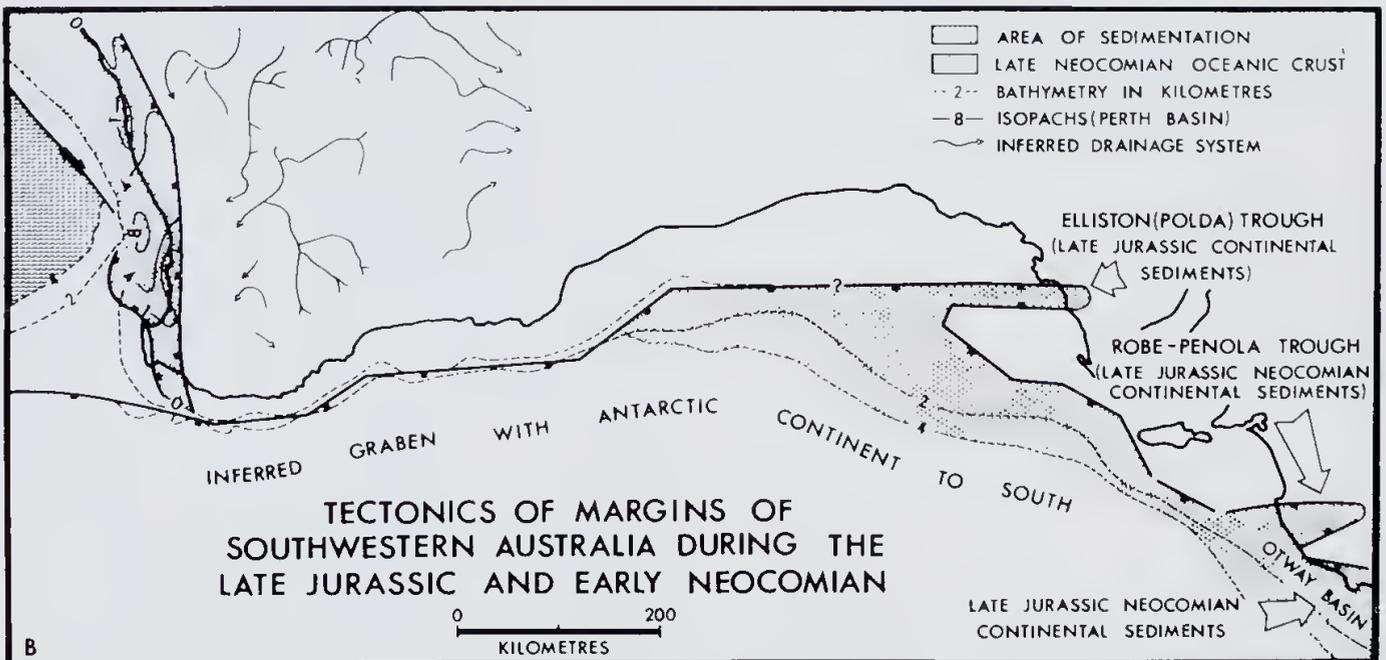


Figure 2B.—Late Jurassic to Neocomian sedimentation marginal to southwestern Australia and the inland drainage system.

In the vicinity of Perth, the Cardup Group can be dated as younger than the widespread pegmatite formation and dolerite intrusions of 700-750 m.y. (and probably no younger than 500-590 m.y.); and 350 km north of Perth, the Billeranga Group (Fig. 1) has been tentatively dated at 1,400 m.y. (Compston and Arriens, 1968).

In summary, it can be seen that the western and southern margins of the Archaean Yilgarn Block are marked by zones of Proterozoic high grade metamorphics, granites, and some un-metamorphosed sediments, the depositional and structural trends of which bear no relation to those of the Archaean nucleus. As can be demonstrated in other parts of Gondwanaland, these Proterozoic orogenic zones provide the lines of weakness along which the initial graben formation ("rifting") and final drifting apart occurred (Fig. 2).

Older Palaeozoic

In the northern Perth Basin, more than 1050 m of cross bedded, fine to coarse fluvial sandstones of probable Ordovician to Early Silurian age crop out (Konecki *et al.*, 1958). The Tumblagooda Sandstone may be a piedmont deposit associated with early movements on the northern portion of the Darling Fault for, although the entire sequence appears to be fluvial or deposited in extremely shallow water, geophysical evidence indicates that the unit may be up to 3000 m thick.

In the Officer Basin during the Ordovician, very extensive basalt flows covered folded Proterozoic sediments. Subsequently in the Ordovician, Devonian or Carboniferous, there was widespread deposition of two fine grained sandstone units (Lennis Sandstone and Wanna Beds; see Lowry *et al.*, 1972). The units are interpreted as shallow marine sediments deposited under the influence of strong tidal currents in a sea that probably extended from the Canning Basin around the southern side of the Musgrave Block into South Australia.

Permo-Carboniferous

In the northern Perth Basin, the older Palaeozoic fluvial deposits are overlain unconformably by a sequence of poorly bedded, poorly sorted, sandy siltstones containing abundant boulders (usually up to 50 cm in diameter, but exceptionally up to 6 m) of a great variety of Precambrian igneous, metamorphic, and sedimentary rocks. The variety of provenance, variety of size, and incompatibility of these boulders with their fine-grained host sediment leads to their interpretation as icerafted detritus dropped into an epeiric sea from icebergs. Although no more than 130 m can be measured in any one section, it is thought that they may attain a total thickness of 350 m. Their age is Late Carboniferous to Early Permian (Sakmarian). Up to 2400 m of similar sediments were deposited in the Carnarvon Basin to the north, and similar, but thinner, deposits are known down the length of the Perth Basin and in the Collie, Canning, and Officer Basins, so the glaciation was widespread in Western Australia

(Fig. 3). Sediments associated with this glaciation are known from Eastern Australia, and the other Gondwanaland continents, notably India, Africa and Antarctica.

In the northern Perth Basin, the glacial sequence is capped by 530 m of black marine shale (containing the Sakmarian goniatite *Metalegoceras jacksoni* Etheridge Jr.) which culminates in shellbanks rich in brachiopods, crinoids, and bryozoans. This, in turn, is capped by 330 m of fluvial and coal swamp deposits, indicating an amelioration of the harsh, glacial climate. Three hundred metres of marine siltstone complete the sequence (Johnstone and Willmott, 1966). Mild faulting and erosion of this sequence preceded the deposition of a Late Permian sandstone which precedes thick (300-1000 m) Early Triassic marine shale.

Analysis of the structure and stratigraphy of the sequences indicates that, whereas the Early Permian glacial and later marine siltstones were linked with the sea by a gulf which connected with the Carnarvon Basin to the east of the Northampton Precambrian Block, the seas of the Late Permian and Early Triassic came into the basin from the west of the Northampton Block. Thus the minor faulting in the Late Permian of the Dongara area (Hosemann, 1971) actually dates the initiation of a set of north-northwest-south-southeast trending faults and rifts which produced the deep graben of the Perth Basin from Triassic to Neocomian times. This fault trend marks a crustal weakness which also controlled the inferred large transform fault which permitted India to move away from Western Australia during the Neocomian (Falvey, 1972).

The lower part of the Permian sequence (including minor glacial deposits at the base) is thin in the southern part of the Perth Basin, and in the Collie and Wilga Basins which were probably part of the same basin of deposition at the time. However, the accumulation of more than 2000 m of Late Permian coal measures in the southern Perth Basin suggests that rifting began in this area in the Late Permian. There is little evidence of marine conditions reaching this part of the basin during any part of the Permian.

There is no evidence of Permo-Carboniferous to Triassic sediments along the south coast. In the Officer Basin, the Paterson Formation and the Wilkinson Range Beds are thin (60-100 m), flat-lying, glacially derived, boulder-bearing sandstones of Early Permian age. These lie unconformably on the older Palaeozoic and are overlain disconformably by the Early Cretaceous Bejah Beds.

Triassic to Early Neocomian

In the northern Perth Basin, the quiet deposition of the Early Triassic marine shales and the Middle Triassic deltaic sediments in a gently subsiding trough was interrupted in the Late Triassic by intense uplift of the margins of the trough and the dumping in the rapidly subsiding graben of more than 2000 m of coarse grained fluvial sandstones (Jones and Pearson, 1972). In the southern Perth Basin, coarse dominantly fluvial sandstone was deposited throughout the Triassic. Deposition continued

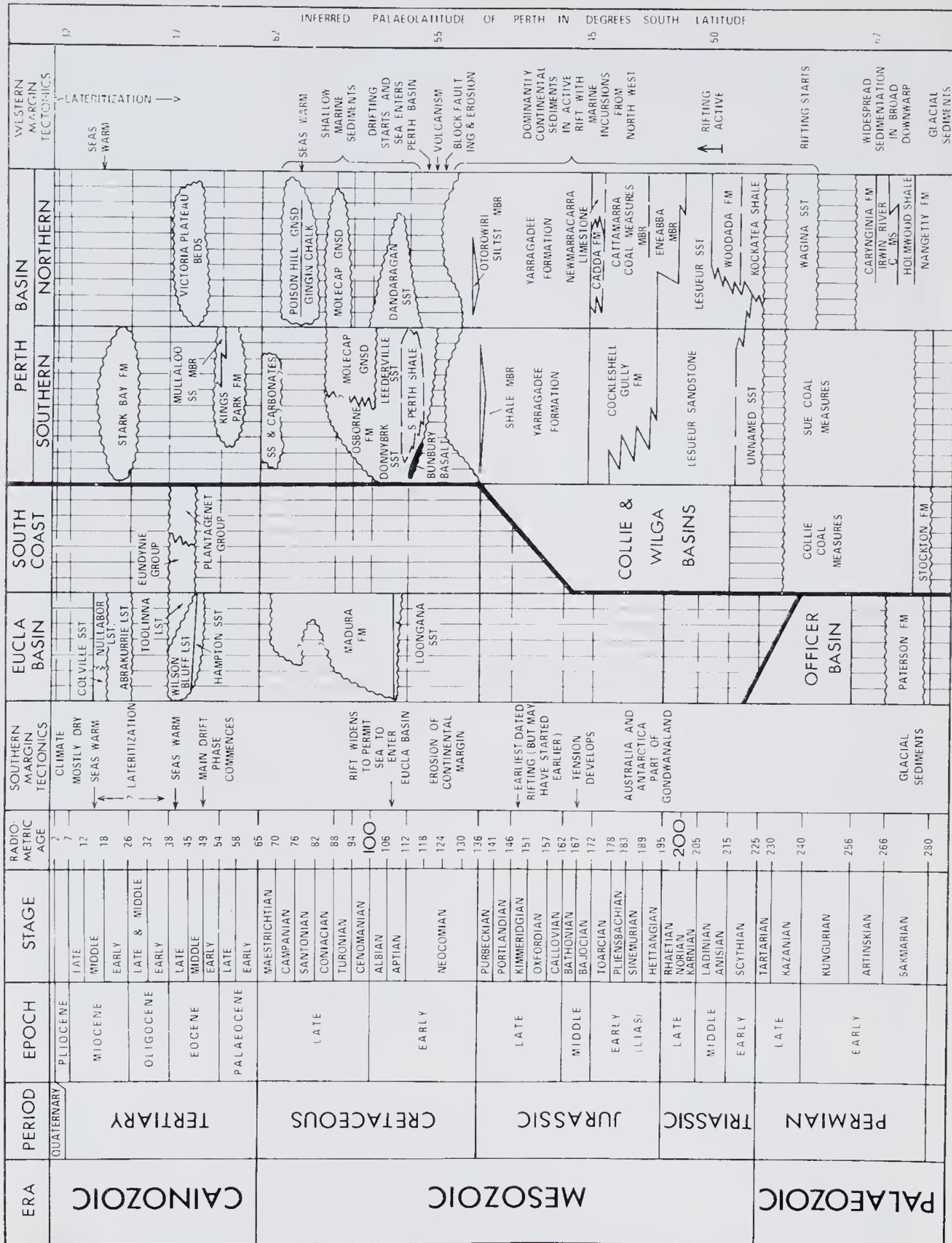


Figure 3.—Stratigraphic columns of the areas of sedimentation marginal to southwestern Australia.

uninterrupted into the Early Jurassic when up to 2400 m of sandstone and claystone grading upwards into coal swamp deposits were laid down. The climate of the Early Jurassic was thus favourable for the development of a dense coal swamp vegetation. In the Middle Jurassic, a minor marine incursion from the northwest deposited a widespread blanket about 250 m thick of shallow water marine shale, sandstone and limestone containing ammonites, pelecypods and gastropods of Bajocian age (Arkell and Playford, 1954).

Major movements of the trough and its borderlands in the Middle to Late Jurassic caused further deposition of the coarse fluvial sediments similar to those in the Triassic. Up to 4250 m of coarse sandstones were deposited during this major development of the Perth Basin rift.

In the Neocomian, the locus of intense down-faulting moved westwards into the offshore Vlaming Sub-basin where up to 6000 m of fluvial sand and estuarine shale and sand were deposited immediately before (and possibly during) the violent jostling of the fault blocks in the Perth Basin graben which preceded the active initiation of the transform fault which moved India away from the western coastal basins of Australia. The stage was then set for the next phase in the evolution of the west coast basins.

No sediments of Triassic to Neocomian age are known from the south coast area or the Eucla Basin. However, geophysical surveys and drilling in the Elliston (or Poldo) Trough and the Duntroon Basin on the eastern side of the Eucla Basin, show that graben formation commenced in this area as early as Late Jurassic (Smith and Kamerling, 1969). This graben formation continued eastward into the Robe-Penola Trough in the Late Jurassic and had reached the eastern Otway, Bass, and Gippsland Basins by the Neocomian (Griffiths, 1971). These graben were the precursors of the spreading which separated Antarctica from Australia. Thus, although there is no published evidence for rocks of this age off the southern coast of Western Australia, it is logical to assume that the graben between southwestern Australia and Antarctica had formed by Late Jurassic times, and possibly even by Middle Jurassic or earlier.

Neocomian-Maestrichtian

Tectonism in the Perth Basin reached a climax in the Neocomian (Jones and Pearson, 1972). The sequence of events included major subsidence of the Vlaming Sub-basin (up to 6000 m); a period of arching and faulting causing local uplift and erosion of as much as 2500 m of the recently deposited soft sediments; eruption of the Bunbury Basalt at the southern end of the basin, and subsidence of the continental margin causing a marine transgression. These events mark the change from continental "rifting" to "drifting". With generation of sea floor between India and Australia the tectonic stresses were relieved, and the Darling Fault and

most others ceased to move. Late subsidence within the graben was due to compaction of underlying sediments and general sagging of the continental margin. The precise mechanics of the split are still conjectural; however, it is likely that the Perth Basin is a rift controlled by an ancient crustal weakness that developed into a transform fault (Falvey, 1972).

Sediments deposited later in the Neocomian and Aptian include a thick marine shale west of Perth (South Perth Shale) and shallow marine and paralic glauconitic sandstone (Leederville Sandstone) (Fig. 4). Deposition at the southern end of the main Perth Basin was continental, but it presumably extended around the west side of the Leeuwin-Naturaliste Block, where marine sediments of this age have been recovered in deep sea cores (Burckle *et al.*, 1967).

The present salt lake system (Jutson, 1934), a relic of ancient drainage systems, is indicated on Figure 2B and has been discussed in several papers by Bettenay and Mulcahy (see their 1972 papers for full reference list).

The system seems to be a relic of the Late Jurassic-Early Cretaceous drainage, which was most active in filling the basins at that time, but which has had only a relatively minor sedimentational history since. Voluminous terrigenous sediments of Late Jurassic age (Perth Basin only) and Early Cretaceous (Perth and Eucla Basins) attest to well developed drainage systems to supply them. No sediments younger than Early Cretaceous seem voluminous enough to justify such a drainage system. Late Eocene sediments in Rollos Bore, Coolgardie (Balme and Churchill, 1959), show that the system is pre-Eocene. Although the present salt lake system is a relic of the most active (Late Jurassic to Neocomian) phase, it could also mark the drainage system which supplied sand to the Early Triassic.

In the Albian-Cenomanian and Senonian, thin greensands and a chalk bed were deposited north of Perth (Osborne Formation, Molecap Greensand, Gingin Chalk, and Poison Hill Greensand; see McWhae *et al.*, 1958). Maestrichtian sandstone and calcilutite occur offshore in Warnbro No. 1.

In the Eucla Basin, a marine transgression began in the Neocomian-Aptian (Ingram, 1968; more probably Aptian, A. Williams, *pers. comm.*). The beds of carbonaceous and glauconitic sandstone and shale (Madura Formation; see Lowry, 1970) lie on a deeply dissected granite surface in the southern portion of the basin, near the edge of the continental slope. The valleys, which are as much as 500 m deep, may have formed in the Late Jurassic and Neocomian by up-arching of the flank of a graben that developed along the impending Australia-Antarctica rupture. During the Aptian, much of the Australian continent was submerged and sea covered parts of the Canning, Officer, and Great Artesian Basins (Skwarko, 1967). In the central Eucla Basin, deposition of greensand continued, perhaps intermittently, into the Senonian.

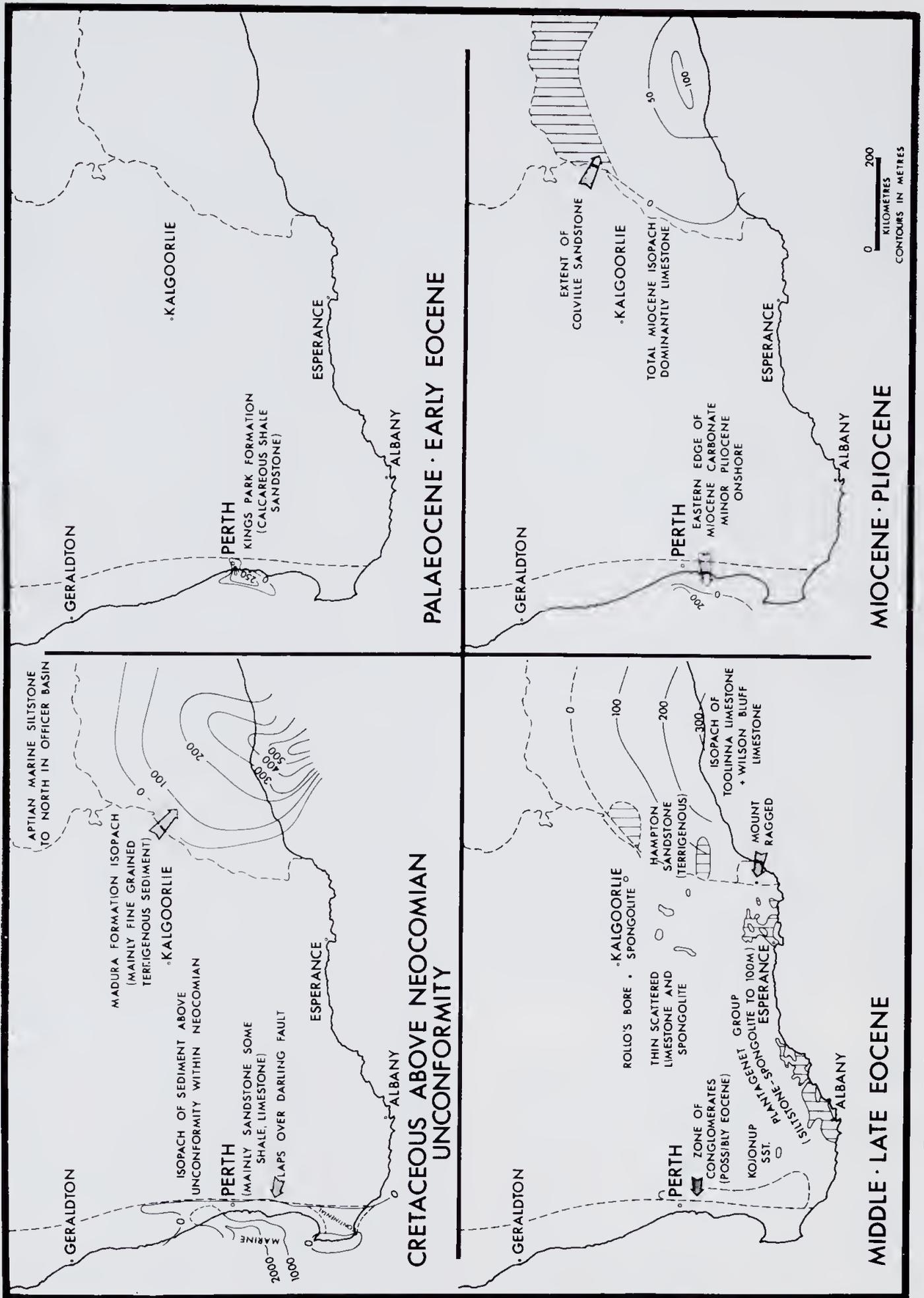


Figure 4.—Major cycles of deposition around southwestern Australia after the unconformity within the Neocomian.

The epeirogenic subsidence of the Eucla Basin is possibly part of a general subsidence of a newly developed southern continental margin following minor generation of sea floor between Antarctica and Australia. This interpretation is consistent with the palaeomagnetic data of Wellman *et al.*, (1969) and Weissel and Hayes' (1972) interpretation of sea floor magnetic anomalies. Although the latter interpretation is taken to indicate that the major motion of Australia away from Antarctica was initiated in the Eocene, stratigraphic evidence from the Eucla and Otway Basins indicates that a pronounced marine gulf extended across the southern part of the Continent during the Late Cretaceous. Thus Australia became an isolated continental mass by the uppermost Cretaceous, with only a tenuous link joining Tasmania to Antarctica across a transform fault.

Late Cretaceous faunas in the Gingin area and from the offshore Perth area contain abundant *Globotruncana* which Bandy (1967) would take to be an indication of warm water conditions. The presence of carbonate-rich sediments also supports this view. These warm water indicators are absent from the Eucla Basin but this absence could be due to facies control or water circulation rather than purely climate. It is unlikely that warm waters from the Indian Ocean would circulate freely into the narrow gulf separating Australia and Antarctica until at least the Middle Eocene when the southern tip of the Tasmanian peninsula had cleared Antarctica and thus permitted the warm Indian Ocean waters to flow through the widening gulf into the South Pacific Ocean. However, once the warm currents could penetrate the widening gulf, warm water forms from the Indian Ocean could migrate in an easterly direction along Australia's south coast. Hence the Eocene faunas of Australia's south coast should show marked similarities.

Rates of sedimentation and runoff had decreased markedly by this time and the drainage system probably became very subdued. This pattern of minimal influx of terrigenous material from the defunct river systems would have continued into the Tertiary.

Paleocene—Early Eocene

The only sediments of this age known are from the vicinity of Perth (Fig. 4) and have been documented by Quilty (*in press*). The maximum thickness of the Kings Park Formation near Perth is approximately 500 m of shale and sandstone with some carbonate content. The sediments can be differentiated into a northern sandy marine facies and a more southerly marine shale facies. The former may be related to the ancestral Swan River where it enters the Perth Basin near Walyunga National Park. The shale facies is likely to have been deposited by smaller streams (Canning and Helena Rivers) flowing into a deep embayment—probably an old submarine canyon eroded during the Late Cretaceous and/or Early Paleocene into Cretaceous terrigenous sediments.

The drainage at this time is very minor compared with the Early Cretaceous but probably it ran in the same stream channels.

Very little can be said of the climate at this time as foraminiferal faunas are almost cosmopolitan. *Globorotalia rex* Martin, *G. dolabrata* Jenkins and other keeled *Globorotaliae* may indicate warm water conditions (Bandy, 1964).

Middle and Late Eocene

Marine sediments of Middle and Late Eocene age occur in the Eucla Basin and along the south coast between Esperance and Albany (Cockbain, 1967, 1968, Lowry, 1970, Quilty, 1969)—see Figure 4.

In the Eucla Basin, both Middle and Late Eocene are present but the Plantagenet Group to the west is so far known to contain only Late Eocene faunas.

The Eucla Basin sediments (Hampton Sandstone, Wilson Bluff Limestone, Toolinna Limestone) consist of up to 300 m of biogenic carbonate sediments containing the warm water bivalve *Spondylus*. The thin sandstone at the base suggests minor terrigenous material being supplied by the poor drainage, probably from the northwest.

The Plantagenet Group consists of up to 100 m of fine sandstone, spongolite and minor limestone. Near Esperance, the limestone contains the large warm water foraminifer *Asterocyclina* and the tropical alga *Neomeris* (Cockbain, 1967, 1969).

Thus the Middle and Late Eocene sediments attest to warm water sedimentation and also the presence of minor southerly drainage.

Early and Middle Miocene

Sediments of Early and Middle Miocene age occur in both the Perth and Eucla Basins (Fig. 4).

In the Perth Basin, friable limestones with some dolomite and chert (Stark Bay Formation of Quilty, *in press*) occur offshore from Perth and attain a thickness of some 200-250 m. There is no terrigenous content. They contain abundant bryozoans and foraminifera including *Lepidocyclina* and keeled *Globorotalia*, both warm water indicators.

The age of the sediments is latest Early Miocene and earliest Middle Miocene.

Sedimentation in the Eucla Basin took place over a longer period, beginning before and ceasing after that in the Perth Basin. The age limits of the Eucla Basin Miocene are not as well established as those in the Perth Basin. The older Miocene sequence (Abrakurrie Limestone) seems to be Early Miocene (Longfordian of southeastern Australia) and underlies the Nullarbor Limestone and Colville Sandstone disconformably. The Nullarbor Limestone and Colville Sandstone are coeval and laterally equivalent. Both contain Middle Miocene warm water benthonic foraminifera which may indicate sediments slightly younger than the Middle Miocene of the Perth Basin. The Colville Sandstone occurs on the northern rim of the Eucla Basin and is probably derived from Palaeozoic sandstones by marine erosion.

Pliocene

Pliocene marine sediments occur in small, scattered, poorly-known lenses to the north, east and south of Perth. Darragh and Kendrick (1971) reported ages based on mollusc faunas and Kendrick (*pers. comm.*) has since substantiated a Pliocene age from Redcliffe (a Perth suburb) on the basis of the pelagic gastropod *Hartungia typica typica* Bronn.

The knowledge of the Pliocene is so far too imperfect to make any comments on palaeoecology.

Pleistocene—Recent

A wide variety of Quaternary units is developed around the coastal margin. On the west, the sediments of the central Perth Basin have been eroded to form a coastal plain with alluvium inland and a series of dune systems, lakes, interdunal swamps, and relict estuaries nearer the coast (McArthur and Bettenay, 1960). The calcareous dune sands show varying degrees of lithification and leaching, according to age. The lithified dune systems and intercalated marine lenses are known as the "Coastal Limestone". These form prominent hills along the coast and the backbone of several offshore islands and reefs. The total age range of the "Coastal Limestone" is unknown but the unit is still forming along the coast and probably on the seabed. The greatest known age is $100,000 \pm 20,000$ years for reef limestone on Rottnest Island (Teichert, 1967).

Palaeontological age control is very poor but Kendrick (*pers. comm.*) notes the presence of early Pleistocene marine molluscs at Jandakot. He also (Kendrick, 1960) has discussed the significance of a Late Pleistocene mollusc fauna in the "Coastal Limestone" at Peppermint Grove. Details of these various Quaternary rock and soil units are given in Dr. Seddon's excellent review of the Swan Coastal Plain (Seddon, 1972).

Similar dune systems occur along the south coast and, in the Eucla Basin, the Roe Calcarenite is tentatively referred to the Pleistocene. The formation is marine with a warm water fauna which may indicate an interglacial age for the unit if it is Pleistocene.

Other young sediments in the Eucla Basin include kankar and dune sands discussed in some detail by Lowry (1970).

Lateritization

Details of laterites in the southwest of Australia will be dealt with in a subsequent article in this volume, but some comments will be made here on stratigraphic evidence for the time of lateritization. In eastern arid areas the laterite is Miocene or Oligocene in age. The evidence is that the Late Eocene Eundynie Group around Norseman, the Plantagenet Group around Esperance and the Early Cretaceous Bejah Formation of the Officer Basin are all lateritized whereas the adjoining Middle Miocene Colville Sandstone of the Eucla Basin is not.

In the extreme southwest, Pleistocene alluvium and dune sands have been lateritized and laterite appears to be forming at the present day on the coastal plain where there is a temperate climate with a strongly seasonal rainfall of 750 to 1000 mm.

In coastal areas north of Perth, Late Cretaceous sediments are lateritized but there are no datings to indicate a minimum age. However, the laterite is considerably dissected, and a Tertiary age is likely. Farther north, in the Carnarvon Basin, lateritization has affected rocks of Late Eocene and older age but not Middle Miocene and younger.

Thus there was a major period of lateritization in the Oligocene and/or Miocene. Earlier periods have been assumed by other workers, but there is no geological evidence for them. Since the Middle Miocene, lateritization has occurred (presumably intermittently) only in coastal areas of the southwest that have a moderate and strongly seasonal rainfall.

Crustal movements in the Cainozoic

Whereas the Eocene sediments along the south coast of Western Australia accumulated in very shallow water and are now only a few metres above their level of deposition, the old beach levels associated with this cycle of sedimentation are now at about 300 m at Mt Ragged (Lowry, 1970) and the Stirling Range (H. Schumann, *pers. comm.*). Also, marine sediments of Eocene age now at 300 m at Lake Cowan near Norseman, and in the Kennedy Range in the Carnarvon Basin, near the northern margin of the Yilgarn Block. Thus it appears that the whole shield area (apart from the present coastal margins) has been uplifted by approximately 300 m since the Eocene, but the relative importance of marginal warping and eustatic sea level changes cannot be determined.

Perhaps the most perplexing structural unit near the south coast of Western Australia is the Stirling Range. This feature, which lies just south of the southern margin of the Archaean Shield, thrusts metasediments of the Albany-Esperance Block to a height of 1200 m above sea level (about 1000 m above the level of the flat shield to the north). The abruptness and straightness of the north front of the range suggest that this is a very young feature, but the presence of the Late Eocene marine bench at 300 m and the concordance of this with other Eocene levels indicates that the Stirling Range was in existence prior to the Late Eocene. Perhaps its elevation was a final adjustment of the continental margin before block faulting ceased with Eocene drift.

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2.—Landforms and soils of southwestern Australia

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Abstract

The landforms of southwestern Australia are outlined as a basis for a description of the distribution of the extremely weathered materials and superficial deposits on which the soils are formed. While soils on younger landscape elements change predictably with climatic change, a major factor controlling soil distribution is the degree of erosional modification of the leached and deeply weathered profiles associated with the older landforms which are extensively preserved, both in higher rainfall areas and the arid interior. The significance of the soil patterns and their characteristics are briefly discussed.

Introduction

The area dealt with in this paper lies to the south of the latitude of Geraldton, and extends from the west coast eastwards to include Kalgoorlie and Esperance. It forms part of the Great Plateau of Western Australia (Jutson, 1914) consisting of a stable Archaean shield, characterized by low relief, extending over the Mesozoic rocks of the Perth basin in the north west, all flanked by narrow coastal plains of younger sediments.

It is part of the landscape described by Hills (1961) an "ageless and undatable old land". Woolnough (1927) associated the widespread deep weathering with peneplanation, and Prescott (1931) pointed out the occurrence of leached, acid, lateritic soil materials extending from the humid coastal areas to the now arid interior.

Early soil maps such as that of Prescott (*loc. cit.*) and later Stephens (1961) influenced by the Russian school of pedologists, emphasized climatic zonation, and south-western Australia tended to be shown with soil boundaries parallel to the isohyets. Teakle's regional soil classification, published in 1938, and subject to the same influence, left out of account the "azonal" lateritic soils, dealing mainly with the more fertile soils of the younger landscape elements. This was good sense at that time since the technology necessary for agricultural development of the lateritic soils, including the use of minor elements, was only just then becoming available, and the use of soils in the higher rainfall areas as a bauxite ore was still some years away. A later compilation in the form of the Atlas of Australian Soils (Northcote *et al.*, 1967), based on much more detailed information, indicates a strong relationship between soil distribution and drainage pattern as well as climate, while Mulcahy *et al.* (1972) have shown that geological structure and the extent of drainage rejuvenation are also important.

Stephens (1946), in his classical paper on pedogenesis following the dissection of lateritic regions by downcutting streams rejuvenated after uplift, suggests a fairly simple picture of lateritic materials preserved on peneplain remnants and removed from the slopes below. Playford (1954), on the other hand, pointing out that lateritic materials are frequently found at many levels in the one landscape, and assuming laterite formation during some single period in the past, concluded that this must therefore have been postuplift.

Subsequent investigations in soil-landform relationships, on which this account is based, show that the situation is probably rather more complex than the early workers believed. It appears that laterite profiles, including both surface ferruginous horizons and underlying pallid zones (Walther, 1915), are to be found extensively in a wide range of topographic situations, ranging from piedmont deposits of the Swan Coastal Plain (McArthur and Bettenay, 1960), and older alluvial terraces in well-incised valleys such as that of the Avon River (Mulcahy and Hingston, 1961), to the most extensive divides of the Great Plateau. While the laterites of some of the younger landforms, particularly those of the Swan Coastal Plain, may be regarded as forming today in the sense of meeting the classical environmental requirements for laterite formation postulated by Prescott and Pendleton (1952), those of the older landforms clearly cannot, being either in unsuitable topographic situations or in semi-arid and arid climatic conditions, or both. Further, in all but highest rainfall areas the extremely leached and weathered pallid zones now contain an appreciable store of soluble salts (Dimmock *et al.* in prep.) so that leaching conditions are clearly less effective than in the past.

Physiography

Figure 1 shows some of the main physiographic features of south western Australia, to which the soil pattern may be related.

The Darling Scarp marks the western margin of the shield and Great Plateau, beyond which the Precambrian rocks are buried by a considerable thickness of sediments of the Perth Basin and Swan Coastal Plain. To the south the shield slopes gently into the Southern Ocean, with a discontinuous, thin veneer of Tertiary and Recent sediments. The section (Fig. 1, ABC) shows clearly the relatively high relief and elevation of the Darling Range, regarded by King (1962) as a marginal upwarping of the shield rocks. It is separated from the gradually rising plateau levels of the interior by a belt of

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lower country showing partial coincidence with an important zone of seismic activity, the "Yandanooka/Cape Riche Lineament" (Everingham, 1968).

A little further inland is another important, but not so obvious physiographic feature, the Meckering Line (Mulcahy, 1967), which marks a striking change in the drainage pattern. Inland of it the drainage is sparse, open and sluggish, with chains of salt lakes in the main trunk valleys. A large proportion of the westward-flowing lake chains joins the headwaters of the Swan-Avon system, off the mouth of which is a prominent submarine canyon on the continental shelf (Von der Borch, 1968). Most of the remainder reaches the Moore and the Blackwood Rivers (Bettenay and Mulcahy, 1972). A major continental divide separates these systems from a generally eastward trending one draining to the Nullarbor Plain and Great Victoria Desert in the interior. In most years under the present climatic regime the system as a whole does not flow, acting as a sump in which the salts accumulate in the playa lakes. In exceptionally wet years, however, it becomes functional, and flowing water flushes out the accumulated salts into the downstream drainage lines (Fig. 1).

Downstream of the Meckering Line in the west, the drainage lines form a closer network, have steeper gradients, are more sharply incised, and thus form a much more effective drainage system functional in all normal winters. Depth of incision of the streams increases progressively, with a change from shallow flat floored valleys to deep V-shaped valleys where they issue from the Darling Scarp.

Thus the zone marginal to the Meckering Line, particularly in the Darling Range, is one of considerable relief relative to that inland of it. Nevertheless, many of the more extensive divides in the marginal zone are upland areas of low relief, with features such as lakes and swamps associated with sluggish drainage lines comparable with those inland. Their broad, flat-floored valleys characteristically have grey sandy valley fills, and some are known to have sedimentary sequences of considerable thickness, such as the Kirup Conglomerate (Hobson and Matheson, 1949), or the Permian sediments of the Collie Basin (Lord, 1952). While it is tempting to regard these features collectively as dismembered remnants of the old drainage systems now preserved only in the interior, such an interpretation is undoubtedly too simple. It could not account, for example, for the Kirup Conglomerate which, with its smoothly rounded cobbles in a finer sandy and clayey matrix, is obviously a deposit resulting from a high energy means of transport. A conclusion must await further investigations in a field of enquiry as yet virtually untouched.

Laterites, superficial deposits and soils

Distribution of lateritic materials

Figure 2 illustrates the broad regional distribution of lateritic and other soil materials in south western Australia, based largely on Northcote *et al.* (1967).

The map distinguishes between the low level laterites of the Swan Coastal Plain, the "iron-stone gravels" or bauxitic laterites of the Darling Range and adjacent high rainfall areas to the south, and the extensive "sand and gravel plains" inland and to the north. All may be classed as laterites in that they have surface horizons of accumulation of iron oxides, frequently, but not invariably overlying deeply weathered kaolinized country rock, the pallid zone (Walther, 1915). The Darling Range laterites, together with the sandplains, are associated with Jutson's (1914) Old Plateau and Woolnough's (1918) Darling Peneplain, but the Section ABC of Fig. 2 shows the considerable relief of the lateritic surfaces of the Darling Range—only inland of the Meckering Line does the low relief traditionally postulated for the lateritized peneplain become apparent. In both the Darling Range and the sandplain areas the lateritic pallid zones are most widespread and deepest. They may be up to 30 metres in thickness, beneath the floors of the trunk valleys of the inland drainage systems, while they are much shallower beneath the sandplains of the divides (Bettenay *et al.* 1964). Downstream of the Meckering Line deepest weathering is probably associated with the older valley forms of the low relief upland divides.

On the Swan Coastal Plain, west of the Darling Scarp, deep pallid zones are common on the older piedmonts, but associated ferruginous duricrusts are less frequent, except near the foot of the scarp on slightly elevated spurs corresponding with the Ridge Hill Shelf described by Prider (1948).

It is evident (Fig. 2) that areas free or almost entirely free of lateritic materials are restricted, being confined to the deeply entrenched valleys of the downstream sections of streams as they issue from the Darling Range, or further inland, to the entrenchment of streams associated with the Yandanooka/Cape Riche Lineament. High points above the general level, such as the Stirling Range, and a number of others too small to show because of scale, are also almost completely free of laterite.

The principal remaining area of the map (Fig. 2) shown as "Dissected Laterites" is one of considerable complexity in terms of landforms and soils. The small divides and valley side spurs tend to be capped with lateritic materials, and bounded by prominent, erosionally-active scarps or breakaways, the long pediment slopes below them being underlain by pallid zones of the truncated laterites. These features are best developed immediately west of the Meckering Line, where available relief is greatest, while rainfall is still low, less than 500 mm per annum. Towards the coast, and in higher rainfalls, these typically arid-zone landforms are replaced by more gently inflected concavo-convex slopes associated with less active erosion. Only adjacent to sharply incised streams and on the steeper valley sides are fresh rock materials locally exposed.

Superficial deposits

Many of the lateritic materials mapped in Fig. 2 are detrital. Those of the high relief areas of the Darling Range often consist of fragments of ironstone, and sometimes fresh rock, recemented with skins of iron oxide (Mulcahy, 1961). These materials may extend downslope as colluvial sheets overlying a variety of substrates, including relatively fresh country rock (Mulcahy *et al.*, 1972).

The sandplain materials too have been shown to be colluvial deposits of local origin derived largely from the ferruginous duricrust of pre-existing laterites (Mulcahy, 1961; Brewer and Bettenay, 1973). Further, they are multiple deposits, not all of the same age; some, the most extensive, carrying undifferentiated sandy yellow earth soils, are clearly very young, while others are older, and have developed segregations of iron oxide which harden on exposure. Both forms, the undifferentiated younger deposits overlying the older, may be found capping classical lateritic residuals bounded by breakaways (Mulcahy, 1964). It follows that the surfaces of such residuals cannot be uncritically accepted as any kind of time marker or datum.

Colluvial and alluvial deposits derived from fresh rock outcrop are important though limited in extent. They are confined principally to the valley sides and floors, and to limited areas on the Swan Coastal Plain, where they give rise to the more fertile soils in comparison with those derived from lateritic materials. Fresh colluvial deposits are also occasionally found on upland divides where rock outcrops are exposed by the stripping of the pre-existing laterites to form the sandplain deposits downslope.

Aeolian activity and dune formation are not common on the sandplain surfaces, except perhaps in the arid interior, in the east of the area considered. There is some aeolian activity associated with the drainage lines. Bettenay (1962) has described the formation of "lake parna", a silty, calcareous and saline deposit blown out of the salt lake chains, which may account for the extensive calcareous soils shown in Fig. 2. They may, on the other hand, be due in part to the more extensive occurrence of basic and ultrabasic rocks in the eastern goldfields. Aeolian sands blown out of stream channels have been reported by Northcote *et al.* (1967) from the higher rainfall areas. Windblown coastal beach dunes are almost continuous, particularly on the west coast, and show age sequences related to Pleistocene sea levels (Fairbridge, 1954; McArthur and Bettenay, 1960). Aeolianite limestone dune and beach rocks, the result of leaching of the original calcareous sands and consolidation of the lower layers by deposition of carbonates, are prominent in the coastline, offshore reefs and coastal islands (Fairbridge, 1953).

Soils

Only a brief outline of the nature of the soils, related to the foregoing account of the geomorphology and superficial deposits, can be

given here. A considerable amount of further information within this framework may be extracted from the published Atlas of Australian Soils (Northcote *et al.*, 1967), with careful study of the map legend and the accompanying Memoir. Reference to areas of detailed study on which this account is based is also given where relevant.

Relatively little has been published on the Darling Range soils, apart from a broad scale study by Mulcahy *et al.* (1972). Smith (1951a, 1951b) has published accounts of the rather similar patterns in the Donnybrook Sunkland and towards the south coast. In the latter of these, on the Frankland-Gordon river valley, he drew attention to the sequential change of valley form from the broad valleys of the inland areas to the more sharply incised forms downstream. The dominant soils are, of course, the lateritic gravels (KS-Uc4.1 and KS-Uc4.2)*, consisting of up to 5 metres or more of ironstone gravels in a yellow sandy matrix and the related lateritic podsolics (Dy3.61) with ironstone gravels in a sandy surface overlying a mottled yellow-brown clay subsoil. These materials frequently overlie a pallid zone up to 30 metres or more in thickness. Massive ironstone pavements are common on ridgetops and occasionally on slopes. It is worth emphasizing that, apart from more extensive divides, there is some considerable relief (Fig. 2), with slopes up to 8°. In general, the gravels tend to become finer downslope, sometimes grading into sandy yellow earths (Gn2.21) in the lowest positions. The mid-slope gravels are those currently being mined as bauxite. The broader valleys of the more extensive divides carry grey sands over ironstone gravels (Uc2.3) or solonetzic profiles (Dg3.81), both overlying deep pallid zones. Further downstream the sides of the more incised valleys have a range of soils including red and yellow podsolics (Dr2.21 and Dy3.21) and red and yellow earths (Gn2.14, and Gn2.21).

The complex soil pattern of the zone of dissected laterites has been described by Mulcahy and Hingston (1961), and Bettenay and Hingston (1964). West of the Meckering Line the truncated laterites and limited exposures of fresher rock give rise to a range of solodic and podsolc soils (Dy3.82 and Dy3.81) and some red-brown earths with generally neutral reaction trends (Dr2.22). Further inland, with longer, gentler slopes and lower rainfall, reaction trends of the red-brown earths become alkaline (Dr.2.33).

The soils of the predominantly sandplain areas and the associated broad valleys, forming the larger part of the agricultural area of Western Australia, have been described by Bettenay and Hingston (*loc. cit.*) for an area representative of the shield and by Churchward (1970) where they are extensively developed over the Jurassic sediments, often sandstones,

*Notation in parentheses after names of great soil groups refers to the classification of Australian soils by Northcote 1971.

flanking the shield to the north. The sandplain soils are predominantly sandy yellow earths (Gn2.21) with some sands over ironstone gravels (Uc5.22). The limited areas of fresher rock outcrop on the valley sides, and the alluvial deposits of the valley floors carry sodic brown soils (Dr2.33) with calcareous subsoils. Both upland and valley floor are, however, underlain by lateritic pallid zones, deepest in the latter situation, where the ground water is similar in composition to sea water, though it may exceed it in the concentration of salts. Thus the relatively fresh materials of the soils of the valley floors, which are calcareous and alkaline, overlie acid and saline substrates. Bettenay *et al.* (1964) calculate that 90% of the salts stored in the landscape are in these valley ground waters, and only a small proportion in the rather more obvious playa lakes.

The aeolian lake parnas (Bettenay, 1962) give rise to the silty, saline calcareous earths (Gc1.12 and Gc1.22) adjoining the salt lakes, usually on the eastern or south eastern (downwind) margins. The greater inland extent of these soils (Fig. 2) may be due to the greater extent of the lakes as a source area, or alternatively to a greater relative abundance of fine textured basic and ultrabasic rocks.

The Swan Coastal Plain provides two important age sequences of soils covering a period extending as far back as the Mindel-Riss interglacial (McArthur and Bettenay, 1960) or perhaps beyond it. One is developed on the coalescing piedmonts near the foot of the scarp, and the other on the wind blown sands of the coastal areas.

The older, and most widespread, alluvial deposits have been lateritized, but also have been extensively stripped, so that the dominant soil is a meadow podsollic (Dy5.81) consisting of a sandy surface over a poorly structured subsoil clay of low permeability developed in the lateritic pallid zone. Younger deposits, in the form of the terraces incised in these older materials, or of alluvial fans laid over them, carry a sequence of red and yellow podsolics (Dr2.81 and Dy2.21) and of undifferentiated soils on the relatively fresh youngest deposits. Thus McArthur and Bettenay (*loc. cit.*) were able to establish the age relationships of the soils by the frequently observed and invariable order of superposition of the deposits.

The youngest beach dune systems are at the present coastline, consisting of a highly calcareous shell sand (Uc1.1). Inland they are succeeded by slightly podsolized yellow sands (Uc4.2), almost entirely quartz, but with some local areas where heavy minerals are abundant. The yellow sands are invariably underlain by aeolianite rock which, however, extends beyond them far to the west, underlying the present day dunes at the coast and on the offshore islands, so that the system must have been at one time far more extensive. The oldest system furthest inland has now lost its dune morphology, and is of low relief compared with the younger systems nearer to the coast. Its soils

are extremely leached and podsolized white quartz sands with B horizons of iron and organic matter accumulation (Uc2.3). They are important intake areas for the coastal plain aquifers and are underlain by fresh ground waters at shallow depths.

Discussion and conclusion

The account of soils and landforms given here is necessarily brief and incomplete, partly because a comprehensive treatment is impossible in a short paper, and partly because of gaps in our knowledge. Similarly, a discussion of the significance of the data presented must also be limited, since it would involve consideration of a large number of aspects, ranging from fundamental questions of soil and landscape development to practical and applied problems as diverse as minerals exploration, agricultural technology, or land use planning. Some of the more important are briefly considered below.

Landscape development

Preoccupation with questions of the age and development of laterite is a common and understandable characteristic of discussions of this topic in Western Australia. One or perhaps two periods of formation in the past are assumed (e.g., Prider, 1966), and thus the possibility of using a lateritized surface as a time marker is raised.

The evidence reviewed here shows that well-developed, deep laterite profiles may be found on surfaces as young as (early?) Pleistocene on the Swan Coastal Plain, where the process may still be continuing. They are most widespread on the older landscape elements of the Old Plateau, which Johnstone *et al.* (1973) considered to have been established in its present form by the mid-Cretaceous. The older laterites, except in the highest rainfall areas, now contain appreciable quantities of soluble salts in their pallid zones indicating that the necessary leaching conditions for their development are no longer operative. These facts, together with the detrital and transported nature of many lateritic materials, makes their use as a stratigraphic marker suspect, though they are, of course, likely to be preserved where erosional forces are least effective, i.e., on gentler slopes and in well vegetated higher rainfall areas.

Age of landscape is much more likely to be indicated by a combination of landscape characteristics rather than the occurrence of a single characteristic such as laterite. These would include low relief, widespread deep weathering, ineffective drainage systems, and widespread retention within the landscape of weathering products and sediments derived from them. These are the conditions found most extensively inland of the Meckering Line.

Tectonics are, of course, an important factor in landscape development. In this connection the correspondence of entrenchment of the drainage and greater relief with the Yandanooka/Cape Riche lineament (Fig. 2) is noteworthy, and is reflected in the soil pattern with

the exposure of fresher rocks as soil parent materials and the truncation and dissection of the lateritic profiles.

Ecological implications

Southwestern Australia is probably unique in its great extent of deeply weathered and leached soil materials, and consequent extremely low levels of natural soil fertility. An account of the natural vegetation adapted to these conditions is given elsewhere in this volume. Isolation by climatic barriers, particularly that of aridity, is often invoked to account for some of the unique features and speciation in the Western Australian fauna and flora. An additional factor may be the formidable barrier presented by the great extent of infertile sandplain soils on the major continental and regional drainage divides shown in Fig. 2.

Minerals exploration

The great extent of deep weathering and of superficial deposits, particularly the sandplains, not directly related to the underlying geology, obviously makes location of ore bodies difficult. In many areas the nature of the surface materials is very poorly understood; for example, the mullisols of the eastern goldfields, which may be either aeolian deposits blown from the lakes, or formed directly from ultrabasic rocks.

The old drainage lines of the interior and possible remnants of them in marginal areas are also of importance in this context, since they drain catchments now deeply weathered, including those in which ore bodies have been discovered. Deep leads are well known in the eastern goldfields (e.g., Campbell, 1906), and have been described from the extreme south west at Greenbushes, where some of the tin mined is alluvial (Hobson and Matheson, 1949). The study of these and other fragmented remnants of old drainage and sedimentary systems shown in Fig. 1 may lead to further discoveries of economic value.

Agricultural development

Early pastoral and agricultural development was confined to the more fertile non-lateritic soils of the valley floors and flanking rock outcrops, where, too, water supplies and natural grazing for stock were more readily available.

With the identification of the nutrient deficiencies, including the minor elements zinc, copper, cobalt and molybdenum, which limit crop and pasture establishment on the lateritic soils, and with the growth of a fertilizer technology, agricultural development has been, until recently, proceeding at an extremely rapid rate on these soils. This has been possible, however, only where rainfall is adequate, so that inland of about the 250 mm isohyet, where sandplains are extensive, neither farming nor grazing is possible, due to the low nutritive value of the native vegetation and the frequent occurrence of poisonous legumes. Only further inland again, in the vicinity of the eastward draining salt lake systems, does pastoral activity become possible.

Hydrology

The store of soluble salts in the widespread lateritic pallid zones (Dimmock *et al.* in prep., Bettenay *et al.*, 1964) presents a peculiar hydrologic problem. It is continually being replenished by atmospheric accession in rainfall at rates of the order of 200 kg/ha NaCl in high rainfall areas of the Darling Range, falling off rapidly inland (Teakle, 1937, Hingston, 1958). Its retention within the landscape is apparently a matter of an extremely delicate balance. This is easily disturbed by clearing of the perennial native vegetation with its deep rooting systems and growth habit persisting into the dry summer season and its replacement by short lived shallow rooting, winter growing, annual crops and pastures. As a result evaporative losses of water from surface soils decrease and ground water recharge increases, with increased discharge of water and salts in streams. Agricultural development on sandplain areas inland of the Meckering Line has thus increased the frequency with which the salts from the lake chains are flushed into the headwaters of the major rivers, so increasing the salt content of the latter. Where drainage systems are ineffective the salts accumulate in the valleys, so that agricultural development has led to soil salinity in those situations (Lightfoot *et al.*, 1964). Peck and Hurlle (in press) in a study of water and salt balances of farmed and forested areas show that catchments with average annual rainfalls less than 1000 mm/annum, if extensively cleared, become unsuitable for damming for water supply purposes due to the salinity of the water. Their analysis also shows that where the salt balance is so disturbed the achievement of a new equilibrium at an acceptably low level of salinity may take times of the order of tens, or more commonly, hundreds of years.

Land use planning

Development of different forms of land use in southwestern Australia has proceeded very largely on an *ad hoc* basis. Gold, and later other minerals, were mined where most readily accessible, and when technological development and growth of world demands made them transportable and marketable.

Agricultural development has proceeded similarly, where the current state of farming technology permitted, and in response to the fluctuating demands of overseas markets. While farming has built up soil fertility by importing phosphate and through the use of legume nitrogen, it has been at the cost of considerable effects on water supply and quality. Only forestry, with its traditional attachment to the policies of sustained yield, under management by a single State authority, has developed on a conservative basis. Even so, the native hardwood forest today compares badly with the few isolated areas within it still untouched by the timber fallers and sawmillers. But the extent to which the forest has been preserved is the extent to which the delicate hydrologic balance,

on which the water supplies of the south-west depend, has been conserved.

As the population and industrial and mining development increases in the south west of Western Australia, with its relatively equable climate, competing demands on the agricultural, forestry, mineral, public amenity and water supply resources especially in the Darling Range, will increase. Of these, the last is most likely to be limiting, so that its conservation is of highest priority.

A continuing objective of agricultural and forestry research should be the restoration of the hydrologic balance through the strategic deployment of land-use systems more efficient in the use of water, since its misuse and wastage through inability to utilize the abundant winter rainfall is the root cause of water supply and salinity problems.

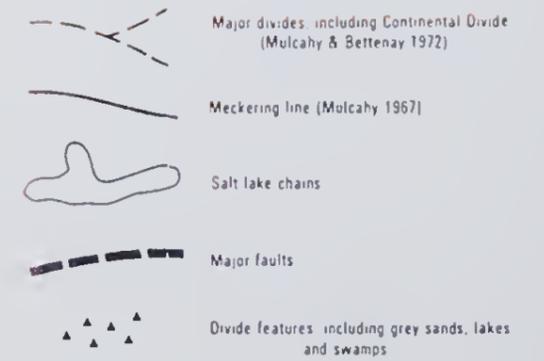
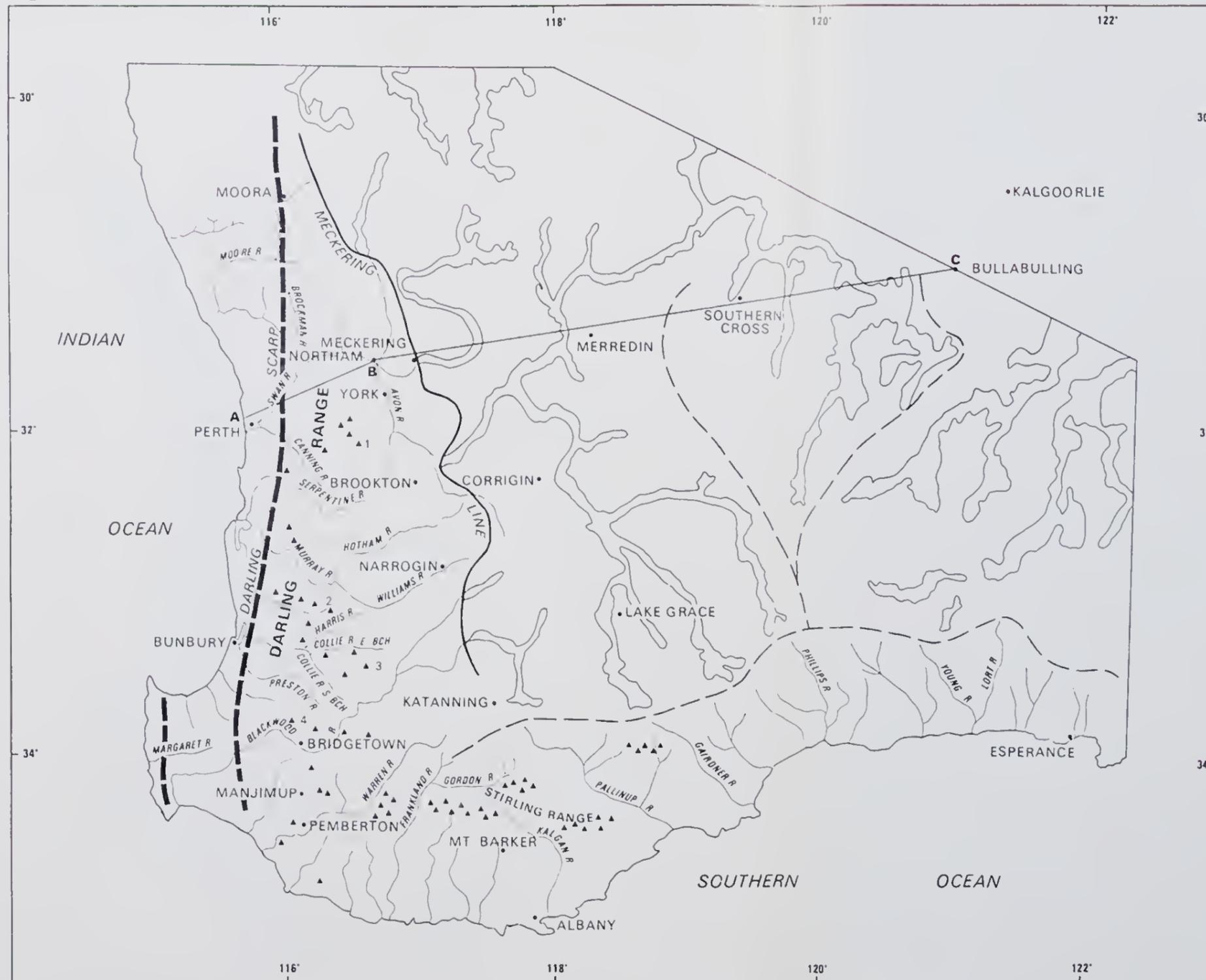
Acknowledgement.—I am grateful to Mr. W. M. McArthur for compilation of the figures, and for valuable criticism of the text.

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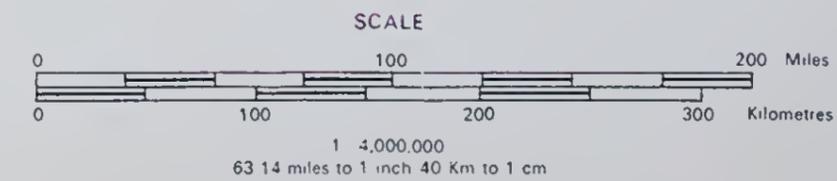
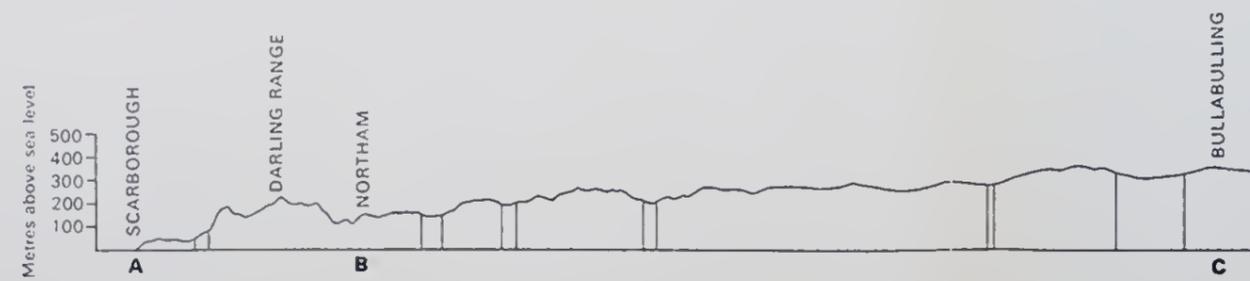
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Figure 1. PHYSIOGRAPHY OF SOUTH WESTERN AUSTRALIA.

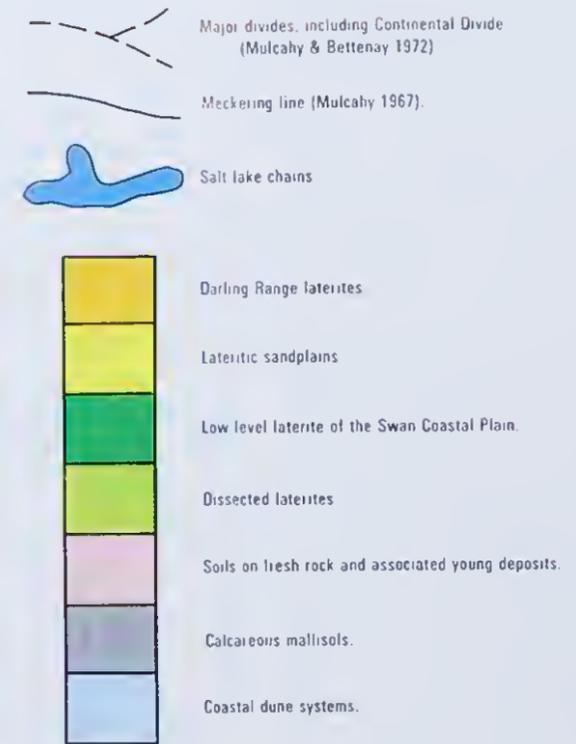
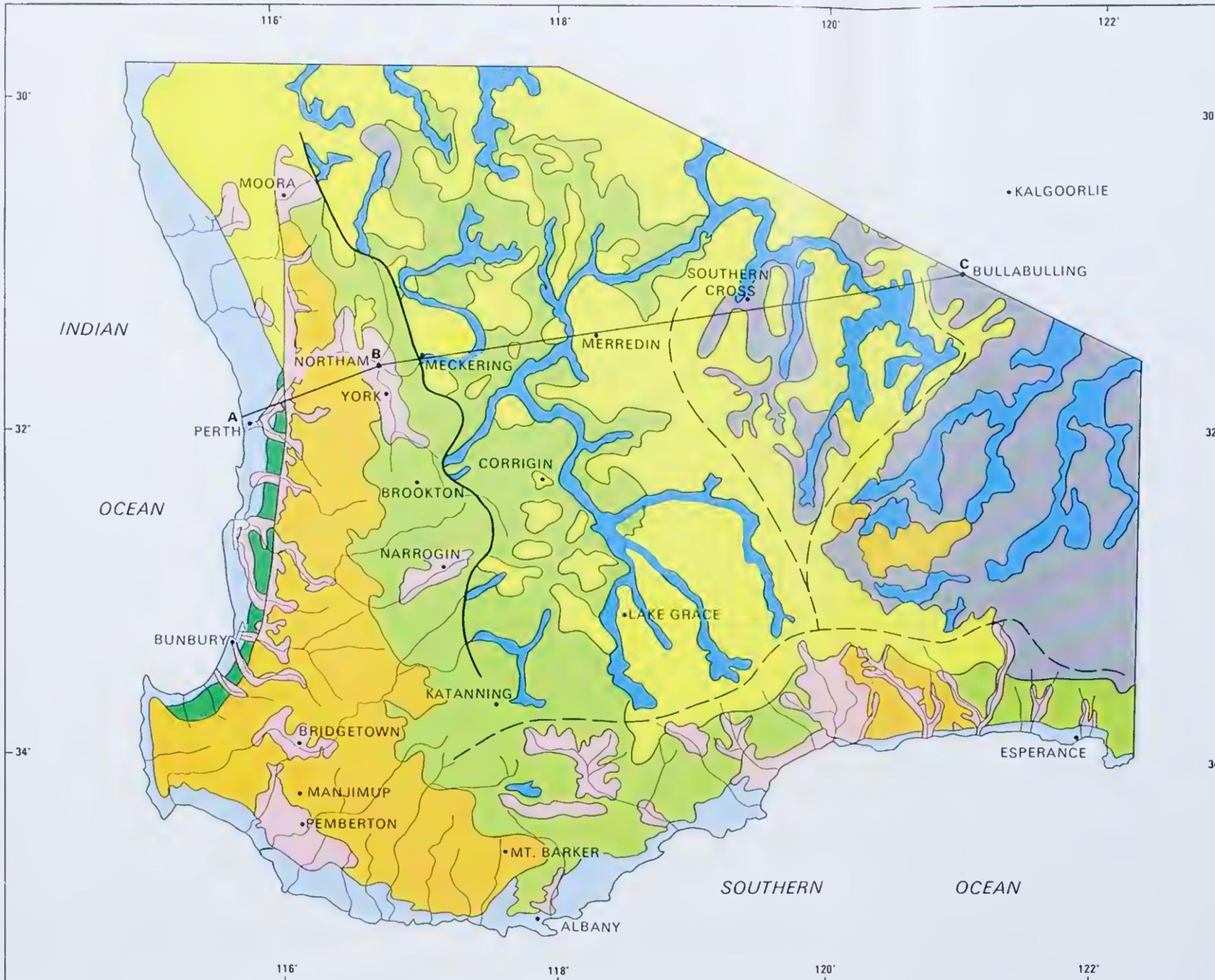


- DIVIDE FEATURES INCLUDE
- 1 Grey sandy valley floors with swamps (Mulcahy et al. 1972)
 - 2 Old valley fills indicated by cobble traces (Churchward and Bettenay, in preparation)
 - 3 Grey sands overlying Permian sediments (Lord 1952)
 - 4 Kirup conglomerate (Hobson and Matheson 1949)



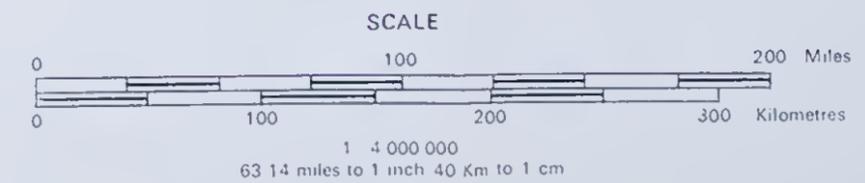
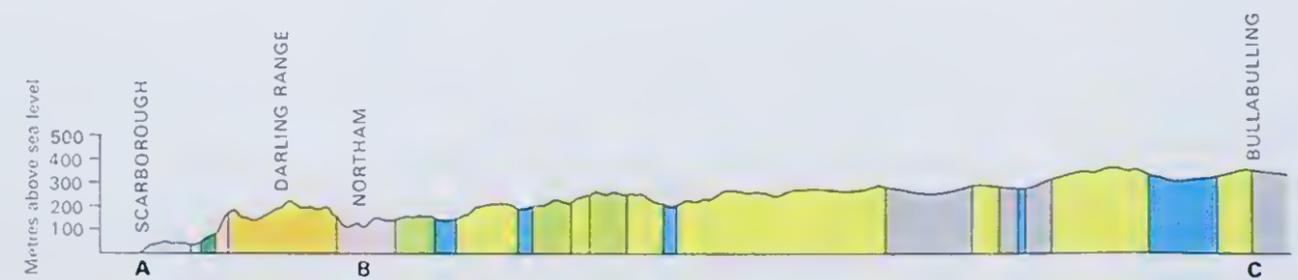


THE SOILS OF SOUTH WESTERN AUSTRALIA.



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AGRICULTURAL EDUCATION,
EDUCATION DEPARTMENT
OF WESTERN AUSTRALIA



3.—Species diversity in the southwestern flora

By N. G. Marchant¹

Abstract

The South West Botanical Province is noted for its floristic richness and high degree of endemism. Over 30% of the total species of *Epacridaceae*, *Myrtaceae* and *Proteaceae* are recorded in the Province. The percentage of species restricted to the area, calculated from available data, is 68%.

The flora is clearly related to that of eastern Australia with only tenuous links with the flora of South Africa and Malagasy.

The richness has arisen through the relative isolation of the area, major climatic fluctuations, and the diversification of the flora on sandy and gravelly soils with a marked summer drought.

Introduction

The South West Botanical Province of Western Australia is the southwestern corner of the State, where there is a reliable winter rainfall and marked summer drought. The boundary has been variously defined by Diels (1906) and Gardner (1942; 1956) as a line extending from Shark Bay (latitude 26° S, longitude 114° W) in the north to Israelite Bay (latitude 33° S, longitude 124°) in the south. The crescentic area west of this boundary is approximately two hundred thousand square kilometres.

Nowhere is the boundary between the South West Province and the Eremaean Province well-defined. Gardner (1942) relied upon a 175 mm winter (May to October) isohyet to substantiate his field observations on the distribution of what he considered South-Western and Eremaean species. Diels (1906) used the 300 mm annual isohyet, a line slightly to the west of Gardner's. Burbidge (1960) also accepted this line, using the 10" isohyet. These are presented in Figure 1.

Floristically the South West Province is delimited by the inland extent of many heath components such as *Conostylis*, *Anigozanthos* (Haemodoraceae) and the Restionaceae and Epacridaceae. The eastern limits of low heaths on sand or gravel, mallee and mallee heaths and certain woodlands also delimit the South West Province. Further east are the Mulga, Salmon Gum woodlands and shrublands dominated by species of *Acacia* and species of Chcnopodiaceae and Myoporaceae.

Floristic diversity

Few studies have been made on the lower plants of Western Australia. Bibby and Smith (1954) list 36 lichens for the whole state and an estimate of the numbers of Bryophytes can only be made from a few localised studies.

¹Western Australian Herbarium, Department of Agriculture, South Perth.

Smith (1962) lists the number of Bryophytes on granitic slopes in the well-watered Porongurup Range as 14. Willis (1954) has listed some 33 mosses, 20 of which occur in the dry Goldfields region.

The number of ferns and fern allies for Western Australia is only 49 (Smith, 1966). Of these, 26 occur in the South West Province, most being associated with moist microhabitats on granitic monadnocks. To this list must be added five or six south-west species of *Isoetes*.

Only 11 Gymnosperms are recorded for the province. This includes one widespread *Macrozamia*, a shrubby species of *Podocarpus* with morphological affinities with the eastern species *P. spinulosus* (Dallimore and Jackson, 1966) and six species of *Callitris* as well as three species of the endemic *Actinostrobus*.

Beard (1969) records a total of 3,611 Gymnosperms and Angiosperms in the South West Province. This record was based on data, extracted from species folders in the W.A. Herbarium, which were published as a "Descriptive Catalogue of West Australian Plants" (Beard, 1965). These data are limited because so much of the Western Australian flora still remains to be studied.

In comparison with most parts of the world the recorded number of ferns, Gymnosperms and Angiosperms in the South West Province is relatively high, though a survey of recent literature reveals other areas which have greater numbers of species per square kilometre. These data are presented in Table 1, arranged in decreasing species density. Species numbers have been obtained from Adamson and Salter (1950), Allan (1961), Beadle *et al.* (1972), Black (1929), Burbidge and Gray (1970), Chippendale (1971), Curtis (1969) and Willis (1962).

Table 1

The numbers of plant species in the floras of different regions

	Area sq. km	Estimated no. of species	Species per sq. km
Cape Peninsula, South Africa ...	471	2,622	5.567
Australian Capital Territory ...	2 359	1,037	0.440
Sydney District ...	28 500	2,000	0.070
Tasmania ...	68 330	1,200	0.018
South West Province ...	220 150	3,637	0.017
Victoria ...	227 620	2,500	0.011
New Zealand ...	268 670	1,457	0.005
South Australia ...	984 380	2,500	0.003
Northern Territory ...	1 347 525	2,736	0.002

The incredible diversity of the Cape Peninsula flora is no doubt partly due to its diverse

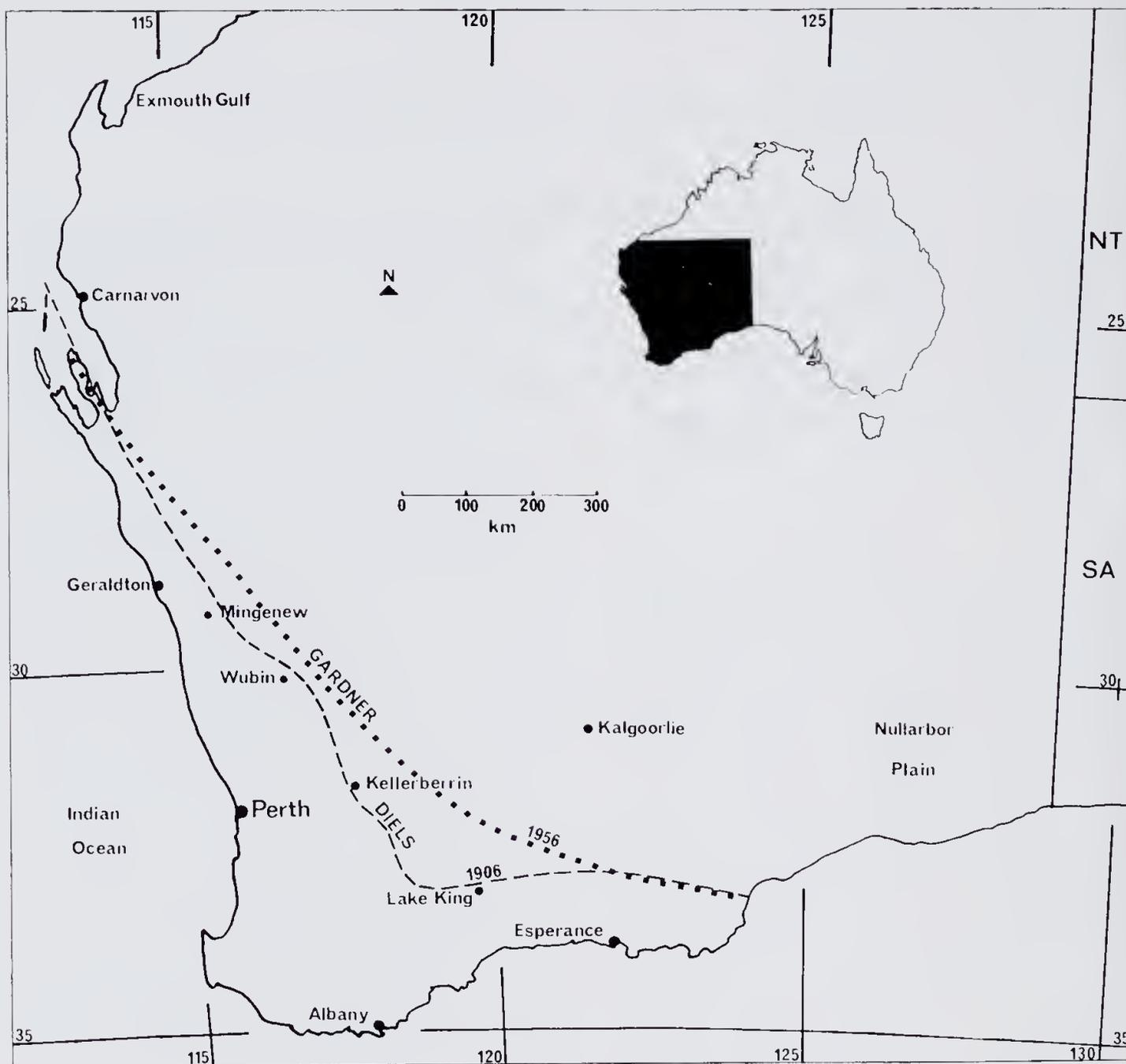


Figure 1.—The South West Botanical Province as defined by Diels (1906) and Gardner (1956).

physical features, which modify the climate so that various locations receive from 50 to over 200 cm annual rainfall. The higher elevations also receive summer mists, which must alleviate the summer drought to some extent. Of the species total recorded by Adamson and Salter (1950), 846 are monocots. In comparison, Beard (1965) lists less than 700 monocots for the South West Province, a lower proportion than that of the Cape Peninsula, due to the absence of many bulbous plants in the former.

In comparison to the data available on the number of species in other Australian states the South West Province compares favourably. The richness of the flora and its high degree of endemic species have been commented on by

many authors. Burbidge (1960) in a detailed analysis of Australian genera listed 462 genera in 96 families in the South West province. Of this total 111 genera are restricted to the Province. Only five families are endemic. These are Cephalotaceae, (1 sp.); Eremosynaceae, (1 sp.); Emblingiaceae, (1 sp.); Ecdeiocolaceae, (1 sp.); Anarthriaceae, (5 spp.). The last two families are morphologically and anatomically related to the Restionaceae but are regarded as separate families by Cutler and Airy Shaw (1965).

Among the families which are well represented by a number of genera in the province are the Restionaceae (16 genera), Liliaceae (21), Xanthorrhoeaceae (9), Myrtaceae (26), Epacridaceae (15), Leguminosae (31), Rutaceae (13).

Goodeniaceae (10) and Asteraceae (30) (largely from Burbidge, 1960).

At the species level, Gardner (1942) lists the families well developed in the province as Tremandraceae, Proteaceae, Leguminosae, Rutaceae, Rhamnaceae and Verbenaceae.

An indication of the number of species in some of the larger families of the province and the percentage of the total species estimated for Australia is presented in Table 2. Data have been extracted from Burbidge (1963) and Beard (1965).

Table 2

The numbers of species in selected families of plants from the South West Province and the whole of Australia

	Estimated total Australian species	Estimated S.W. province species	Percent. of Australian species in S.W.
Centrolepidaceae	35	23	66
Dilleniaceae	107	63	59
Epacridaceae	499	170	34
Goodeniaceae	309	128	41
Myrtaceae	1,918	603	32
Proteaceae	1,211	408	34
Restionaceae	82	57	70
Stylidiaceae	144	102	71

The three large families Epacridaceae, Myrtaceae and Proteaceae, which are regarded by Good (1964) as large Australian families, have between them over 3,600 species, over one-third of the total number of species in the Australian flora estimated by Good (*loc. cit.*). The South West Province total of these three families is just under 1,200 species, which is one third of the total number of species of the families and one third of the species total of all families recorded for the province.

In contrast to the richness in the south-west of the families presented in Table 2 are the distribution patterns of the other large Australian families listed by Good (*loc. cit.*). For example in the Poaceae, Gardner (1952) records only 82 species native to the Province in comparison to 278 native Western Australian grasses. Figures for the Orchidaceae (George, 1971) reveal the same degree of paucity in the South West Province, only 128 species out of an Australian total of approximately 600. The numbers of species of Australia's largest genera *Acacia* and *Eucalyptus* show the same pattern. Only 161 *Acacia* species are recorded and 79 eucalypts out of a total of very approximately 600 species for each genus. The southwestern representatives of the two genera respectively contribute only 27% and 13% of the Australian total.

Endemism

Good (1964) comments on the difficulties in comparing species richness and degrees of endemism. No attempt will be made here to present the facts using the methods outlined by Exell and Williams (*vide* Good *loc. cit.*).

The high degree of endemism in the flora of southwestern Australia has been commented on by Hooker (1860), East (1912) and Gardner (1942; 1959). The number of species restricted to the South West Province has been estimated at 75% of the southwestern flora (Gardner, 1959) and as 86-87% by Beard (1969). The latter paper, based on the descriptive catalogue mentioned above (Beard, 1965), and a survey of the literature, presents figures for the number of both widespread and restricted species for the South West Province, the Eremaean Province and the Northern Province. The percentages of endemism recorded in the analysis are not clearly comprehensible, as there is some confusion between the use of the terms "endemic" and "solely southwestern" as well as errors in calculation. On the basis of figures by Beard, the number of species restricted to the South West Province is 2,472 and the total number of species in the province is 3,611. This means that the percentage of species restricted to the province is 68%.

In comparison with this percentage of endemism Good (1964) suggests that the Cape Peninsula, South Africa, has more than 90% endemism. Malagasy is also quoted as perhaps having 85% of the species being restricted to the island. It must be remembered however that the larger an area the higher the proportion of endemic species. Australia for example probably has a greater proportion of endemic species than any other major geographical region.

Figures for species endemism also exist for Tasmania (Curtis 1969) as 17% and for Darwin and the Gulf region of the Northern Territory, 57% (Chippendale 1971), though this latter figure apparently refers only to the percentage of endemism of that region in comparison to the Northern Territory and not the neighboring States.

There is no doubt that the South West Province does have a high degree of endemism in comparison to other regions of comparable size. It is also worth noting that a considerable area of the South West Province is covered by forests and woodlands which are dominated by a single or very few species of *Eucalyptus*. For example, prime forests of Jarrah (*Eucalyptus marginata* Donn ex Sm.) cover over 17,000 sq. km yet harbour only a few hundred associated species. The incredible richness and uniqueness of the local flora is to be found on the heaths or so called sandplains of sandy or lateritic soil which occupy considerable areas, particularly in the northern and eastern parts of the province. Diels (1906) and Gardner (1942) comment on this richness at the "cusps" of the province. Diels (*loc. cit.*) quotes the total number of recorded species and the percentage endemism in each of the six botanical districts he designated within the Province. Even though his total figures are low and it is not clear if he uses the term "endemism" to refer to the species restricted to the district or whole Province, the results are interesting. Endemism is quoted as 6% for the extreme south-west corner, 37% for the most

northerly district and 33% for the most easterly. The districts in between range from 20 to 33%.

An indication of the species richness of heath areas of the province is given in Table 3, which presents recent information on the species total in three reserves.

Table 3

The numbers of species in selected National Parks in southwestern Australia

	Area (sq. km.)	No. of species
Tutanning (32° 30'S, 117°E.)	18.2	400
Stirling Range (34°S, 118°E.)	1 093	550
Fitzgerald River (32° 30'S, 117°E.)	2 444	700

With more field work the figures for the species of the Stirling Range and Fitzgerald River reserve will rise. Already it has been found that 10% of the plants of the Fitzgerald River reserve are restricted to that area. Most of these local endemics are restricted to the slopes of the Barren and Eyre Ranges which rise to over 500 m. It is worth noting from the above data that the species density of Tutanning, the most intensively studied reserve, is 22 species per square kilometre. This figure is probably typical of many small areas of heath in the south-west, particularly along the southern coast on some monadnocks such as Mt. Manypeaks and Peak Charles and some mountain ranges such as the Stirling Range, the Barrens and Mt. Ragged. A similar situation exists in the Grampians, Victoria, with approximately 750 species of angiosperms and ferns, 30 of them restricted to that location in Victoria and some of these having Western Australian affinity (Willis, 1962).

Disjunctions and links with other floras.

The closest relationship of the South West Province judging by the number of shared genera and species is with southeastern Australia. Beard (1969) records 491 species which occur in the south-west and in eastern Australia. Of these 211 are widespread in Western Australia while 280 are restricted in Western Australia to the South West Province and also occur in the south-east of Australia.

Green (1964) mentions that several hundred species occur in the south-west and in the eastern states but not in the intervening regions of Western Australia and western South Australia. He selected 35 of these with a minimum intervening distance in their distribution of 1200 km and a maximum of 2500 km. A recent unverified collection of the species quoted with the greater disjunction, (*Stylidium perpusillum* Hook f.), reduces the intervening distance to 1600 km. In the same paper, Green lists 48 pairs of species, the members of which are regarded as morphologically related and far removed geographically. Some of these are considered by Green to be true vicariads which

have been separated by unfavourable climatic conditions in the intervening region and have diverged morphologically.

The explanation for some of the disjunct species listed by Green is regarded as long distance wind dispersal. To support this suggestion the author refers to the high proportion of minute-seeded species such as Orchidaceae, *Stylidium* and *Levenhookia* in his lists. Recent work on the Orchidaceae at the Western Australian Herbarium has revealed other species which could be added to list of southwestern and southeastern Australian species. One of these, *Thelymitra mathewsii* Cheeseman, occurs in a few localities at the northern tip of New Zealand (George, 1971). This is only a few degrees of latitude south of the Western Australian occurrence, and approximately 5000 km to the east.

Disjunctions between southwestern and south-eastern Australian species with large propagules require an explanation involving geological and climatic history. Disjunctions within the South West Province itself, particularly between the northern and southeastern sections and between the south-west and the granitic monadnocks of the interior, can also be explained on the basis of past climatic fluctuations. This subject will be dealt with later.

A floristic relationship between southern and east Africa and Western Australia is often quoted in the literature on plant geography and continental drift. This relationship has been discussed by Gardner (1942), Specht (1958), Burbidge (1960) and Good (1964). Specht *loc. cit.* lists four genera which range from East Africa and Malagasy to Australia. These are *Adansonia*, *Diplopeltis*, *Keraudrenia* and *Rulingia*. These genera except *Adansonia* are well represented in the South West Province. The record for *Diplopeltis* from Malagasy has recently been refuted (George and Erdtman, 1969) though Hoogland (1949) adds the genus *Hibbertia*, which is very well represented in the south-west, to those genera which occur in Malagasy and Australia.

Gardner (1942) and Burbidge (1960) discuss in detail the distribution of the families Centropetalaceae, Restionaceae and Proteaceae and their links between southwestern Australia, southern Africa and southern South America. These links are well developed only at the family level. Weimarck (1941) listed only four genera which occur in the Cape Peninsula and in the South West Province. These are *Restio*, *Leptocarpus* and *Hypolaena* (Restionaceae) and *Caesia* (Liliaceae). As pointed out by Burbidge (1960) there is no certainty that the respective taxa in the two regions are congeneric. Certainly very little is known at the present time of the generic limits within the local Restionaceae.

The case of the distribution of the Proteaceae is frequently regarded as a keystone in phyto-geographical interpretation, rivalling the position of *Nothofagus*. The study of the distribution of genera (Rao, 1971) reveals that none of those represented in Western Australia occur

outside Australia and that there is a greater relationship between Australia and South America than between South Africa and Australia.

The concept of a close relationship between the flora of southern South Africa and the South West Province has arisen largely because of the incredible morphological similarity of some genera, particularly in Proteaceae and Papilionaceae, in the respective regions. This similarity, as well as the parallel floristic diversity and localised richness of the two areas, suggests not recent contact but a parallel in environmental history.

Thus the relationships of the southwestern flora are clearly with that of eastern Australia and, in common with that region, the northern regions of Australia and the neighbouring islands. Through the relationship of the flora of eastern Australia to that of New Guinea, New Caledonia, New Zealand and South America, the western flora is more related to these as well, than it is to that of southern Africa and Malagasy.

Discussion

A considerable amount of controversy has raged over the location of the origin of the angiosperms. The most widely accepted view at present is that they arose in the area which now lies between Assam and Fiji, most probably in what is now south-east Asia (Takhtajan, 1969).

Hooker (1860) suggested that the South West Province was a cradle of angiosperm development but later workers such as Crocker and Wood (1947) dispute this, pointing out that the area is merely a centre of diversity. The figures presented earlier showed this diversity in some of the families represented in the south-west. Cytological evidence on the origin of the Myrtaceae and Epacridaceae (Smith-White, 1959) points to an eastern Australian origin for most of the genera within these families. Rao (1971) also suggests an eastern origin for the Proteaceae. Thus the South West Province is only a centre of diversity in a few families which are usually considered as typical "Australian elements". The origin of the Australian flora then, lies either in the eastern Australian region or, as is probably more likely, in the area to the north of that region.

Smith-White (1959) believes that the angiosperms developed outside Australia and that the orders and families were established before the predicted massive invasion of Australia after the mid-Cretaceous. Beadle (1966) also follows this view.

It is significant to note that the suggested period of the drifting apart of the pre-Cretaceous great southern continent was the Neocomian, the same period as that of the earliest fully-authenticated Angiosperm remains (Takhtajan, 1969). It is possible that the flowering plants were well developed at the time of this separation but it is doubtful if many present day families had appeared. Thus the very

tenuous botanical relationship between the South West Province and Africa could possibly be due to continental drift. As well, if we accept that the final breaking up of the southern continental mass into Australia, Antarctica and South America occurred at a much later date then we would expect the greater degree of botanical relationship between Australia and South America, as has been found.

Burbidge (1960) discusses the affinities of the floras of the southern continents, pointing out that the reconstruction of "Pangaea" by Carey (1958) fails to explain the strong generic affinities between South America and Australia and the lack of them with South Africa. More recent reconstructions of the supposed southern continent by Griffiths (1972) and the paper dealing with geological history in this volume, show how it is possible for Australia to have more affinities with South America than South Africa. However it must be pointed out again that Africa is supposed to have separated from "Gondwanaland" before most modern plant families had appeared.

Far more important considerations than continental drift and links with other floras are those dealing with the entry of angiosperms into Australia, and for the present study, a discussion of the factors which have led to diversity in the South West Province.

Knowledge of the Australian Angiosperm flora in the early Tertiary is considerably better than that of the earlier periods. The Eocene and Miocene are presumed to have been periods of adequate, reliable rainfall over southern Australia. This enabled the development of a so-called pan-Australian mesophytic flora which included *Cinnamomum*, *Nothofagus*, *Podocarpus*, *Casuarina*, *Banksia* and perhaps *Eucalyptus* (Crocker & Wood, 1947; Wood, 1959). In southwestern Australia sediments of Eocene origin have revealed evidence of *Araucaria*, *Banksia*, *Nothofagus* and *Gleichenia* (McWhae *et al.*, 1958). From this evidence it is presumed that the climate of southern Australia was warm and wet. There is no evidence of climatic conditions in the mid-north of Western Australia, though warm water marine faunas are recorded during the Tertiary for the Carnarvon basin (Brown *et al.*, 1969). If the present climatic zones were applicable in the Miocene then it is possible that the area which is now North West Cape and the Hamersley Range experienced a Mediterranean type climate.

The Miocene period has been noted as an important one in Australian plant geography by Wood (1959). It marked the end of a long period of peneplanation, it was the beginning of earth movements in the south-east of the continent, and it was the beginning of the partial isolation of the South West Province from the rest of southern Australia.

In the Miocene to the Pliocene a marine transgression deposited the limestones which now constitute the Nullarbor Plain. This became an edaphic barrier between the east and west though, as will be suggested later, not a completely effective one.

Smith-White (*vide* Burbidge, 1960) suggests a pre-Miocene origin for many genera in the Rutaceae and Myrtaceae. It is likely that if this is the case, the diversification and development of endemism in the South West Province commenced in this period. Perhaps the Eocene transgression, which may have extended over much of the southern part of the Western Shield marked the beginning of the diversification. At this time the higher mountains and ranges along the south coast of Western Australia would have been islands and as such would have acted as refugia. It is in refugia such as these that much evolutionary change could occur, especially during the subsequent migration and intermingling of these refugial floras on newly liberated soils of the Oligocene and Miocene.

Another important factor contributing to the development of the flora in the Miocene was probably the development of laterite in the humid climate. Lateritization of the whole plateau commenced in the Eocene or Miocene but subsequent aridity restricted formation to the wetter south-west. The shield could have been colonised by laterite-tolerant species from the south or north-west to give a widespread flora adapted to the post-Miocene drier conditions. This flora was to a certain extent cut off from the eastern parts of the continent.

Later weathering of the laterities on the central part of the shield would have broken the continuous flora: two large remnants of these which exist today are the northern and southern sandplains, which have numerous disjunct species, i.e., only occurring in these regions or in isolated areas in between.

The scanty evidence of the post-Miocene floras has been discussed by Burbidge (1960). It is possible that the *Cinnamomum* type vegetation moved northward in response to a cooling of the climate leaving behind some of the present flora which had adapted to the changed conditions.

Specht and Rayson (1957) suggest that the present day sclerophyll genera developed in a warmer, wetter climate. The growth of these plants occurs at a time of great water stress in the late summer. This is interpreted as being out of phase with the present climatic conditions and a result of their origin in a more humid climate. It is possible that the leafy shoots which initiate and differentiate small, rigid cells in a period of stress would have an evolutionary advantage under arid conditions.

A number of authors, including Wood (1959), Smith-White (1954), Burbidge (1960) and Green (1964), stress the importance of the Miocene inundation and the subsequent development of limestone and arid land to the north, as a major barrier to plant migration between the east and west. Recent surveys of the area to the north of the Nullarbor Plains have revealed a surprising number of genera and species which are normally considered as southwestern. These include *Acacia leptopetala* Benth., *Daviesia ulicifolia* Andr., *Leptospermum roei* Benth. and species of *Micro-myrtus*, *Thryptomene* and *Logania*.

It is evident from the existence of pockets of southwestern flora at North West Cape (lat.

22°S, long. 114°E) and Roe Plains, especially at Twilight Cove (approx. lat. 32°S, long. 116°E) as well as others of southwestern species on granitic monadnocks as far east as Kalgoorlie, that the present day vegetation of the South West Province was of much greater extent in the past. Evidence for climatic fluctuations in the recent past (4000 to 3000 BC) have been provided by Churchill (1968). Under pluvial conditions it can be imagined that the area north of the Nullarbor Plain could provide an effective corridor between the southwest and southeastern Australia. The importance of this corridor for birds has been presented by Ford (1971).

Crocker and Wood (1947) postulated a mid-Recent period of aridity which, with subsequent amelioration of the climate causing contraction and expansion of the vegetation, had profound effect on the ecological and species complexity. During a period of severe southern Australian aridity the South West Province would have suffered greater decimation of the vegetation than the southeastern Australian region. The southeast in contrast to the west has a greater latitudinal and altitudinal variation. In the south-west three refugial areas could have been important. One of these is the Hamersley Range (approx. lat. 22°S, long. 118°W). The refugial nature of the present day Hamersley Range flora has been commented on by Burbidge (1959). If the arid period in southern Australia postulated by Crocker and Wood (*l.c.*) was due to a relative southwards movement of the weather zones in the mid-Recent as has been proposed by Keble (1947), Gentilli (1961) and Specht (1958), then it is likely that more of northern Australia came under the influence of monsoonal weather patterns. The Hamersley region could not only have provided a refugium for some southwestern species but also allowed some mixing of these with species of northern origin.

Two areas of refugial nature are postulated in the south-west. One is the deeper valleys of the Darling Scarp which because of uplift of rain-bearing westerly winds would always have a higher rainfall than the neighbouring plateau and coastal plain. From these refugia the recolonization of the laterites to the east of the scarp and the coastal plain could have taken place.

The remaining refugia could have been provided by the monadnocks and ranges, particularly along the south coast. These were probably the most important areas because of the variety of habitats available and the relative reliability of rainfall. If the mean path of the high pressure wind systems was much lower than at present, the on-shore winds would have brought more or less reliable rains to the south coast as they do in summer today. Such refugia as the Stirling Range and Barrens could have developed a species diversity and degree of endemism similar to that of the present Cape Peninsula.

The South West Province is not a centre of origin of the Australia flora but a centre of great diversity of some of these elements and of some relict groups. Continental drift occurred too early to have a profound effect on relationships with southern Africa. The diversity is

due to the long standing stability of the western plateau with diversity beginning in the Miocene and continuing with limited migration between east and west and north and south. The whole Southwestern corner of Australia developed into a virtual island which underwent drastic climatic change which must have favoured species adapted to sandy and gravelly soils. The South West Province can be regarded as a relatively isolated area with a latitudinal spread of only 9° and a limited altitudinal variation. This "island" has always been well away from any migration routes. Eastern Australia, in contrast to the south-west, has a latitudinal range of over 35° with a wide altitudinal variation. According to Burbidge (1960) this part of Australia is also a well developed migration route parallel and related to other routes from New Guinea to New Caledonia and New Zealand.

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4.—Animal and plant speciation studies in Western Australia

By H. E. Paterson¹ and S. H. James²

Abstract

Speciation studies involving Western Australian, and especially southwestern, animals and plants are reviewed. The paper presents different approaches to the problems of integrating cytogenetics, ecology and taxonomy, and falls into two parts.

Current studies on animals in Western Australia illustrate some of the consequences of the evolutionary process of speciation, as well as some aspects of the mechanism bringing it about.

Cytocoevolutionary responses in ten groups in the Western Australian flora are reviewed. Cytogenetic innovations in evidence include polyploidy, apomixis, complex hybridity, aneuploidy, lethal systems and B chromosomes, and in general, these are interpreted as conservative devices, conserving either heterozygosity, adapted gene combinations, or both.

These studies support Mayr's arguments for a discipline covering the speciation process and its consequences.

Introduction

Speciation studies amongst Western Australian animals and plants are not extensive, but they illustrate differing points of view in a number of areas. Firstly, the application of a species definition to taxonomic practices varies between zoologists and botanists; for example, the existence of infraspecific polyploidy in plant species must often, perhaps invariably, combine genetically distinct though morphologically similar biological species into a single taxonomic species. Comparable genetic barriers in animal species would normally be taken to delimit taxonomic species. Secondly, there is a continuing discussion concerning the importance of postmating isolation and its reinforcement in the speciation process. In this paper, the theory of allopatric speciation involving an initial attainment of premating isolation is vigorously, and profitably, applied to animal speciation studies. On the other hand, while recognizing that the theory of allopatric speciation may well be of great utility in interpreting the evolutionary origin of many plant species, the plant speciation studies reviewed here have been selected, and in many cases the work actually directed, with a view to seeking out situations in which alternative processes of speciation may be demonstrable. Thus, these latter studies do not concentrate on an integration of genetically-determined ecological attributes with geohistorical circumstances, but attempt to investigate situations where endophenotypic attributes, the attributes of which postmating isolation is made, are of adaptive utility at the infraspecific level.

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Animal species studies

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The species concept

In 1957 Ernst Mayr proposed that a Science of Species could be justified as a legitimate field of study. It was conceived as including not only the study of the process of speciation itself, but the study of many of its sequelae as well. Such a field of study would clearly be most closely related to population genetics because it is based on the genetical concept of the species, which, in turn, has the idea of a species-specific gene pool at its centre. The studies reported on here are mostly still in progress. They are diverse in approach and cover a wide range of animal species, but they all fall within the scope of Mayr's Science of Species. By presenting them together it is hoped that they will provide support for Mayr's suggestion by revealing something of the breadth, interest and even utility of such a discipline.

At the outset it is necessary to outline clearly what is meant by the genetical concept of the species, because the species in genetics does not always correspond to any species currently recognised in taxonomy. This usually means that insufficient time has elapsed for the necessary adjustments to be made. A gene pool can only exist in organisms which reproduce sexually, though it could be argued that it is applicable to certain prokaryotic organisms characterised by at least one of Haldane's "alternatives to sex" which would enable recombination to occur (Haldane, 1955; Sanderson, 1971). In sexually reproducing organisms all reproductively mature members of a species can contribute to, and share in its gene pool. Furthermore, the gene pool of this species is isolated from the gene pools of other species due to the functioning of genetically determined isolating mechanisms. For these reasons the gene pool of a species is able to be distinct in genetical properties and structure from those of all other species.

These ideas can be expressed in other ways. For example, the essential characteristic of an animal species is that it comprises a number of individuals each of which is able to recognise reproductively mature mating partners of the same species. This is achieved by means of a genetically-determined, co-adapted behavioural signalling system. Members of a particular species, because of this system, do not usually respond effectively to the analogous signals of members of other species under natural conditions.

The explosive diversification of forms of organisms which apparently followed the evolution of eukaryotic cells in late Precambrian times cannot be attributed to the newly evolved methods of generating genetic diversity alone. Recombination will generate variation, but will not on its own lead to the radiation of forms which we observe. Radiation will, however, be initiated if recombination is restricted to occurring within discrete gene pools. This raises the key question how did the species as an evolutionary phenomenon first arise? No general answer to this question will be attempted because it is very likely that species arose on several independent occasions following the independent acquisition of sexual reproduction by several different eukaryotic Protista (Margulis, 1970). In the following discussion only the animal lineage will be considered. Most animals are dioecious or can be shown to have had dioecious ancestors. This suggests that the whole animal kingdom evolved from an early dioecious protistan ancestor. Because we are discussing the origin of the species as an evolutionary phenomenon, such an ancestral form must have lacked an isolating mechanism as such. However, being dioecious it must have had a genetically-determined mechanism which enabled the one mating type to recognise the other. Credibly, this system could have provided the basis for the first isolating mechanism which brought the first two animal species into existence, because the principles of allopatric speciation long advocated by Mayr (1942; 1963) are as applicable to this basic system as to more advanced ones. In simple terms the mechanism behind allopatric speciation may be as follows. Once an extrinsic barrier has split the original "gene pool" into two, the genetic structure of each will begin to deviate in response to selection from its distinct environment. Some of the gene substitutions brought about in this way will have a pleiotropic effect on the mate selection mechanism. In this way the mechanisms of the two populations will progressively diverge to the point when the signals of members of the one population are no longer effectively recognised by members of the other. At this stage speciation will have been achieved. An example of a gene with pleiotropic effects of the sort invoked is *yellow* in *Drosophila melanogaster* Meigen. When compared with "wild type" flies homozygotes for this allele are more resistant to starvation (Kalmus, 1941) and the males have a modified courtship pattern (Bastock 1956). Following effective long term isolation, the mate recognition systems of the two sub-populations may, thus, also function as premating isolating mechanisms, which effectively protect the integrity of their gene pools. This in turn enables the two populations to continue to diverge adaptively even though their ranges may come to overlap.

Details of the speciation scheme outlined above will be disputed by some, but if it happens to be correct it will be noted to have the following implications. Species come into existence as by-products of adaptive evolution. They are

not products of selection for diversity, though selection may decide whether a newly evolved species will survive for long. Diversity is not selected for as such, and it is ultimately dependent on factors which favour speciation. However, selection does decide the specific pattern of diversity which comes into existence in a particular environment at a particular time.

In Western Australia the work of A. R. Main and his students on Leptodactylid frogs is the pioneer work on animal species studies. This work is still continuing and has recently been reviewed (Main, 1970), which provides an indication of how young a field this is within this State.

Studies on the origin of species

The term "speciation studies" is often used loosely to mean almost any type of species study. Here it is used in a stricter sense to mean the study of the mechanism by which isolating mechanisms, which protect the gene pool of a species from introgression, come into existence.

Earlier work (Main, Lee and Littlejohn, 1958) showed a rich frog fauna in southwestern Australia, an area almost free of geographical barriers of the kind which have proved important in initiating speciation. These authors compared the faunae of southwestern and southeastern Australia, using as particular criteria male call structure and genetic divergence as judged from the results of *in vitro* crosses. They concluded that during the Pleistocene three distinct pluvial periods, separated by interpluvials, had allowed the entry into Western Australia of faunal elements from the east. The arid interpluvial periods effectively led to the splitting of populations into western and eastern sub-populations, thus providing the conditions for subspeciation and speciation to occur. Main (1970) has modified details of the original model, suggesting that the last Pleistocene pluvial, and one of the two earlier connections, were only wet enough to allow frogs from seasonally arid environments to invade from the east. During the third pluvial, however, both wetland and semi-arid country frogs were able to penetrate westwards. This modified model accounts for why there is only one western species representing certain eastern wetland (Bassian) species, while numbers of eastern semi-arid (Eyrean) species each have three western representative species. These ideas have proved applicable to spiders of the tribe Aganippini (Main, 1962), horseflies (Tabanidae) (Mackerras, 1962) and, if allowance is made for the biological features of the group, to birds (Serventy and Whittell, 1951).

The genus *Calliphora* (Diptera) has radiated enormously within Australia, so much so that most of the world's species are endemic here. These flies offer excellent opportunities for testing Main's ideas on speciation at a new level of sophistication. Most species are easily cultured, and pre- and postmating isolation between members of western and corresponding eastern populations can be studied with considerable precision. The eastern and western populations can also be compared with great precision at the cytological level because these flies possess

excellent polytene chromosomes (Thomson, 1969). Their large size make them very suitable for biochemical studies using gel electrophoresis, for example. Such a study is at present in progress. N. Monzu is exploiting some of the techniques mentioned to compare Western Australian species with close relatives in eastern Australia (Table 1).

Table 1

Western Australian species of the genus Calliphora with closely related species in the eastern states of Australia

Western form	Eastern form
<i>Calliphora nociva</i> Hardy <i>Calliphora albifrontalis</i> Malloch <i>Calliphora varifrons</i> Malloch	<i>Calliphora augur</i> (F.) <i>Calliphora stygia</i> (F.) <i>Calliphora hilli</i> Patton

R. W. George* has in recent years paid attention to the rather neglected field of speciation in the sea (George and Main, 1967; George, 1969). The organisms with which he has worked are the rock lobsters, Palynuridae. By considering and taking into account the biological properties of present day species of the genus *Jasus*, for example, he was able to propose credible models of speciation in the sea, which do no violence to the well-accepted ideas of how speciation occurs on land. In this case speciation of a group of six contemporary species which occur in the waters of the southern hemisphere was explained in the following broad terms: George accepts that their close similarity implies a common ancestral species which formerly had a circumpolar distribution. Because global temperatures were formerly higher on the average than now, the ancestral species was thought to have occupied an area occupied by the subantarctic zone today. With climatic cooling this temperate zone must have moved to lower latitudes, forcing the species northwards until it could colonize appropriate regions of the southern continents and several islands (New Zealand, Tristan da Cunha, St. Paul's Island and Juan Fernandez). In this way the original single circumpolar species was effectively fragmented into isolated populations, each of which would then have been subjected to a different set of selection pressures. The isolation could have been maintained by specific local conditions resulting from local currents due to the configuration and position of the island or continent with respect to the prevailing major currents.

In a comparable way speciation in other genera was accounted for. In general, a study of the biological attributes of present day species was considered to provide the key to elucidating the pattern of speciation proposed for each genus.

Earlier work by Littlejohn and Main and his students on the isolating mechanisms operating to maintain the integrity of the gene pools of the frogs *Crinia insignifera* Moore and *C. pseud-*

insignifera Main has been repeated in considerable detail by M. Bull. These two species meet along the Darling Scarp. *C. insignifera* occupies the coastal plain and *C. pseudinsignifera* extends over large areas of the interior of southwestern Australia. Bull has demonstrated clearly that post-mating isolating mechanisms between these species are absent as judged by the *in vitro* cross method. Reproductive isolation between them is therefore largely at the premating level. In transects across the rather sharp line of contact between the species no indication of reinforcement of the premating mechanisms, such as the male calling characteristics, has been revealed. It seems that in this case the premating isolating mechanisms did not come into existence through natural selection acting to reduce gene flow between two partially diverged populations as postulated by Wallace, Fisher and Dobzhansky, among others.

The study of isolating mechanisms

It is generally accepted that postmating isolating mechanisms arise as pleiotropic by-products of adaptive evolution in isolated populations. This is because it is not easy to see how they could be evolved directly by natural selection. Less agreement exists over the origin of premating isolating mechanisms, because less difficulty exists in proposing models which account for their evolution by selection acting against inferior hybrids, as an alternative to their production in the same manner as postmating mechanisms. Many cases of "reinforcement" of premating isolating mechanisms have been reported (Levins, 1970), but it should be appreciated that the mere demonstration that selection strengthens premating isolation can in no way be regarded as compelling evidence in support of the thesis that premating isolating mechanisms evolve in this manner. This is because no satisfactory mechanism has been proposed to explain how genes, selected at a parapatric interface between two populations for their property of reinforcing premating isolation, can spread through the body of each population outside the zone of contact. Because premating isolating mechanisms are properties of species as a whole, models of speciation must account for this fact. This is an old objection (Moore, 1957) but one which is still avoided by many advocates of the hypothesis of the selective origin of premating isolating mechanisms.

S. J. Miles, R. Irving-Bell and I are particularly interested in reproductive isolation between the four members of the *Culex pipiens* L. complex which occur in Western Australia, *C. fatigans* Wd., *C. molestus* Forskål, *C. australicus* Dobr. & Drumm. and *C. globocoxitus* Dobr. here treated as distinct biological species. *C. australicus* has not yet been cultured successfully, but the other three species are readily cultured and can be crossed in the laboratory. Except in the crosses between *C. globocoxitus* and *C. fatigans*, there is little evidence of postmating isolation between them. In cages the premating isolation is detectable but is by no means complete. Yet in nature very little hybridization

*Western Australian Museum.

has been detected, and then only between *C. molestus* and *C. fatigans*, which often share the same breeding place. This is of interest because *C. molestus* was introduced from Europe, *C. fatigans* was introduced, possibly from the oriental region where it almost certainly originated, while the remaining two species are confined to the Australasian region. Thus *C. molestus* and *C. fatigans* do not naturally coexist with each other, or with the two endemic species. Yet they are all very effectively reproductively isolated when brought into coexistence due to man's interference.

Yvonne Henderson is applying the pioneering studies of Margaret Bastock, Aubrey Manning and Herman Spieth to a comparative study of the courtship behaviour of members of the *Drosophila melanogaster* species sub-group, recently reviewed by Bock and Wheeler (Bock and Wheeler, 1972).

N. Monzu's studies of the genus *Calliphora* include the measurement of reproductive isolation between sympatric and allopatric forms. Studies of pre- and postmating isolation between isolated demes of the frog species, *Crinia insignifera*, Moore, by J. Blackwell, have failed to substantiate the suspected existence of a deviation between demes breeding on sand and demes breeding on clay (Main, 1970).

An aspect of the study of isolating mechanisms is the detection of unsuspected sibling species. Using the methods of polytene chromosome cytology C. A. Green has been investigating the taxon *Anopheles annulipes* Walker which has a wide distribution within Australia and its neighbouring islands. Thus far he has detected four sibling species which he has temporarily designated as Species A, B, C and D. The species are readily identified by their X-chromosomes, which have been involved in extensive rearrangement during the course of evolution. Species A and B are sympatric over considerable areas of Western Australia (at least between Kalbarri and Geraldton). Species A and species C co-exist in Southern Queensland. Species D extends southwards from the Ord River possibly as far as Geraldton, though the southern record requires confirmation by means of crossing experiments with an Ord River stock. So far no hybrids have been detected in nature. Studies in this complex are hampered by the need to maintain them in culture by means of artificial mating methods. Crosses are performed in the same way.

Julian Ford and S. A. Parker have recently shown that the Australian Wedgebill comprises two sibling species *Psophodes cristatus* (Gould) in the east, and *P. occidentalis* (Matthews) in the west. The ranges of these two bird species overlap in the region of Oodnadatta, South Australia. The fact that the two gene pools exist was revealed by the use of song analysis (Ford and Parker, 1973).

R. J. Mahon has made use of the gel electrophoresis of heart muscle enzymes to demonstrate that the common blue and orange rock crabs, hitherto referred to as *Leptograpsus variegatus*

(F), actually belong to two distinct species. Until this demonstration *L. variegatus* has been generally regarded as a single polymorphic species.

The study of the genetic structure of species

The study of the genetic structure of species poses particular problems which have been considerably alleviated in recent years with the introduction of gel electrophoresis as a tool with which to score populations for variation at loci determining certain enzymes and other proteins.

Crinia insignifera Moore is a very small Leptodactylid frog found on the coastal plain of south-west Western Australia. The species is broken up into a large number of unusually discrete demes each occurring near a winter breeding site. Because of the small size of these frogs their vagility is considered to be rather low. This situation has been exploited by J. Blackwell to study genetic divergence between demes within a species. Here again use has been made of gel electrophoresis to study variation at loci determining enzymes. Using eight enzyme systems she will have data on at least 10 loci. This information will enable her to study the divergence of demes, and to estimate how effectively each population is isolated from its nearest neighbours. To facilitate the scoring of the gels she has studied the genetics of each system utilized. Studies such as this are much needed as checks on population genetic theory, which has moved well ahead of the studies which are actually feasible.

J. den Hollander is studying the structure of populations of *Musca domestica* L. using loci involved in determining maleness, and by studying variation involving the sex chromosomes. Most Australian housefly populations are characterized by the absence of a Y-chromosome, in sharp contrast to most populations of the species which have been studied elsewhere (Rubini, 1964; Milani, 1964). By using marked chromosomes den Hollander has shown that in the Western Australian flies so far examined there is a male-determining locus only on chromosome III. This is in contrast with Wagoner's (1969) report on a strain from Brisbane which carried male-determining loci on chromosomes II, III and V, and one from Canberra which showed holandric inheritance of a chromosome II (Kerr, 1961). The strain from Canberra was XY in the males and XX in the females, but Wagoner's Brisbane strain was XX in both sexes. In this study den Hollander has only found strains without a Y-chromosome: these stocks came from Sydney, Canberra, Melbourne, Adelaide, Perth, Albany, Kalgoorlie and Kununurra. The results presented in Table 2 have been obtained from crosses between the Perth stock with the others mentioned. Controls and stocks maintain a sex ratio very close to 1.

With further elaboration it is hoped that methods will be developed with which populations of *Musca domestica* from anywhere in the world can be characterized.

Table 2

Sex ratios of crosses between various stocks of *Musca domestica*

Cross	♂ off-spring	♀ off-spring
Perth ♀♀ x Canberra ♂♂	510	115
Canberra ♀♀ x Perth ♂♂	262	229
Perth ♀♀ x Melbourne ♂♂	420	31
Melbourne ♀♀ x Perth ♂♂	553	503
Perth ♀♀ x Ord ♂♂	668	322
Ord ♀♀ x Perth ♂♂	362	388
Melbourne ♀♀ x Canberra ♂♂	659	713
Canberra ♀♀ x Melbourne ♂♂	296	292

Ecological studies

Darwin pointed out that the ecological interactions of closely related species are of particular importance in understanding evolution. For this reason the studies, discussed above, which deal with the *Culex pipiens* complex, the species of the genus *Calliphora* and the crabs of the genus *Leptograpsus*, are all concerned with this subject.

In the *Culex pipiens* complex there are quite marked differences between the four West Australian species. The two native species are not closely associated with man. They breed in natural pools, usually low in organic content, and they rarely feed on man. *C. australicus* will not breed in cages, no doubt because of its ecological requirements for mating-swarm formation. *C. globocoxitus* will mate in small cages and, therefore, it is very probable that its requirements for swarm formation in nature are quite distinct from those of *C. australicus*. This contrast in mating behaviour between the two sympatric endemic Australian species is reminiscent of the differences between the two endemic members of the complex in Europe, *C. pipiens*, which resembles *C. australicus* in requirements and *C. molestus* which is comparable with *C. globocoxitus*. *C. australicus* has been recorded as feeding on rabbits and birds (Lee *et al.*, 1954). Neither endemic species appears to bite man in nature. *C. fatigans* and *C. molestus* both bite man and poultry. The latter species can survive without blood meals (i.e. it is autogenous) since females in their first gonotrophic can ripen their ovaries on reserves laid down during the larval stages. Autogeny has a relatively simple genetic basis, but nevertheless, it has a striking effect on the ecology of the species by freeing it from dependence on vertebrate hosts. This enables it to penetrate the far north of Europe by invading sheltered underground cellars, underground railway tunnels, etc., provided breeding places are available, and despite the fact that it cannot hibernate. This in turn might be expected to lead to a greater degree of inbreeding than is found in the anautogenous members of the complex. These ecological topics are being explored by R. Irving-Bell.

N. Monzu's study of blowflies of the genus *Calliphora* includes an attempt at defining the niche of each common carcass-breeding species. Much work has been done on blowfly ecology, but most of it has been done in the laboratory and relatively little in the field. Yet studies on interspecific competition, for example, are only realistic if they take into account such factors as the behaviour patterns which determine choice of oviposition site and the seasonal peaks of abundance of the species. Other factors to be considered are adaptations such as ovoviviparity and fecundity, the behaviour of larvae in relation to parasites and predators, geographical distribution and interactions with exotic blowflies which have intruded into the Australian scene.

The sibling species of the rock crab genus *Leptograpsus* show slight but palpable ecological differences which were first detected by Shield (1956), but recently studied in greater detail by Mahon. The blue species is more resistant to desiccation than is the orange, and as a consequence it can move and feed at a greater distance from the splash zone to which the orange species is more or less limited. The two species show slight differences in breeding season as judged by the numbers of females carrying eggs attached to pleopods on their abdomens, differences in habitat preference as shown by clumping in transects along the reefs, and in geographical distribution.

The role of symbiosis in the *Culex pipiens* complex of mosquitoes

Early workers on the *Culex pipiens* complex found that crosses between certain colonies of *Culex molestus* from various parts of Europe were incompatible in one or both directions (Marshall and Staley, 1937). This phenomenon was later studied in detail by Laven (1953) who demonstrated that the incompatibility involved mosquito genotypes and cytoplasmic "factors". This has suggested to several authors (e.g., Rai, 1967 and Irving-Bell and myself), that the factors may in fact be symbiotic microorganisms analogous to the sigma factors in *Drosophila melanogaster* (L'Heritier, 1970). This idea has been resisted by Laven (e.g., 1967). He has considered the factors to be RNA (Laven, 1967) and more recently his colleague Jost has suggested that they are DNA particles (Jost, 1970). However, Laven's basis for rejecting the symbiont hypothesis does not appear very impressive. The early work of Hertig & Wolbach (1924) and Hertig (1936) suggested to Yen and Barr (1971) and independently, to Irving-Bell and myself (Irving-Bell & Paterson, 1973) the hypothesis that the cytoplasmic factors of Laven are rickettsiae. Yen and Barr and we have confirmed the work of various earlier workers (Hertig, 1935; de Zulueta, 1964 and Byers & Wilkes, 1970) by detecting rickettsia-like symbionts in the ovaries of members of the complex. The species in which they have been found by us are *Culex molestus* and *C. fatigans* from Australia and *C. pipiens pipiens* L. from England. We have failed to find them in the

endemic Australian species, *C. globocoxitus* and *C. australicus*, but have detected virus-like particles in their place in these two species.

Our attempts at relating the micro-organisms to the phenomenon of cytoplasmic incompatibility have been held up by our inability to detect incompatible populations in *C. fatigans* or *C. molestus* in Australia, despite their reported existence (Dobrotworsky, 1955). However, Irving-Bell has recognised in *C. fatigans* and *C. molestus*, an apparently new form of degeneration in the oocytes which is distinct from that found with natural abortion. This type of degeneration coincides with a large increase in the numbers of symbionts, and she is now investigating the connection between the two phenomena. The symbiotic relations which have been described above are evidently of long standing, since the one appears to be older than the species *C. pipiens*, *C. fatigans* and *C. molestus*, and the other evidently predates the divergence of *C. globocoxitus* and *C. australicus*. Experiments now in progress are investigating whether the two types of symbiont can be obtained in the same cytoplasm, and the interaction of the various genotypes with the various symbionts.

Concluding remarks

The studies reported on here will give some impression of the scope of Species Studies as defined above. All the studies mentioned were designed from a purely scientific point of view, but it will be noted that those involving pest animals are of considerable practical value as well. All are essentially studies of single species. In other words, they are studies at the population level of complexity. Species Studies are also an essential first stage in the study of ecosystems. This is, of course because the organisation which is apparent at the community level results from selection acting at the level of the individual within a species. The ecosystem comprises a physical environment occupied by a number of species. Ultimately its structure depends on the process of speciation although, more immediately, it may depend on the migration of species. In turn, the coadjutment of a migrant species and the ecosystem provides the selective pressure which lead to speciation under the system outlined in the introduction to this section of the paper.

The significance of Species Studies might seem obvious, and yet they are rarely pursued in the way which Mayr had in mind. That much remains to be done is shown by the fact that disagreement is still widespread over so fundamental a matter as the process of speciation. We find population biologists of high standing quite unable to agree on the answer to a question such as: "Are species the product of direct selection for diversity, or are they by-products of adaptive evolution?". And yet each alternative carries with it far reaching and contrasting evolutionary implications.

Cytogenetic aspects of the speciation process in plants

by S. H. James

Perspective

The more characteristic elements of the Australian flora have been investigated cytologically, mainly by Smith-White, and his findings and those of other cytologists have been integrated with a geological history of the continent to produce a rather satisfying, yet suggestive, picture of the evolution of our flora. In summary, the hypothesis developed is as follows (Smith-White, 1959). The angiosperms originated elsewhere than in Australia. Before their entry into Australia they achieved geographical expansion over the major continents and underwent adaptive diversification. The major orders and families were established whilst the Australian continent remained geographically isolated and unavailable. Isolation of Australia was temporarily broken down during the middle Cretaceous, and a massive angiosperm invasion occurred, leading to the replacement of the older more primitive flora. The invading angiosperms included only those lineages which were near the "bridgeheads". Subsequent isolation of the continent has allowed the immigrant flora to indulge in a second evolutionary cycle which has resulted in the establishment of the present day autochthonous groups. These groups (e.g. Boronieae of the Rutaceae, Chamaelaucoideae-Myrtaceae, Proteoideae and Grevillioideae-Proteaceae, and the Section Cryptostomae of *Casuarina*-Casuarinaceae) show remarkable variation in chromosome number; they contain considerably more gross cytological variation than their extra-Australian relatives. Generally, this variation is shown by differences between the chromosome numbers characterizing genera, but within the genera the numbers are constant. The diversity in generic chromosome numbers originated during the early phase of the Australian evolutionary cycle, just as the diversity in numbers between orders and families developed in the earlier extra-Australian primary radiation, and in a pan-Australian flora. Dissection of this pan-Australian flora into its eastern and western components occurred in the Miocene, after the establishment of present day genera, and this dissection, established first by marine intrusion, has been maintained by the Great Australian Desert (Crocker and Wood, 1947), and progressive evolution within these isolates has led to the development of their own suites of species within common genera. Continentally, recent phytogeographical events include a partial breakdown in isolation allowing the entry of modern Indo-Malayan elements; changes of climate and topography, particularly the relatively recent (Quaternary) establishment of alpine conditions in Eastern Australia, which has allowed the establishment by long distance dispersal and by intrusion from the north along the montane tableland route of a "Southern" element showing affinities with New Zealand and South America; and a general

contraction, in Western Australia, of the autochthonous elements to the south west corner, associated with a general increase in aridity (Crocker, 1959; Churchill, 1961).

The recent immigrants, especially the herbaceous ones, are of particular interest. They may be expected to show, and do show, a third order cycle of adaptive diversification. By studying the distribution of cytogeographical races and their genetic systems, it should be possible to gain information which, in time, may contribute to a coherent picture of the dynamic phytogeography of the Quaternary. Significant work in this field, for mainly eastern taxa, has been done by Hayman (1960), Briggs (1962) and Peacock (1962).

In his essay on the cytological evolution in the Australian flora, Smith-White (1959) developed an hypothesis to account for the chromosome number variation discussed. He suggested that adaptive diversification of the original immigrant lineages was mediated by a multiplicity of newly available habitats, and by reduced biological competition. Consequently, the immigrant flora underwent an evolutionary cycle which "favoured genetic experiments, including experiments in structural changes and in chromosome number". This hypothesis implies that the changes in chromosome structure and number involved are basically innovative in nature. On the other hand, it is frequently argued (Darlington, 1958; Lewis and John, 1963) that such changes find their adaptive utility as conservative devices.

Much of the current cytological research on the Western Australian flora, reviewed below, is directed towards an understanding of the genetic systems operating in particular, mainly herbaceous, plant groups to determine how, and with what consequences, these groups have responded to the vicissitudes of a new environment. A major aim is to evaluate the role of chromosome changes as innovative and conservative devices, and to determine whether in fact, particular types of genetic architectures, at the population level, are associated with particular types of cyto-evolutionary responses. In this way, it may be possible to account for the cytological diversity characterising the endemic Australian tribes.

Calectasia cyanea—ancient and unchanging

Green (1964) has listed the species which occur in both Eastern and Western Australia. Of these, many are equipped with small seeds or other such devices that might allow for long distance dispersal. A few species showing this disjunct distributional pattern, however, are not so equipped, and their occurrence poses an important problem. What is the basis of their conservatism? Anyway (1969) investigated the variation pattern and genetic system of *Calectasia cyanea* R.Br., the blue tinsel lily, and noted there to be little morphological and phytochemical variation between populations within its distributional range. However, the difference in habit exhibited between the extensively rhizo-

matous plants of the eastern populations and the shortly rhizomed plants of Western Australia was taken as a key character in differentiating these taxa at varietal rank. The general exophenotypic constancy, however, was shown to be associated with a conservative genetic system in which Anyway was able to demonstrate a close relationship between the frequency of chiasma formation in the long arm of chromosome no. 9, which constitutes some 20% of the total genetic material, and the percentage frequency of sterile pollen. It appears that all *C. cyanea* plants are self pollinating and heterozygous for differentiated chromosome 9 long arms, and that recombination between these "supergenes" results in the synthesis of gene combinations lethal in the haploid phase. As Anyway concludes: "The lack of .. (genetic) .. flexibility has prevented significant evolutionary change, and the species is now restricted to those limited areas which provide the ecology to which it is adjusted. *Calectasia* is a true relic, apparently committed to ultimate extinction by the adoption of an ultra-conservative genetic system."

Isotoma petraea—recent complex hybridity

Isotoma petraea F. Muell. is another species which has evolved a system of permanent hybridity. It is a largely autogamic species which occurs in discrete populations on granite outcrops and other rocky areas throughout the Ereman Province of Australia. In the southwestern corner of its distributional range in Western Australia, complex hybridity has evolved; the populations are made up of plants heterozygous for multiple interchanges, made permanent by the operation of its autogamic breeding habit and a system of balanced lethal genes. A detailed hypothesis concerning the evolutionary origin of this genetic system from structurally homozygous progenitors has been developed (James, 1965; 1971).

Beltran (1971) has investigated the generation of hybrid vigour in interpopulational crosses in *I. petraea*. He has shown that the degree of heterosis achieved in such crosses depends in large measure upon the genetic systems of the parents involved. Intropopulational hybrids between structural homozygotes will show substantial heterosis if the parental populations exhibit little outcrossing, and little or no heterosis if the parental populations exhibit substantial amounts of outcrossing. Intropopulational hybrids between complex heterozygotes exhibit either no or negative heterosis. These results suggest that the *I. petraea* population system may be viewed as a series of lineages inbred to varying degrees; amongst the structural homozygotes, crossing generates heterosis, the degree and significance of which depending upon the relative degree of inbreeding characterising the parents, but all the structurally homozygous populations constitute a single coadapted gene pool in that the union of gametes drawn from different populations produces a hybrid as vigorous as or more vigorous than the

parents. On the other hand, amongst the complex hybrid populations, the absence of heterosis in interpopulation hybrids conforms with the hypothesis that the complex hybrids are already conserving high levels of genetic hybridity, and the negative heterosis observed in some inter-population hybrids suggests that coadaptation no longer exists between the complex hybrid populations.

Laxmannia—responses to autogamy

Laxmannia, a member of the tribe Johnsonieae of the Liliaceae is one genus which promises rewards for detailed biosystematic studies (Keighery, unpublished). Possibly the most striking morphological feature in this genus is the development of shortly to strongly pedunculate inflorescences in most species, with sessile inflorescences in *L. sessiliflora* Dene. This suggests that natural selection has favoured a more effective presentation of flowers and, therefore, cross pollination. More importantly, *L. sessiliflora* has an open pollinating mechanism while the rest of the species so far examined have a floral mechanism in which open flowers are presented for cross pollination, but closure of the flowers in the evenings causes the anthers, still with pollen attached, to be pressed on to the stigma, to effect self pollination. However, a comparison of seed set following selfs and crosses shows that the products of self pollination in these latter species are to a large extent eliminated by lethals operating post zygotically. This seems to be a rather inefficient system, involving the wastage of many ovules, a situation particularly important in *Laxmannia* where, it is interesting to note, the number of ovules per flower is three in *L. sessiliflora* and increases to 15 to 21 in species with lethal systems. Additionally, in *L. ramosa* Lindl., certain populations on the coastal plain around Perth exhibit high frequencies of interchange heterozygotes as well as the automatic self-pollination system and the elimination of selfed products by lethal systems. Again, there is a conjunction of interchange exploitation and the generation of lethal systems in association with a change in the breeding system towards autogamy, but the system has not achieved the rigidity of that exhibited by *Isotoma petraea*. *Laxmannia squarrosa* Lindl. is a highly variable species, and with *L. grandiflora* Lindl., *L. sessilis* Lindl. and several other forms, constitutes a complex of some taxonomic confusion. These species exhibit the automatic self-pollination mechanism described above, post-zygotic elimination of selfed products, and a variety of other cytogenetic devices including chiasma localization, polyploidy, aneuploid reduction, and a complex but as yet unresolved pattern of genetic coadaptation between forms. It is clear that an understanding of the genetic architecture and strategies of this group will greatly facilitate the construction of a meaningful taxonomy.

Stylidium—lethals and aneuploidy

Stylidium is one of the more remarkable components of the Western Australian flora. It is by far the largest genus of the Stylidiaceae, a family restricted to Australia (including Tasmania), New Zealand and Antarctic South America, plus a few species penetrating back into the Indo-Malayan region. Of the 140 species currently recognized, 102 occur in the south-west of Western Australia, 30 occur in northern Australia and beyond, while 8 occur only in the eastern states. A comparison of the cytological information presently available indicates that the base chromosome number is $x = 15$, a number constant, except for polyploidy, amongst all the eastern states and New Zealand records. However, associated with the radiation of species that has occurred in the south-west of Western Australia, is a massive propensity for aneuploid reduction. In Western Australia, chromosome numbers ranging from $n = 16$ down to $n = 5$ have been recorded, with polyploidy occurring on 15, 14 and 13 (James, 1973; Banyard, 1973). Aneuploid reduction series are in evidence in most sections of the genus as recognised by Mildbraed (1908), with possibly several independent reduction series occurring in some of the larger sections. Carlquist (1968) has commented upon the bio-systematic interest of the Stylidiaceae and upon the lack of published information. He speculated upon the factors which may have contributed to its striking speciation in Western Australia, and suggested that adaptation to pollination vectors and to soil mosaic patterns may have been of prime importance. The information on chromosome number variation, which was not available to Carlquist, is indicative, however, of important cytogenetic situations.

The genetic systems and biosystematic relationships in several species groups in *Stylidium* have been investigated. Farrell (1973) has shown that *Stylidium calcaratum* R.Br. and *S. ecorne*,* the latter formerly considered to be a variety of the first, differ in chromosome number ($n = 11$ and $n = 13$ respectively). *S. ecorne* having the higher number, may be considered primitive to *S. calcaratum*, and this directional reading of the evolutionary sequence conforms with the proposition that the well developed floral spur and the adaptation to more xeric habitats characteristic of *S. calcaratum* are derived conditions. Seed set following selfing in both species is as good as that following intrapopulation crosses. However, interpopulation crosses in *S. ecorne* yield high seed sets, but in *S. calcaratum* reduced seed sets, relative to intrapopulation crosses, are found. Thus, the evolution of *S. calcaratum* from *S. ecorne*-like ancestors has involved not only the acquisition of a perfected floral spur and an increased ecological amplitude, but also an aneuploid reduction of chromosome number, and a loss of coadaptation between the *calcaratum* populations.

**S. ecorne* is a manuscript name to be formally published in Farrell (1973), the taxon so named is equivalent to *Stylidium calcaratum* var. *ecorne* F. Muell. ex Erickson and Willis.

Banyard (1973) has made comparable studies on *S. elongatum* Benth. (n 13 and 26), *S. confluens** (n=14) and *S. crassifolium* R.Br. (n 14 and 28), three distinct species considered by Carlquist (1968) to form a continuous variational cline. In all three species, at the diploid level at least, comparison of seed set following selfing and intrapopulation crossing demonstrate the elimination of most selfed products by the operation of post-zygotic lethals. Inter-population crosses show that there is again, in all species, a breakdown in coadaptation. Best seed set is obtained in interpopulation crosses involving parents drawn from populations some 15 to 40 miles apart. When the interparental distance is 100 to 150 miles, the seed set is reduced to levels comparable to that obtained in intrapopulation crosses. Thus, it would seem that in these species, individual plants are heterozygous for several to many recessive lethal genes, and these lethals are shared by most or all members of a population. The arrays of lethals vary from population to population and populations sufficiently distant have fewer lethals in common. However, increasing distance between populations is associated with increasing genetic divergence, and this may be fostered either by exophenotypic adaptation to differing environmental circumstances, or by random, perhaps neutral, endophenotypic variation.

Tetraploid races occur in both *S. elongatum* and *S. crassifolium*. In the latter, the tetraploids occur towards the centre of the species range; the species is characteristically distributed in this region as very small localized populations which must perforce be relatively inbred. Since the ancestral diploid populations contain arrays of recessive lethal genes within their gene pools, it seems certain that the role of tetraploidy here is to conserve hybridity. A similar role may be attributed to tetraploidy in *S. elongatum*, but in this case, the species occurs as small scattered populations in yellow sandplain, in contiguous association with diploid *S. elongatum* to the west and diploid *S. confluens* to the south and east. Thus, it may well be that the adaptive utility of tetraploidy here is found in the genetic barrier it establishes between these three ecologically-differentiated contiguous forms.

Stylidium brunonianum Benth. (n=9) is an extremely variable species. Typically, local populations are made up of one or a few forms differing from each other in various morphological and ecological attributes. Each biotype appears to have its own suite of characteristics. One infraspecific taxon, sub sp. *minor*, seems of valid rank, but within sub sp. *brunonianum* the variation pattern cannot be partitioned into a satisfactory infraspecific taxonomy. The limits and relationships of *S. striatum* Lindl. *S. rigidifolium* Mildbr. and *S. brunonianum* sub sp. *brunonianum* are most confused. Ling (unpublished) and Stone (unpublished) have in-

vestigated the genetic systems found in this group. Again, post-zygotic lethals operate to eliminate the products of self pollination, and inter-population crosses reveal a breakdown in genetic coadaptation between populations as in *S. elongatum*, *S. confluens*, *S. crassifolium* and *S. calcaratum*. However, in *S. brunonianum*, the loss of coadaptation with interparental distance is much more rapid than in the other species mentioned; the optimum interparental distance being in the order of miles rather than tens of miles. *S. brunonianum* shows further developments in its genetic system in that many populations exhibit high frequencies of male-sterile plants in which the anthers abort soon after pollen mother cell meiosis, and the stigma develops precociously within unopened buds. In addition a high proportion of the male-fertile plants exhibit substantial degrees of pollen sterility, although no cytological aberrations have been associated with this. In one population examined, Stone (unpublished) found a multimodal distribution of pollen sterilities among plants, with a pronounced peak around the 50-60% sterility level. This suggests the existence of synthetic gametic lethals, in which recombinant products from an independently assorting bifactorial system are lethal.

The extent to which lethal systems have been developed in *Stylidium* appears to be quite novel, if not unique, and it seems safe to predict that causal association between lethal system exploitation and the aneuploid speciation method involved will accumulate in the future. Although the details of the speciation methods operative in this genus have yet to be resolved, it is incontestable that the phenomena reviewed above have anything but profound effects on the biosystematics and evolutionary potentials of the group.

Dampiera linearis—polyploidy and B-chromosomes

Dampiera linearis R.Br. is a species of the Goodeniaceae to which attention was initially drawn by Peacock's (1963) observation of intra-specific polyploidy. Bousfield (1970) has shown that in this species there is a wide-ranging hexaploid race in the southwestern corner of Western Australia, a tetraploid race on the lower western coastal plain and two disjunct areas of diploids, one near Albany, the second confined to the Wicher Range below Busselton. The diploids are cross incompatible with the tetraploids and hexaploids, and all forms exhibit a self-incompatibility system based on an interaction between pollen tubes and stylar tissue. Detailed analyses of the Wicher Range area has shown that the diploids are confined to the elevated lateritic caps of the old land surface, while the tetraploids occur on the alluvial soils of the erosion valleys incising the plateau and on the coastal plains. In addition, the diploid populations on the ecotonal slopes contain many plants with from one to five B chromosomes, indicating yet another cytoevolutionary response. Bousfield has clearly demonstrated B chromosome/A chromosome interactions, including

**S. confluens* is a manuscript name to be formally published in Banyard (1973). The taxon so named is presently embraced in *Stylidium crassifolium* R.Br. subsp. *crassifolium sensu* Carlquist.

physical associations between B's and A's during meiotic prophase, and a polarized nondisjunction of A chromosome bivalents at anaphase-1 which is directed such that the nondisjoining bivalents become associated with nuclei containing high numbers of B chromosomes. A survey of the population concerned showed that plants without B chromosomes were either highly pollen fertile or had substantial pollen sterility, while plants with one or more B chromosomes were never associated with the "substantial" pollen sterility levels. There is, then, a striking lack of substantially pollen-sterile plants with one or more B chromosomes in the population. From this, it is inferred that there are plants which are potentially capable of exhibiting substantial pollen sterility, and these are postulated as "interpopulational hybrids", but which have had their fertility restored by a B chromosome effect, and this effect is postulated as being a system of bivalent co-orientation which reduces the segregational fractionation of the divergent genomes combined in these interpopulational hybrids.

Thus, the biology and the cytogenetics of the situation have been integrated into an evolutionary hypothesis which proposes the following. The primitive diploids on the lateritic caps are unable to penetrate the coastal environment. However, genetic recombination at the diploid level in peripheral ecotonal situations has allowed the construction of genotypes which are better adapted to the novel ecology of the coastal plain, and systems contributing to the conservation of such newly fabricated genetic combinations are subjected, therefore, to strong positive selection pressure. The B chromosome system is the conservative device selected in this case. A consequence of B chromosome activity here, however, is A bivalent nondisjunction in interpopulational hybrids. It is proposed also, that this aberration may lead to the production of totally unreduced gametes and hence provide a mechanism for the origin of polyploids adapted to the coastal plain environment. This interpretation for the evolutionary origin of tetraploidy in *D. linearis* is strengthened by the finding of a single tetraploid plant carrying some six B chromosomes.

Although the interpretations of the observed phenomena are somewhat speculative at this stage, *Dampiera linearis* offers an exquisite opportunity to study in detail the evolutionary process of biological speciation. Present information suggests, then, that the invasion of the coastal plain by the derived tetraploids is not due to an increased ecological amplitude of tetraploidy *per se*, but that tetraploidy provides a mechanism of totally conserving genotypes assembled at the diploid level, the whole process being mediated by the unique properties of the B chromosome system.

Eremophila glabra-polyploidy and ecological preference

In *Eremophila glabra* (R.Br.) Ostenf., Ey and Barlow (1972) have demonstrated a relationship between chromosome number and ecolo-

gical preference. Although their intensive work was centered around the gulfs area in South Australia, the species is widespread in Western Australia. In this group, the diploid progenitors occur as localized populations in temperate refugia. The tetraploids are more widespread, but still relatively restricted compared to the hexaploids, and occur in temperate to semi-arid areas, while the hexaploids are of widespread distribution throughout the arid region. Thus progressive adaptation to the arid environment is associated with increasing euploid levels. Similar patterns of geographical replacement of euploid races in other species of *Eremophila* have been documented by Barlow (1971) on a less detailed scale, with "strong indications that the ancient land surfaces of Western Australia are a reservoir of relic diploid populations of *Eremophila*". Barlow discusses the possible roles of polyploidy in the genus, and suggests that "the conservative genetic effects of polyploidy in reducing segregation in newly arisen, highly adaptive heterozygous outbreeding biotypes are . . . of far greater evolutionary value than its supposed role of restoring fertility to partly sterile hybrids." In this he is in accord with the conclusions reached by Bousfield (1970) concerning the role of polyploidy in *Dampiera linearis*. A similar interpretation of the role of polyploidy is considered by Banyard (1973) concerning the tetraploid race of *Stylidium elongatum*.

Cassia—polyploidy, hybridization and apomixis

In *Cassia* (Caesalpinaceae) the species of the series *Subverrucosae* of the section *Psilorhegma* exhibit a very complicated biosystematic situation. Randell (1970) has extensively surveyed this group throughout the Eremean Province, and although her work was largely concerned with central Australian populations, probably similar situations obtain in Western Australia. The following interpretation was developed. Polyploid forms are widespread throughout the Eremaea. The diploid species are confined to mountain refugia such as the Macdonnell, Flinders and Kimberley Ranges, and are apparently fairly strongly isolated from each other in that no evidence of hybridization at the diploid level has been obtained. However, infraspecific polyploid races occur and interspecific hybridization at the tetraploid level, and between tetraploids and diploids, apparently occurs with considerable frequency, generating taxonomically confusing hybrid swarms containing several chromosome numbers. In addition, facultative pseudogamous adventitious polyembryony occurs in the polyploid forms, leading to a competition between the single sexual and up to nine apomictic embryos within the single embryo sac. There is some evidence that the components necessary to assemble this genetic system, namely mechanisms for generating diploid gametes and inducing adventitious polyembryony, may be found at the diploid level.

Once assembled, this remarkable system provides for many things. Sexual reproduction and hybridization between disparate forms generates

hybrids which may themselves have an adaptive advantage in heterotic vigour, and from which the sexual process may assemble a limitless array of novel genotypes. Any genotype is potentially conservable by the apomictic mechanism, but the pseudogamous and facultative nature of this mechanism requires sexual experimentation to proceed. The products of sexual fertilization are subjected to a competitive screening against adventitious embryos of maternal genotype during seed formation. Thus ovules carrying "inferior quality" sexually produced embryos are not wasted, but instead they carry embryos of an already tested genotype. These *Cassia* population systems seem to have achieved a remarkable balance between innovative sexuality and conservative apomixis.

Other groups—possibilities

Several other groups have been investigated cytotaxonomically, and here interesting situations which may well respond to detailed cytogenetic analysis are in evidence. For example, intra- and interspecific polyploidy have been observed by Brittan (unpublished) during his wide-ranging experimental taxonomic study of the genus *Thysanotus*. Polyploid cytotypes have been found in 13 of the 27 species so far investigated cytologically. There appears to be some correlation between the occurrence of polyploidy and a change in the pollination mechanism towards inbreeding. In some of the polyploid forms the anthers dehisce along their full length by longitudinal slits instead of by terminal pores as is usual in the genus. Under insect-free glasshouse conditions it is found that capsules are regularly developed by non-manipulated flowers as a result of self pollination associated with the freely dehiscing type of anther, whereas capsules only form in the pore dehiscing types when manual self pollination has been carried out. This association of polyploidy and self pollination occurs in *T. patersonii* R.Br., the genus' most widespread species in Australia which exhibits polyploidy at the tetraploid, hexaploid and octoploid levels, in *T. tenuis* Lindl. which is of relatively restricted occurrence and uniformly hexaploid, and in *T. multiflorus* R.Br. Interestingly, in *T. multiflorus*, tetraploids exhibiting pore dehiscence occur as well, and Brittan (1962) has suggested that this form is of amphidiploid origin. It seems that in this genus, further cytogenetic work may be able to discriminate between differing roles for polyploidy, even at an infraspecific level.

Secondly, *Drosera* is well developed in Western Australia, having some 34 species currently recognised. Chromosomally, the genus is quite constant on a base number of $x=10$ except in the section *Lamprolepis*, the pygmy sundews, where aneuploid reduction to $n=5$ has been established (Marchant, unpublished). The pygmy sundews with the lower numbers tend to occur in discrete localized populations whereas the wider ranging species maintain the primitive chromosome number. It will be of interest to learn of any other endophenotypic differences,

as well as exophenotypic differences, which differentiates the section *Lamprolepis* from the rest of *Drosera*.

Similar suggestive observations have been made by Bennett (1972) concerning *Hybanthus*, a shrubby genus of the Violaceae. Here it seems that a primitive aneuploid reduction series, $8 \rightarrow 6 \rightarrow 4$, is represented in present day taxa. In the section *Variables*, the widespread Western Australian taxa, *H. floribundus* (Lindl.) F. Muell. subsp. *floribundas* ($n=6, 12$ and 24), *H. calycinus* (DC. ex Ging.) F. Muell. ($n=6$ and 12) and *H. epacridoides* (C. A. Gardn.) Melch. ($n=12$) include polyploid cytotypes, while four diploid taxa have restricted distributions. This pattern is somewhat confounded, however, by the presence of the polyploid *H. bilobus* C. A. Gardn. ($n=12$ and 24) which is of relatively restricted occurrence, and the diploid *H. monopetalus* (Roem. et Schult.) Domin ($n=4$) which is widespread in the eastern states. Bennett (loc. cit) also notes that pollen fertility is characteristically quite high in the widespread *H. floribundus* and *H. calycinus*, and characteristically rather low in the other Western Australian taxa. It would seem again, that different genetic strategies are associated with different degrees of success, and detailed comparative studies on the cytogenetics of *Hybanthus* species may well prove rewarding.

In like manner, comparative cytogenetic studies involving *Verticordia*, *Darwinia* and other members of the Chamaelaucoideae and members of the cytologically invariant Leptospermoideae may indicate a causal basis for the strikingly different cytological responses in these two tribes of the Myrtaceae. Clearly, such an approach can be extended to any group. Indeed, the Western Australian flora provides a formidable store of materials for research into the processes of biological diversification and speciation.

Concluding remarks

Isotoma, *Laxmannia* and *Stylidium*, and probably *Calactasia*, exhibit lethal systems which eliminate the relatively homozygous products of self-fertilization. The polyploidy in *Eremophila*, *Cassia*, *Dampiera*, *Stylidium* and *Thysanotus* may be interpreted as a system allowing the maintenance of high levels of hybridity within populations, though other bases for its adaptive utility are possible and even preferred. Nevertheless, it would appear that natural selection has favoured systems that facilitate a pursuit of hybridity during the differentiation of these groups in the semi-arid to arid Western Australian environment. Genetic hybridity is necessary for the construction of new adapted gene arrays by recombination, and the evolutionary success of lineages fostering hybridity may well be achieved through default of the relatively homozygous lineages. On the other hand, heterozygosity *per se* may somehow code for a more efficient, flexible and adaptive phenotype than can homozygosity. The occurrence of heterosis in interpopulational hybrids amongst

naturally occurring structural homozygotes in *Isotoma petraea* and the dependence of the extent of the heterotic effect on the breeding system of the parents suggests value in heterozygosity *per se*. In the *Isotoma* complex hybrids and in *Laxmannia* and *Stylidium* hybridity has been fixed by the lethal systems, and these have led to a marked differentiation between populations resulting in what here has been called a loss in coadaptation. The intrinsic barriers to reproduction so established between populations in *Stylidium* and *Laxmannia* may well provide the beginnings upon which speciation may be built.

The self incompatibility system in *Dampiera linearis* would seem to be a much more efficient and less divisive system of excluding self fertilization products. So far, little work on the extent of self incompatibility systems in the Western Australian flora has been done. Another system which prevents self fertilization is dioecy, and McComb (1968, 1969) has concluded that the evolution of dioecy and polyploidy are independent responses associated with the maintenance of high levels of heterozygosity in *Isotoma fluviatilis* (R.Br.) F. Muell. in New South Wales. McComb (1966) has also analysed the frequencies of the various sex forms in the floras of the South-west Province of Western Australia and of the British Isles, and has compared these with each other and with the analysis of the South Australian flora made by Parsons (1958). It was shown, *inter alia*, that the proportions of species with hermaphrodite flowers in South Australia and Western Australia are comparable to each other (88.9% and 90.0% respectively) and significantly greater than in the British Isles (80.7%). Additionally, it was demonstrated that the average number of species in the Western Australian hermaphrodite genera is 9.4 while in the British Isles hermaphrodite genera it is 2.8. The average number of species per genus for non-hermaphrodite genera shows much less disparity, 4.1 for Western Australia and 3.1 for the British Isles. Thus, the Western Australian flora has proportionately fewer sexually differentiated species and, among the hermaphrodites, significantly larger genera than has the British Isles. These differences may reflect the different states of development of plant systematics in the two regions, or it may reflect biologically important differences. The following speculation is irresistible. The Western Australian flora is younger and evolutionarily more dynamic than that of the British Isles; the adaptive diversification of its components is associated with the exploitation of a variety of devices conserving hybridity or adaptive gene arrays, or both, and some of these conservative mechanisms are more divisive than others. Divisive mechanisms must result in the fragmentation of the gene pool, and in speciation. The resources of genetic variation available within each product species would be relatively restricted compared with that available to the whole. As the Western Australian evolutionary dynamism dissipates, those lineages which adopted the less

restrictive conservative systems may be expected to have the better chances of survival. Lineages which have adopted dioecy to maintain hybridity may fare much better than hermaphrodites encumbered with lethal systems and, through natural selection, the spectrum of sex forms in this flora may eventually approach that of the British Isles.

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5.—Aboriginal man in southwestern Australia

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Abstract

Firm evidence from excavations demonstrates that Aborigines have been present in southwestern Australia for about 25,000 years. However, findings from excavated and non-excavated sites could appreciably extend this time-depth to show a much earlier human occupation. Many of these sites are of major scientific importance. Some are listed and located on an accompanying map. One criterion for classifying them is their original nature or use: e.g., ceremonial sites, stone arrangements, hunting devices, rock engravings, quarries, and surface scatter or artefacts. They are now subject to legislative protection. A topographical archaeological approach based on field survey with selective excavation, supplemented by ethno-historical evidence, provides an ecological perspective on the interaction of southwestern Aboriginal populations, through time, with their environment. A special focus here is on the Perth area, particularly in relation to surface artefact assemblages.

The focus then shifts to the contemporary and near-contemporary scene. Various languages and dialects were spoken in this area, but intensive alien contact led to the emergence of one, Njungar (Nyungar), as a general south-west language. Its phonological, grammatical and lexico-semantic characteristics are outlined. The final paper sketches traditional south-west Aboriginal socio-cultural life at the beginning of European settlement. In the wake of that settlement came rapid depopulation and, within fifty years or so, destruction of the traditional systems. Out of this physical, psycho-social and cultural wreckage, have come the mixed Njungar people of Aboriginal descent who now seek an Aboriginal identity of their own.

Introduction

These five papers are devoted to a consideration of what can be called the south-west Aboriginal heritage. Three sorts of data are involved. 1) The archaeological approach takes as its point of departure surviving Aboriginal sites through which the past can be explored. It is building up a picture of Aboriginal settlement that can be related to the situation in other parts of this continent. 2) Because systematic anthropological research was undeveloped during the early settlement of the south-west, reliance has had to be placed on the often incomplete and subjective evidence of the earlier recorders. It is therefore impossible, at this point in time, to obtain a deep understanding of traditional Aboriginal life in this area. These early sources, however, do afford valuable insights. 3) On the other hand, it has been possible to reconstruct aspects of the socio-cultural past from the often fragile memories of elderly Aborigines. And with this, is direct

anthropological research into the contemporary situation, among persons of Aboriginal descent who have more associations with the wider Australian society than they have with their Aboriginal forbears.

The range of accumulating data on the south-west Aborigines, from the far-distant to the near-past and to the present-day, even though so much information is missing, adds up to something approximating an overall statement. And in summarized form, this is what is presented here. Traditionally, these Aborigines belonged to a non-circumcising area: this fact alone placed them, anthropologically speaking, in a minority position *vis-à-vis* other Australian Aborigines. They also possessed some unique or distinctive characteristics which separated them conceptually from the others. In the process of intensive contact, virtually all of these identifying aspects were eroded. Those which survive identify them simply as being of Aboriginal descent in a generalized sense and not distinctively as south-west Aborigines: that has been irretrievably lost.

Early human occupation of southwestern Australia

by D. Merrilees

Sites indicating early occupation

Excavation localities and other sites providing evidence of early occupation of the southwestern part of the continent are included in Figure 1. Notes on these sites are given below, with reference where possible to published information, even if only brief, or an indication of studies planned or in progress. Some of these sites are mentioned below in other contexts by other authors. Occupation sites represented by surface scatters of artefacts not readily dateable are not referred to here. Hallam (1972*b*) gives a relative chronology for such artefact assemblages in the Perth area.

5. Wilgie Mia. Aboriginal ochre mine in use from late Holocene to modern time. (I. M. Crawford, personal communication.)

9. Coolarburloo Pool. Artefact apparently in same geological formation as remains of large extinct marsupial and australite, though not at same site. (Merrilees, 1968*b*: 15) Pleistocene?

36. Hastings Cave. (Lundelius, 1960: as 'Drovers Cave'.) Later excavations have shown charcoal concentrations interpreted as hearths and an artefact; mid-Holocene on radiocarbon dating. (A. Baynes, personal communication.)

47. Caladenia Cave. Artefacts with associated faunal remains in excavation. (R. Roe and D. Merrilees, in progress.) Holocene?

48. Rock shelter near Gingin. Artefacts and faunal remains. (Roe 1971.) Holocene?

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³Director, United Aborigines Mission Language Department, Kalgoorlie, Western Australia.

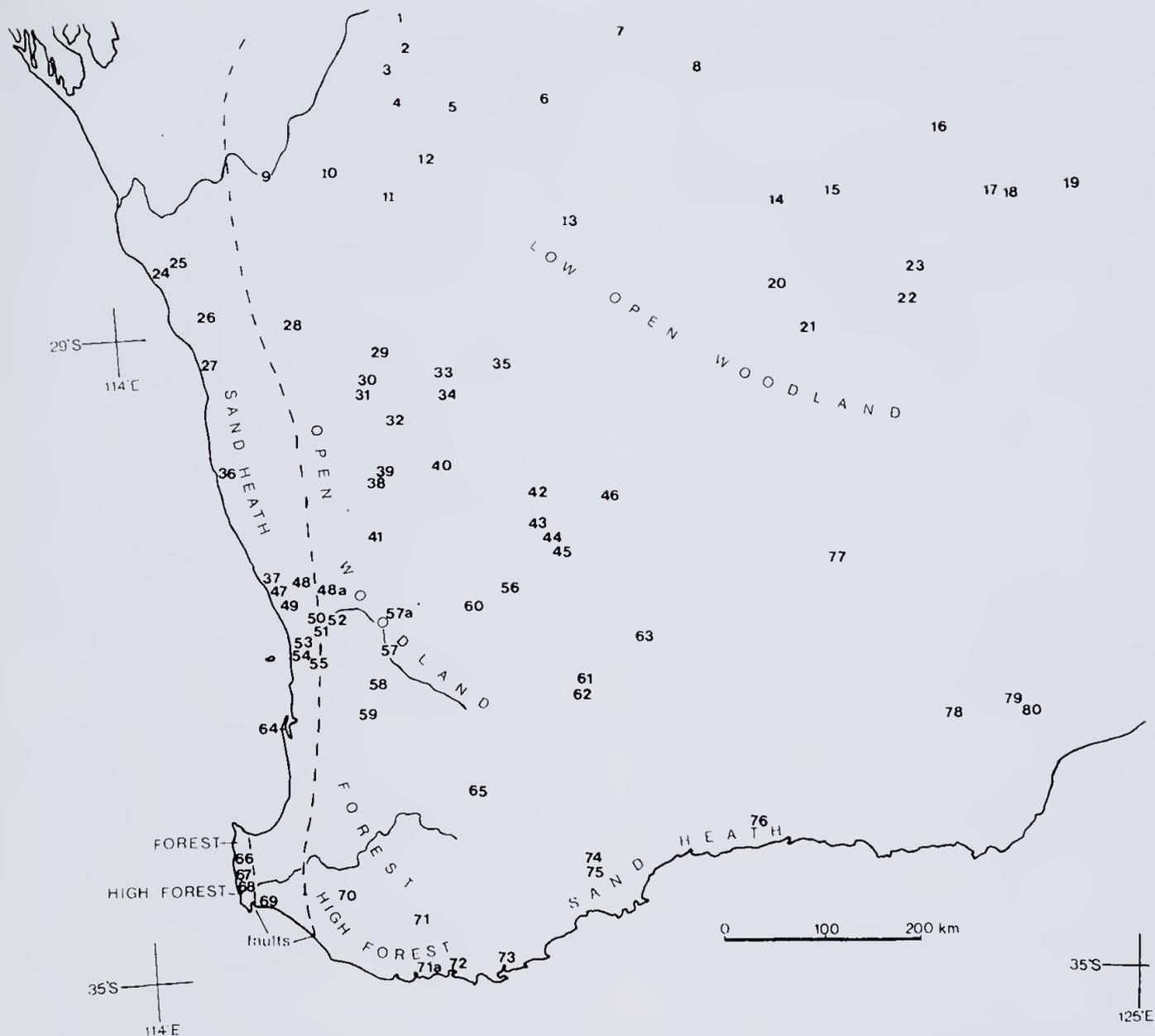


Figure 1.—Sites of excavations and other sources of information on Aboriginal occupation of the south west of Western Australia from prehistoric time to early contact with European invaders. See texts by Merrilees, Dix and Hallam. The map also attempts to give a first impression of vegetation at the time of European contact and of the physiographic nature of the region. The dissected remnant of the long Darling Fault scarp sharply demarcates an eastern plateau from a low lying plain to the west. In the far south west another fault system demarcates this plain from a raised coastal block. The rivers shown are (from N to S) the Murchison, Swan, Avon and Blackwood.

49. Dunstan's Quarry, Douglas. Kendrick and Merrilees (1966) report site as fossil carnivore den, but presence of mussel shell and subsequent recognition of limestone flake as an artefact (A 17553 in Western Australian Museum collections) suggest an archaeological component. Holocene?

49. Orchestra Shell Cave. (Hallam, 1971b.) Roof markings, with artefacts and faunal remains in excavation. Holocene on radiocarbon dates.

49. Murray's Cave. (Hallam, 1971b.) Artefact and faunal remains in excavation. Holocene on radiocarbon date.

49. Yonderup Cave, Yanchep. Excavations by D. S. Davidson, unpublished. Some faunal remains in Museum collection. Holocene?

56, 65. Examples (only) of fossil lake sites in 'wheat belt'. Artefacts and faunal remains reported by Bettenay (1962). Pleistocene? Reconnaissance studies subsequently made by J. M. Bowler.

57. Frieze Cave. (Hallam, 1972b.) Excavation with artefacts, ochre. Late Holocene.

66. Cowaramup Point. Artefacts and faunal remains in well lithified fossil soil. (C. E. Dortch, personal communication.) Pleistocene?

67. Mammoth Cave. (Merrilees, 1968b.) The main source of information on the Pleistocene fauna of the south-west, with many species now totally or locally extinct and some indication of a climate differing from the present (Merrilees, 1968a). Some bones charred, and investigation in progress of possibility that this charring results from man-made fires (M. Archer, I. M. Crawford and D. Merrilees). Radiocarbon date greater than 37,000 yr. B.P. reported (Lundelius, 1960), but there is uncertainty concerning the specimens to which this date refers.

68. Devil's Lair. (Dortch and Merrilees, 1972; 1973.) Deep deposit of 'cave earth' with artefacts, human teeth, and abundant faunal remains. Cave occupied at times by human beings. Self-consistent set of radiocarbon dates indicates man present 25,000 years ago, and bottom of deposit not yet reached. Studies continuing.

68 Strong's Cave. Human remains at shallow depth (Merrilees, 1968b). Holocene? Other caves in Cape Leeuwin - Cape Naturaliste region have yielded similar human skeletal material.

69. Coast south of Scott River. Artefacts and human skeletal and other faunal remains in blown-out dunes (Butler, 1969). Holocene?

79, 80. Guaralya and Wonberna rock holes, Balladonia district. Artefacts associated with faunal remains, some of extinct species, some in well lithified deposit (Merrilees, 1968b: 14). Pleistocene?

Antiquity of man in the south-west

The association of artefacts with extinct animals in a well-lithified deposit at Wonberna, a similar probable association at Coolarburloo Pool, the occurrence of artefacts in a well-lithified buried soil at Cowaramup Point, artefacts at the 'wheat belt' extinct lake sites, and some of the surface occurrences of artefacts mentioned by Hallam (1972b), all suggest considerable antiquity for the human beings concerned, but no firm age estimates are available. An age estimate beyond the limit of radiocarbon dating for the sample concerned from Mammoth Cave is of uncertain application to specimens recovered from the cave, and has not yet been related unequivocally to human presence. Thus the oldest human occupation of the south-west of the continent reliably established so far is that represented in Devil's Lair at about 25,000 years B.P. The bottom of the Devil's Lair deposit has not been reached and might reveal occupation more than 30,000 years ago (Dortch and Merrilees, 1973).

Acknowledgements.—I am grateful to Mrs. P. Kail for preparing Figure 1, to officers of the Western Australian Department of Agriculture for their advice on vegetation, and to Mrs. S. J. Hallam for criticisms of a draft of this note.

Aboriginal Art: Ceremonial and other sites in southwestern Australia

by W. C. Dix

Registration of Aboriginal sites

In 1960, the Anthropological Society of Western Australia began to prepare a list of known or reported Aboriginal sites. The Western Australian Museum undertook to maintain and expand that list, and is continuing to do so. In 1962, a Panel was formed to advise the Government on matters relating to sites. The Panel also prepared a draft of legislation which, after extensive revision, was eventually proclaimed as the *Aboriginal Heritage Act* in December 1972. This Act states that it is an offence to excavate, destroy, damage, conceal or in any way alter an Aboriginal site, even if it happens to be on privately owned land.

As part of the effort to protect such sites, I was appointed in 1970 Registrar of Aboriginal Sites, with supporting staff, having headquarters at the Western Australian Museum. Since then, we have embarked on a programme of verifying reports and have been exploring various methods of physically protecting the sites. In many cases, Reserves and 'Protected Areas' centring on particular places have been established.

Aboriginal sites

Some of the more significant sites listed in our index are noted on the map (Figure 1), and an indication is given below of the nature of the sites. Few have been the subject of detailed published reports. Figure 1 does not show sites from which artefacts have been collected from surface scatter unless these have been published. Locations of stores for sacred ritual objects, and sites reported in confidence, are not indicated. A number of sites which have been excavated are discussed above by D. Merrilees.

a Sacred or Ceremonial Sites: Sites now in disuse are located (in Figure 1) at 16, 18, 33. The only currently significant site shown is the complex at Weebo, 14. Focused on a banded siltstone, now called 'Weebo Stone', the site has attracted considerable publicity in recent years, and the location is generally well known.

b Stone Arrangement (not including stone structures): Authenticated arrangements are located at 4, 6, 8, 13, 15, 17, 20, 21, 27, 28, 30, 31, 32, 34, 38, 41, 43, 46, 58, 59, 63, 70, 74, 75, 76, 77.

c Hunting Devices: Many sites may have had devices for hunting, and these include some stone structures, pits, etc. The purpose of some is quite obvious, and some are known through an information link with early settlers. Fish traps are located at 54, 72, 73. Large animal traps at 71, and small animal or reptile traps at 59, 75.

d Rock Engravings, etc.: Very little engraving is in evidence, probably due to the lack of suitable material, by comparison with the north-west. Some known sites are at 1, 2, 3, 10, 49, 64, 78.

e Paintings: 2, 3, 4, 8, 11, 12, 19, 24, 25, 26, 40, 42, 44, 45, 60, 61, 62, 78.

f Quarries: The well known ochre quarry at Wilgie Mia, 5, has an extensive archaeological deposit. Other ochre quarries are at 16, 29, 39. Significant quarries for stone are known at 7, 22.

g Surface Scatter of Artefacts: Examples include those located at 5, 8, 23, 36, 37, 50, 51, 52, 53, 55.

References: Some of the sites shown on Figure 1, have been referred to, and in some cases described, in the following references:

Butler (1958)	50, 51, 52, 53, 55
Campbell (1914)	24, 25, 26
Cawthorn (1963)	8
Crawford (1963)	5, 61, 62
Davidson (1936)	12, 24, 25, 26
Davidson (1952)	3, 5, 11, 12, 24, 25, 26, 44, 60, 62
Davies (1961)	1, 2, 10, 13
Glauert (1952)	38
Gould (1968)	33, 34
Gould (1969)	34
Glover and Cockbain (1971)	24, 25, 36, 48, 50, 55, 69
Hallam (1971a,b.)	59, 49
Hallam (1972a,b,c.)	57, 64, 49
Hallam (1973)	51
Le Soeuf (1907)	60
McCarthy (1962)	11, 12, 26
Serventy (1952)	57, 60, 61, 62
Serventy and White (1958)	28
Uren (1940)	27
Woodward (1914)	5

Ecology and demography in southwestern Australia

by Sylvia J. Hallam

Pleistocene to Present

Merrilees describes above the earliest decisive evidence for Aboriginal populations in southwestern Australia, as yielded mainly by excavations, and in particular by those in Devil's Lair (Dortch and Merrilees, 1972; 1973), which show the wide range of activities of Pleistocene Aborigines in the south-west—working bone; work-

ing wood; using steep scrapers, adze-fashion; hafting flaked tools and bone (not only at a time similar to Gould's early hafted material from Puntutjarpa [Gould, 1971], but also at a date twice as remote [Dortch and Merrilees, 1973]); utilizing, quarrying and trading a variety of raw materials, including an Eocene fossiliferous chert similar to the 'flint' quarried during the Pleistocene at Koonalda (and later from the cliffs along the Nullarbor coast, and traded hundreds of miles eastward [Wright, 1971]), and also to the chert from surface assemblages throughout hundreds of miles of the west coastal plain (Glover and Cockbain, 1971). Wilgie Mia attests to later large-scale mining and trading; while Orchestra Shell Cave and Frieze Cave provide successive exemplifications and modifications of artistic, mythic and ritual traditions in which serpents, fire, and dark crevices and caves had their part. Stone arrangements and art sites further illustrate that the links between Aboriginal groups and their terrain were mediated through the symbolic as well as the economic aspects of their lore and usages. What other evidence can contribute to analysis of the interacting transformations of Aboriginal life and land between the Pleistocene and European contact?

The role of topographic archaeology

The British, and above all the Cambridge, archaeological tradition has always put stress on field survey as well as excavation, although American archaeologists have only recently realized the importance of ecological and settlement studies. Like Stukley in the eighteenth century, O. G. S. Crawford (1953), Fox (1923), Phillips (1964; 1970), Hoskins (1955), Hallam (1970), Fowler (1972), etc., show a continuing concern with distributions and settlement patterns, with the changing reactions and cumulative impact of human groups to and upon changing regional landscapes—a concern, in brief, with dynamic ecological systems, in which the exploitative, technological and symbolic activities of human societies were major components. Field archaeology, or more properly 'topographic archaeology' (Clark, 1964), comprises the investigation of 'all traces of former human activity' in the landscape. In any Australian region this would include, for example, fords, wells, water sources and their surround of much-burnt ground; yam-diggings, pit-traps, fish-weirs; tracks; belts and nodes of used and fired countryside, open parklike grazing and dense secondary regrowth; artefact-scatters indicating ephemeral stopovers of small hunting groups; the denser artefact-concentrations on camping-spots frequented occasionally, often seasonally or semi-permanently, by smaller or larger aggregates of folk over various timespans and for various purposes (fishing, fowling, taking frogs, turtles, lizards, small mammals, or hunting larger herbivores, digging various roots), leaving the debris of weapon manufacture, woodworking, grinding, etc.; bare sand areas cleared in getting fuel and shelter and kept clear by constant usage; devegetated areas, cleared by fire,

sand-blows and mobile dunes—e.g. (see Figure 1) Williams Bay, 71a (Birmingham *et al.* 1971); Scott River, 69 (Butler, 1969); Moore River, 37 (Hallam, 1972a); as well as sites of art and ritual which patterned Aboriginal activities.

Field surveys may fall into one of several possible categories (Green, 1967): (1) Extensive reconnaissance surveys in relatively little investigated areas, drawing together scattered material, published and unpublished, are an essential preliminary to further investigation (e.g., the Anthropological Society of Western Australia, 1960; Crawford, 1963; the Aboriginal site list prepared by Miss Sarah Meagher of the Western Australian Museum in 1967-8, and amplified recently by the Registrar of Aboriginal sites, Mr. W. Dix). (2) Survey in conjunction with excavation may make clear the range and context of a certain type of site (*cf.* those around the Pleistocene lakes of N.S.W. [Bowler 1971; Bowler *et al.* 1972; Barbetti and Allen 1972]). (3) Problem-oriented surveys concentrate on one particular type of site over a wide area (e.g., Dix's study of stone arrangements [see above]; the art studies of Davidson [1952], Crawford, Bruce Wright, McCaskill, etc.). (4) Intensive surveys 'designed to extract all possible information from each site found' and recognizing the necessity for 'as complete a random sample as possible' must necessarily be relatively localized, but should preferably be sufficiently extensive to include the normal range of a local group and investigate shifts in the demarcation of culture areas. Such systematic field studies have been most effectively adumbrated and pursued in the east and north of Australia (*cf.* McBryde, 1962; 1973, etc.; Lampert, 1971a,b; Stockton, 1970; 1972; and Dortch, 1972) but have been relatively lacking in the South-West (*cf.*, however, Butler, 1958; Akerman, 1969; Bignell, 1971); and valuable local amateur studies are in progress of both the archaeological and the folk evidence of Aboriginal occupation and of the relationship of early European to Aboriginal settlement (e.g. by Gardner near Northcliffe, and Mrs. Roe in the Gingin-Moore River area).

Topographic studies in southwestern Australia

Dr. John Glover* investigated artefact-scatters on the coastal plain in order to define the distributions and proportions of a lithologically-peculiar, exotic raw material (see above), which he found to occur in exposures (e.g. in Figure 1, near 24-5, 36, 37, 48, a concentration of sites around 53-5, and 69) in dune blows mostly overlooking interdunal swamps and lakes (Glover and Cockbain, 1971). No site east of the Darling Fault has yielded more than a few flakes of this Bryozoan chert. It is most abundant, on the whole, on sites near the west of the coastal plain. This suggests a derivation for the Perth Basin material, perhaps from sources now offshore since the rise in sea-level which ended

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around 3000 BC [Churchill, 1959; 1960] in caves or river channels penetrating through Pleistocene deposits into the underlying Eocene. Churchill (1959; 1968) discusses evidence that the Swan River cut a channel down to around 50 m below present mean sea-level, and was still at around —20 m by 7000 BC. Assemblages composed almost exclusively of this fossiliferous chert are also typologically distinctive, comprising flakes, chips, flaked pieces, and a great variety of scrapers—nosed, concave and convex, including many with a steep edge angle and adze-type utilization (e.g. 37; Hallam 1972a). At 37, the fact that there are only two backed blades in the group of artefact scatters suggests that this assemblage, and the similar component in other coastal plain assemblages, is early (i.e. prior to the general floruit of backed-blade assemblages from around 2000 BC [cf. Gould, 1971; Hallam, 1972a,b]).

European glass, sherds, clay pipes, etc., on some sites show that a few continued to be occupied from the early ('pre-blade') phase, through into the middle ('backed-blade') and late ('post-blade') phases, and a very few into the final brief phase after European contact. The analysis of such multi-phase occupations is aided by study of one-phase sites: for example, the early assemblages described above, or the many relatively amorphous late assemblages with a high proportion of quartz chips. Differences due to date must be distinguished from those due to group size, span and frequency of occupation, or exploitative function, as indicated by extent, density of material, presence or absence of grinding equipment; and from regional differences in facies between sites of the same phase. Each assemblage can thus be assigned to a phase or series of phases; and the distribution of numbers and sizes of sites in relation to ecological zones can be analyzed for each phase. Changes over time indicate changes in overall population density, patterning into splitting and aggregating groups, and stress on the different resources which ethno-historical evidence shows to characterize the different zones.

The Perth area project

The Australian Institute of Aboriginal Studies and the University of Western Australia are supporting a survey comprising a transect from the coast eastward to beyond the Avon, centred on the Swan estuary (Hallam, 1971b; 1972a,b,c; 1973). It is too soon to presage full results, but certain trends are suggested by a pilot survey of about 120 sites clustered into about 70 groups and over 10,000 artefacts.

Increasing numbers of sites per unit timespan on the coastal plain show increasing Aboriginal usage and populations. The 'early' coastal groupings using Eocene chert were confined to the (then wider) plain west of the Darling Scarp; later and 'contact' groups, on the evidence both of material distributions and of early European observers, ranged farther east into the good grazing land along the scarp foot and into the Darling Range; with intensive late

usage of the resources of interdunal lakes and swamps.

By contrast, the typologically early (cf. Lampert, 1971a,b) chopper/steep scraper assemblages of the Avon Valley and eastward (e.g. 10 sites in the Grass Valley-Quellington area, —c.55) are richer in numbers, amount of material, and variety of types, relative to later assemblages, than on the coastal plain. They differ in material (largely doloritic) and typology (with their many high-backed 'core' scrapers) from the coastal assemblages, though sharing steep edge and in-biting use wear; and extend west to the foot of the Darling Scarp (e.g. 48a, 50). The line of demarcation between coastal and inland-oriented groups would seem to have shifted eastward with the rise of the sea level, by about 3000-2000 BC. There are relatively fewer and sparser 'middle' and 'late' assemblages inland. I have suggested (1972b; 1973) that the less wooded inland areas offered initially more abundant grazing, supporting high animal and early human populations; that firing will have improved the openness and grazing potential of the 'open woodland' on the inland margin of the forest zone, and also on its coastal fringe. During the drier phase which ensued from before 2000 BC (Churchill, 1968; Gould, 1971), the inland zones proved incapable of supporting as steep a rise of population as the coast, being more sensitive to aridity and possibly also to increased salinity as a result of deforestation. Dr. C. A. Parker* (personal communication) suggests that depletion of nitrogen could be another effect of burning. Burning would, however, continue to develop rather than deplete the grazing resources of the better-watered alluvial piedmont zone, which Stirling was to find open and park-like in 1829; while the more varied fish, fowl, reptile, small mammal, root and water resources of the estuaries, inlets, lakes, and swamps of the coastal plain continued to support steeply increased usage and populations right up to European contact.

Any regional survey must take into account the archaeological and ethno-historical evidence of the symbolic (artistic-mythic-ritual) as well as the technological and economic aspects of the knowledge and skills, the cognitive lore, by which Aboriginal groups grasped and developed the potentialities of their home terrain, creating an ecological system which alien newcomers were to take over (Hallam, 1972c; 1973). Immediately following, Douglas discusses language, which was the mould for these cognitive patterns, and Professor Berndt discusses Aboriginal socio-cultural patterns in traditional terms and under European impact.

The language of southwestern Australia

by W. H. Douglas

Introduction to the 'Nyungar' language

Variant manifestations of the South-West language have been referred to in the historical

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records. Several of the variants are still known today by older speakers of what may be named generically 'Nyungar', which is also the word for 'man' in the language of the south-west. G. O'Grady (in O'Grady and Voegelin, 1966: especially p. 130ff.) has listed four of these dialects as Wadjuk, Balardong, Wardandi, and Minang and indicates that the principle sources of information on these variants are Grey (1840), Moore (1842), Salvado (1850; 1886), and Bates (1914) among others (see Oates and Oates, 1970). Later investigators include O'Grady and Hale in 1958 and 1960. A description of the language as it is spoken today was prepared by Douglas in 1968.

Other known variants of the language include Bibbulman, Kaniyang, Mirnong, Tjapanmay and Kwetjman, all of which names were spelt in diverse ways in the older records (see map in Figure 3). This Nyungar group (Douglas 1968: part 1) contrasted in vocabulary and grammatical structure with Watjari in the north (the boundary today being roughly marked by the Geraldton to Mt. Magnet railway line); with the Western Desert language to the north-east; and with Ngatju or Marlpa in the east (see von Brandenstein 1970). Descendants of the original speakers of the South-Western language number approximately 8,000 today. Many of these, however, have a very restricted knowledge of genuine Nyungar, but speak what the author has labelled 'Neo-Nyungar' (Douglas 1968: 8), a hybrid speech which contains vocabulary items and idiomatic constructions from the original language placed into English grammatical constructions.

The phonological dimension

Orthography: Investigators in the past have used a variety of spelling devices to record this previously unwritten language. In the present description the following symbols, arranged according to point and manner of articulation, have been used:

Consonants	Vowels
b dj d /d g	i u
m nj n /n ŋ	e o
lj l /l	
r /r	
w y	a

A stroke / preceding a letter indicates retroflexion.

The consonant phonemes: There is a series of voiceless unaspirated stops occurring at the labial, dental, alveolar, cerebral and velar points of articulation. The cerebral is retroflexed. A series of nasals occurs at the same five points of articulation. There are three contrastive

laterals—dental, alveolar and cerebral. The two central continuants are the alveolar, which is allophonically flapped and trilled; and the cerebral, which is retroflexed. The semi-vowels are the labio-velar /w/ and the alveolar /y/.

The vowel phonemes: The language at present has a five-vowel system. There is contrast between front and back with the high and mid phonemes, the front vowels being unrounded, the back rounded. The low vowel is central and open.

Prosodic features: Syllable stress is predictable and non-phonemic. Primary stress occurs on the first syllable of multi-syllabic words. E.g., *gudjal* 'two', *nindalinj* 'scorpion'. In reduplicated forms there is equal stress on the first syllable of each component stem: e.g., *gudjal-gudjal* 'four'.

The general syllable structure is CV or CVC (with C representing 'consonant' and V 'vowel'): e.g., *ŋuŋu/lala* 'black cockatoo', *dadj* 'meat'. V and VC may occur initially, followed by CV or CVC: e.g., *aliwa* 'beware', *idjinj* 'to lay (an egg)'. There is also a CVNC syllable in which N represents a nasal which assimilates to the same point of articulation as the final consonant: e.g., *ŋaŋ* 'mother'/'sun', *ŋu/n/d* 'chest body part'.

The grammatical dimension

Nyungar grammatical structure is simple when compared with northern members of the Pama-Nyungan family, in which there are highly complex verbal systems.

The verb does not carry tense, but has the choice of two aspects—'completed action' and 'incompleted action'. Tense is indicated by the use of a series of time words, phrases or dependent clauses, when required.

The noun and pronoun rarely take more than one suffix at a time. Transitive subject marker and direct object marker are used only to avoid ambiguity or to supply a subtle emphasis. For example:

yog-il *mam* *baminj*
woman-subject male hitting
— 'The woman is hitting a man.'
(Emphasis on Subject.)

mam *yog-inj* *baminj*
male woman-object hitting
— 'The man is hitting the woman.'
(Emphasis on Object.)

yog *gudjal* *geb* *ba/raninj*
woman two water fetching
— 'The two women are fetching water.'
(Subject apparent.)

Other inflexional suffixes include the 'locative' *-ag* (as in *bu/nag* 'on the tree/log'); 'instrument' *-ag/-al* (as in *bal bu/n godjag baminj*. 'He (was) hitting the tree with an axe.' [*godj* 'axe']). 'Reason' is indicated by *-aŋ* (as in *bal ga/raŋ njunaŋ*. 'He is angry because of you.' [*njun* 'you']).

The basic clause level constructions are the transitive and intransitive command and statement type clauses and the equational (including the stative) clause type. Expansions of these clauses include the addition of vocative, time, manner, instrument, reason (cause, purpose) and indirect object or benefactive which may be manifested as single words, relator axis phrases or as dependent clauses.

The lexico-semantic dimension

Words: Vocabulary range in old Nyungar could have been quite extensive. Although material culture was not highly developed, knowledge of nature—especially of edible and non-edible plants, animals and fish—was rich in detail. Hunting terminology was also extensive, as were the vocabularies in connection with religious culture, social organization and law.

Phrase words: Body parts feature largely in certain noun phrases which have become descriptive idioms. For example:

- gad wa/ra* (lit. 'head-bad') 'stupid'.
dwaŋ bu/d (lit. 'ear-less') 'unreasonable', 'ignorant'.
ma/da gidj (lit. 'leg-spear') 'bony-legged', 'skinny' (derogatory).
gobu/l wi/d (lit. 'stomach-empty') 'hungry'.

Clause words: Many metaphors, similes, idioms and other figures of speech have survived the clash with the alien language and some of them, as has been mentioned, have found their way into the English of the South-West. Among these are such expressions as:

- ba/daŋinj yoŋga muginj*—'hopping like a kangaroo' (used in various contexts).
ŋjidinj gwiya/r muginj—'cold as a frog' (also used in various contexts).
ge/d-gu/d gu/linj (lit. 'running swiftly')—'darting here and there', 'purposeless'.
geba ŋaninj (lit. 'water-drinking')—now used for 'liquor drinking'.

Discourse analysis of any exhaustive nature has been impossible because of the limited amount of text-material now available, but traditional narratives which have been collected show the Nyungar ability to use all the subtleties of story-telling. Dramatic presentation, mystery and humour are not lacking; nor are cleverness of characterization and development of plot.

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Aborigines of southwestern Australia: The past and the present

by Ronald M. Berndt

Pre-European population

For information on traditional Aboriginal life in the south-west of this State, we must rely on early records which are not detailed and are anthropologically unsatisfactory. The pre-European population could have approximated 6,000 persons—if we take the boundary as a

line drawn diagonally from Esperance to Mullewa. This boundary marks off the non-circumcising zone (see Map on Figure 2), that is, the southwestern corner of the State. If, however, we include adjacent tribes farther inland (within the circumcising area), the population could not have been much less than 7,500. Moore (1884: 115) reported that in 1840 there were about 3,000 Aborigines in the Swan River Colony alone. Radcliffe-Brown's (1930a) estimate of 12,500 Aborigines in the south-west at the time of first settlement is possibly too high (see Makin, 1970: Chapter 5).

The southwestern people felt the full force of the disastrous impact of European settlement. Against that, their traditional life could not survive—not as a living, coherent entity.

Traditional social organization

The 'true' south-west Aborigines, then, did not practise circumcision. However, a merging of social units occurred quite early during the contact period, when members of different tribal groups were obliged to live on mixed-tribal settlements. The map on Figure 2 shows the positioning of 13 'tribal' divisions (after Tindale, 1940) south-west of the circumcision boundary. In 1967, Douglas (1968) located 11 of these; 5, and perhaps 6, of them fall within the circumcisional area: see map on Figure 3. Tindale's list depends on old sources, Douglas's on the memory of elderly persons of Aboriginal descent. Douglas's interest is in language, and these 'tribal' names are really labels and/or dialectal divisions which *in toto* can be classified today as Njungar, or Nyungar, a word meaning 'man' or 'person'.

The internal organization of south-west tribal units was quite diverse. According to Radcliffe-Brown (1930b: 216-19, 220-21, on the basis of Moore, 1842; Salvado, 1851 and 1886; Bates, 1914 and 1923; among others), there were four patterns for this relatively small region (see map on Figure 4). Area 'C' had matrilineal moieties named *manitjmat* and *wardangmat* ('white cockatoo' and 'crow'), with at least four exogamous matrilineal divisions (or clans) grouped under each moiety. Their names had 'totemic' associations. Moore (1842: 4) speaks of them as 'family names': four principal ones, 'resolved again into many local or subdenominations', several grouped under 'one leg', others under another 'leg' and so on. However, this requires further discussion. Ritual affiliation was through the father. The pattern as described by Bates (1923) suggests local patrilineal descent group centring on totemic sites, with mythic connections and correlated with specific stretches of country. Thus, a person belonged to the moiety and totemic clan of his (or her) mother, but also to the local group of his (or her) father. Within the father's land division, a person's conception (or birth) totem, a particular natural species, was mythically defined *vis-à-vis* a centre which was, in turn, the focus of ritual. Area 'B' had a similar social organization, except that the named moieties were patri-

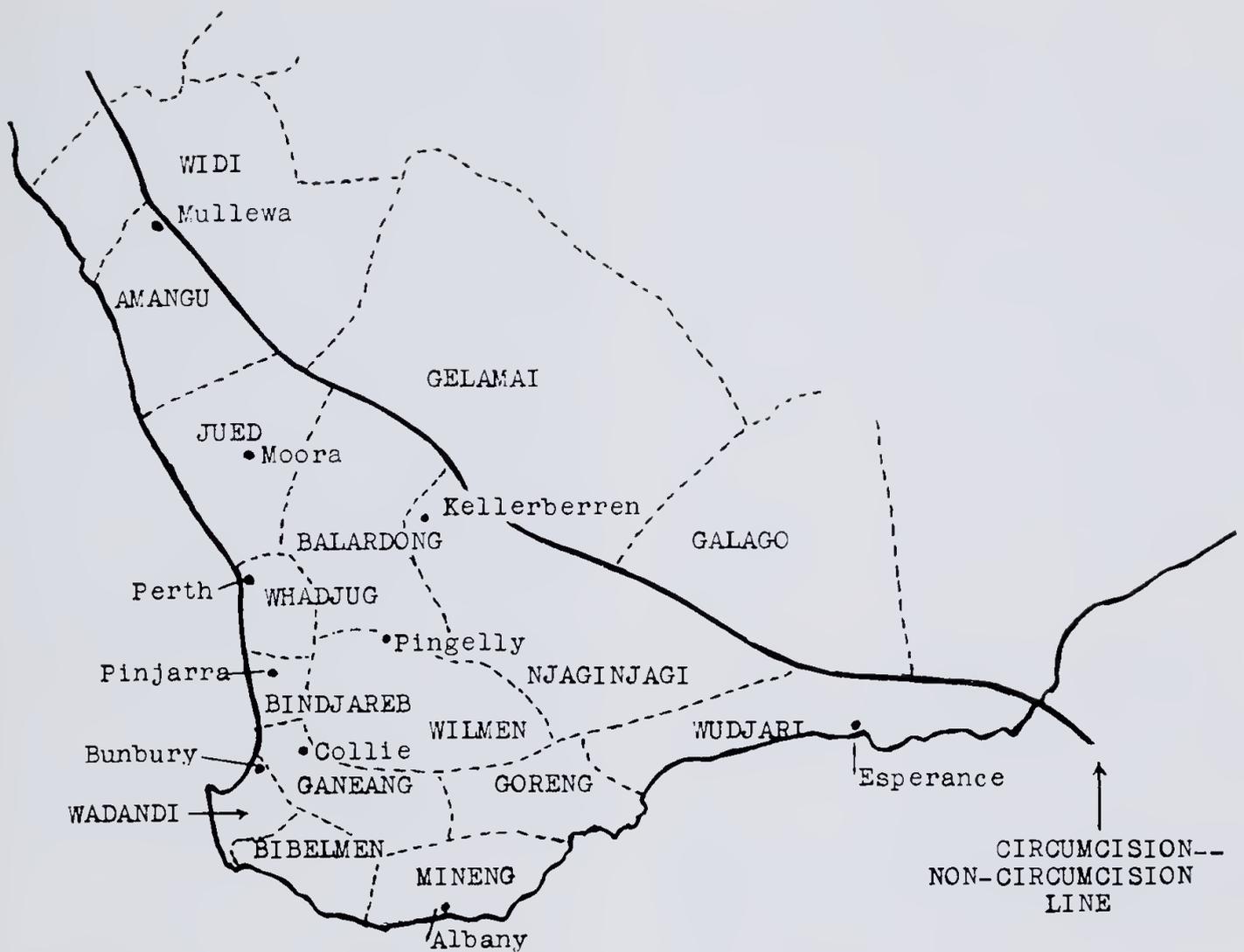


Figure 2.—“Tribal” map of the south west, after Tindale, 1940; tribal names slightly altered.

lineal. Area ‘D’ had two alternating ‘endogamous moieties’ named *birangumat* and *djuamat* (‘kingfisher’ and ‘bee-eater’). These, however, seem to be alternating generation levels similar to the traditional Western Desert type (see R. and C. Berndt, 1964/68: 56-8). The main focus was on patrilineal local descent units. Area ‘A’ seems close to Area ‘D’, with the addition of named totemic groups (probably patri-local descent units).

Generally, the south-west Aborigines were deeply attached to their country through myth-ritual ties. As in other parts of Aboriginal Australia, the local descent group was concerned with religious matters, while the socio-economic unit (a mixed-membership group) moved over limited stretches of territory, hunting and food-collecting. Communication was kept open between members of different territories or districts (subtribal or otherwise). These took structural shape in the *mandjar* or ‘fair’, when Aborigines met to barter a wide range of goods. People living in the Perth area exchanged commodities with those from the Murray River on the south, and also with others from the north.

Cultural background

Environmental and climatic conditions in the south-west made it necessary for Aborigines to protect themselves against cold winters. They constructed bark-covered huts which Hammond (1933: 25) described as watertight. Also, they made *buka* (cloaks), such as were used in southeastern Australia: three or more kangaroo skins, specially treated, were sewn together with sinew or rush and worn with the fur side inward. Distinctive to this area were the kangaroo skin bags used by women: the *goto*, used generally, and the *gundir*, for carrying a small child. And the *kadjo* ‘hammer’ was a unique implement, broad and blunt at one end and sharp-edged at the other: it was affixed to a short thick stick by means of prepared *tudibi*, *Xanthorrhoea* gum.

Initiation was fairly simple, and the major operation involved piercing the nasal septum. The novice was red-ochred during the rites and was given a hairstring, cloak and weapons (Bates, 1923: 236-7). Hammond (1933: 63) mentions that, although there was no circumcision rite in this area, the name of a place near Albany meant ‘circumcision site’. He reports the

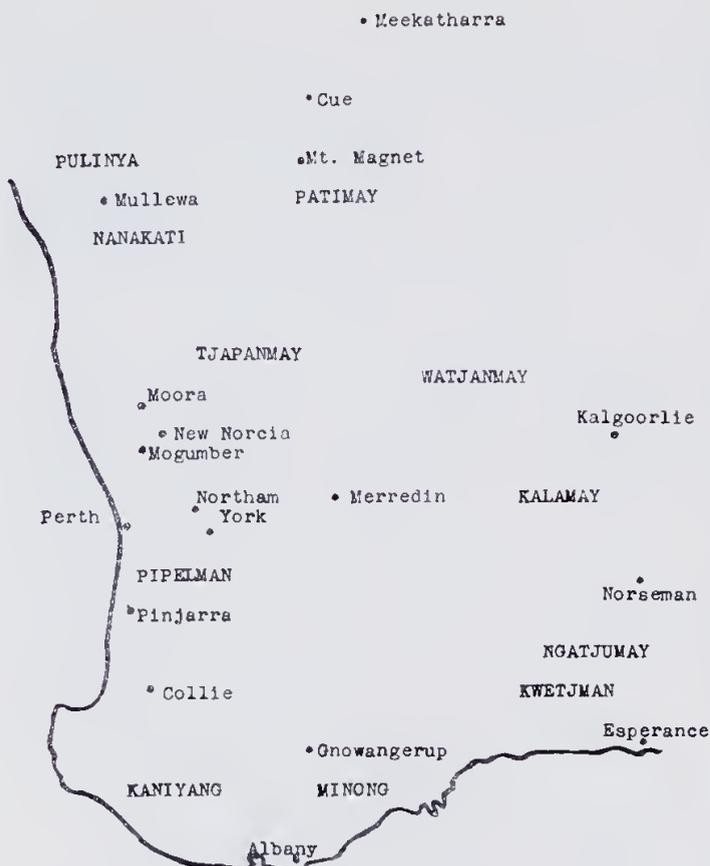


Figure 3.—“Tribal” map of the southwest, after Douglas, 1968.

belief that this operation would have spoilt the natural erection of the penis—but a modified form of the rite, discontinued in the early 1870's, was the removal of the tip of the foreskin.

Salvado (1850) noted that the Aborigines ‘hide carefully from strangers their customs and, in particular, their beliefs’. From the evidence, it would appear that increase rites were held by local groups, and that a reasonably large body of mythology existed, some of which was expressed ritually. Salvado mentioned Motogen (which he translates as god), as a creative being. He also referred to myths about the Sun and Moon, the Morning Star and the great Rainbow Snake. Moore (1842: 103) wrote of ‘a large

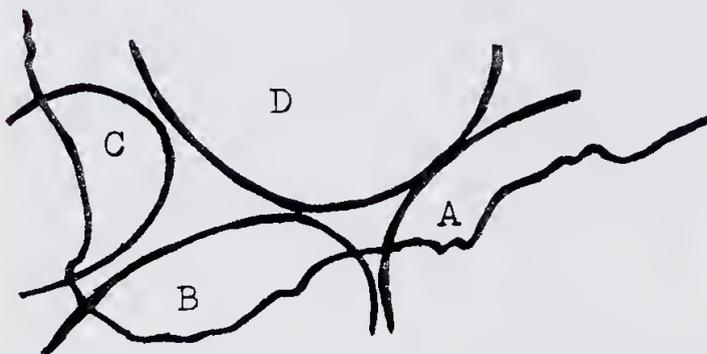


Figure 4.—Social organizational categories, after Radcliffe-Brown, 1930 (map facing p. 42). A.—without moieties and sections, but named patri-totemic units. B.—patrilineal moieties. C.—matrilineal moieties and totemic clans, with patri-local descent units. D.—named pairs of sections or alternating generation levels.

winged serpent’ called Waugal, living in ‘deep dark waters’, who was especially inimical to females but was feared generally as being instrumental in bringing sickness. A similar mythic snake emerged at Mt. Eliza and, crawling its way to the sea, created the Swan River. Mt. Eliza and the high ground where the State Parliament House now stands were called Ga-ra-katta, the site sacred to this snake (see Moore, 1884, and Makin, 1970).

The moon (*miga*) was a man, the sun (*nganga*) a female. A cave at York had a circular figure cut into the rock face, with hand stencils: this was said to have been ‘visited’ by Moon (Moore, 1842: 35). Many stars, too, were mythic beings (or mythic beings had ‘turned into’ stars). Bulgut, a wife of Tdadam or Dedam, was one. Dedam had a sister (of the same name) whom he speared when she allowed his two children to stray: they were represented by stars, and so was the spear. And the star Djingun was a wife of Wurdytch or Wurdoitch. Julagoling, the planet Venus, was an attractive young woman who carried out sorcery. Hammond (1933: 64-5) gives a story of a large tree located east of Northam which was used by mythic eagles who stole human babies to feed their young: the tree was eventually burnt down in revenge.

There was also quite a wide range of dances. However, their significance has not been noted by early recorders. The *dtowalguorryn*, for example, was common among people living in the eastern sector of this area; the *yallor* came from the north; the *kanggarak* from the south; the *yuyltunmitch* (direction unspecified); and the *yenma* from the north and north-east. The *yenma* is undoubtedly the well-known Western Desert *inma*, a general term for an ordinary ceremony. The *yallor* was performed mainly by men, only occasionally by women. They dramatized hunting scenes and the actions of various animals, birds and reptiles, along with the feats of sorcerers. Men were elaborately decorated, wearing ornamental sticks in their hair. It is not clear whether these were cult totemic, but the dancers were ‘surrounded by groups of admiring spectators’. Salvado speaks of songs being ‘handed down with a kind of traditional veneration’. Hammond (1933: 49-53; 63-5) refers to inter-tribal ceremonies during which betrothals were arranged. He gives a diagram showing how participants and onlookers were spatially arranged within a large circle; and he illustrates a serrated-edged bullroarer.

It would appear that women had more to say in tribal matters than has generally been emphasized. The custom of *mony*, conferring the status of *moyran* (or ‘grandmother’) on a woman, gave her authority to arbitrate in quarrels and during armed disputes.

Consistent with the interests of early observers *vis-à-vis* ‘savage peoples’, the material on magic and on death is more extensive. A sorcerer, for instance, was said to be possessed of *boylya* (power) which enabled him to fly through the sky, consume his victim’s flesh, and use quartz crystal (magic stone of the shark). He was able

to raise or calm the wind, and cause rain to fall (Moore, 1842: 18-19). Salvado says that sorcery was under the guardian spirit called Cienga. The sorcerer was also a native doctor and was able to cure his patients (*walbyn*, to cure by enchantment).

Beliefs surrounding death were focused on releasing the deceased's spirit or soul (*kadjin*) from its physical vehicle, the body. There were various forms of earth burial: *gotyt* among the 'mountain tribes', *dyuar* for the 'lowland tribes'. Usually, the corpse was buried in its cloak. A native doctor was present and listened for the sound of the spirit's flight from the body. At that time, it informed him of the name of the person responsible for its death. A small hut of reeds or boughs was constructed over the grave, and a fire lit at its entrance to make the place more comfortable and home-like for the spirit. There it was believed to remain until its death was avenged (see also Nicolay, 1886: 8-10). Bates (1923: 238-40; 1927?) speaks of the *kanya* (soul of the newly dead) going first to the tabu-ed *moojarr* or *moodurt* tree (*Nuytsia floribunda* or 'Christmas' tree), where it rested on its way to Kurannup, the home of the Bipelmen dead located beyond the western sea: here, their old skins were discarded and they appeared 'white'. The ancestors were spoken of as *netingar*, and lived on the island of souls. The first European settlers, because of their light skin pigmentation, were believed to have come from that place: they were called *djanga*, 'the dead'.

Dispersal and the Njungar

The coming of 'the dead' meant death to local Aborigines. The sorry story of Aboriginal-European contact in Western Australia, especially in the south-west, between 1829-1897, has been documented by Sir Paul Hasluck (1942). Hammond (1933: 67-72), too, spells out the disaster which befell them. At first, the settlers were afraid of the Aborigines. They drove them away, destroyed their camps, burnt their huts, made it difficult for them to obtain indigenous food, and employed them as menial workers. Aborigines were threatened, shot at, and in many cases killed. Their traditional territories were no longer their own. The 'battle of Pinjarra' in 1834 was simply one of the more notorious examples which have become part of this State's history (see Neville, 1936: 10-46). Through the early years of settlement, relations between Aborigines and Europeans steadily deteriorated. Shootings, assaults and theft continued. A deputation of Aboriginal leaders waited on the Lieutenant Governor of the time (Captain Irwin) in an attempt to resolve the situation—but without success. The establishment of Rottneest Island prison in 1839, the removal of children from their parents, and the increasing 'mixed-blood' population, all contributed to the destruction of traditional culture. In the 1850's, 'Ticket-of-leave men and parties of convicts in the bush mixed with the natives, supplied them with drink, and there were often hideous orgies.

The dispossessed blacks had become paupers and mendicants and deterioration, already begun, proceeded apace' (Neville, 1926: 40).

The measles epidemic of the early 1880's was another 'killer', and 50 years after settlement (as Hammond puts it, 1933: 70) 'the South-West was left with scarcely a true-blooded aboriginal in it'. Traditional life had by then disappeared. By that time, too, in the early 1890's, Aborigines from other areas were drifting increasingly into the settled areas and inter-mixing with the remaining local inhabitants. An official Western Australian handbook (Hart, 1893: 162-71) claimed that, 'Native labour being cheap, the sheep farmer who might otherwise be unable to work his station is able to do so with profit'; but, as for Aborigines in the settled districts, 'their numbers diminish every year'. Neville (1926: 46) underlines this point: '... here in the South-West . . . between 1829 and 1901 . . . a people estimated to number 13,000 were reduced to 1,419, of whom 45 percent were half-caste'.

The result was to leave the entire south-west with primarily a part-Aboriginal population—few of them directly descended from the original local people, most of considerably mixed Aboriginal affinity, and all possessing little or nothing of their traditional heritage. Hasluck (1939) and Neville (1948: 3-13; 1951: 274-90; 1947), among others, have provided us with surveys of local conditions. In 1948, Neville wrote (1948: 5): 'Years ago I witnessed the passing of the last of the Bibbulmen [a tribal name which he used for the whole of the south-west]. The few full-bloods now in the south-west have come from outside this district'.

It left, too, the majority of these people of Aboriginal descent living on settlement reserves, or occupying squalid camps on fringes of country towns—under the 'supervision' of the then Western Australian Department of Native Welfare. They worked spasmodically for Europeans and were, for all general purposes, culturally but *not* socially European-Australians. Because a tribal background was now irrelevant as far as its content and any of its details were concerned, they saw themselves as being Njungar—different from the non-Aborigines around them.

The story of discrimination and prejudice in relation to these people cannot be discussed here. However, over the last few years conditions have, at long last, been changing radically: more opportunities are now open to them. In 1967, Douglas estimated the part-Aboriginal population as 8,000 in the larger south-west region, not bounded by the non-circumcision line. In 1971, the Central Division (i.e., Perth, Moora and Kellerberrin) had a total population of 5,128. Of these, 58 were 'full-bloods' (from non-south-west areas), and 2,694 were children under 16 years (31 being 'full-blood'). The Southern Division (i.e., Narrogin, Bunbury, Gnowangerup, Albany) had a total population of 2,855. Of these, 60 were 'full-bloods' (from non-south-west areas), and 1,692 were children under 16 years (31 being 'full-blood'). The best recent

studies of these people are by Makin (1970) and McKeich (1971). For general discussions, see Rowley (1970) and Biskup (1972).

Not all the south-west people of Aboriginal descent would regard themselves as Njungar. But, Njungar or not, they are *New Aborigines*—people who seek a social identity of their own in contrast to other Australians. And part of what they seek relates to obtaining some knowledge of their traditional past. For the south-west, unfortunately, only a very little of that knowledge survives.

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6.—European man in southwestern Australia

by G. C. Bolton¹ and D. Hutchison²

Abstract

European man's impact on the south-west of Western Australia may be treated in three periods:

(1) 1829-1850, the period of initial impact. This was characterized by the carrying over of British and European preconceptions in the appraisal of an unfamiliar terrain. Want of labour, capital, and colonial experience led to the simplest forms of adaptation of building and agrarian techniques in the new environment.

(2) 1850-1890, a period of greater prosperity and population growth. The task was envisaged as "subduing" nature and imposing where possible British models of building, landscaping, and agricultural adaptation. Lack of means still led to what could later be considered conservative and exploitative forms of land use.

(3) 1890-1973, initiated by a period of mineral discovery stimulating economic takeoff. This period is marked by increasing urbanization and metropolitan influence on the hinterland, and recently by the uneven growth of a greater official and public recognition of the need for policies of conservation and regeneration.

Introduction

Historians, economists, creative writers, biologists, naturalists, and agricultural scientists have each contributed to our understanding of the impact of western man on the environment of Western Australia. Unfortunately each discipline has tended to work on its own, sometimes apparently ignorant of advances made in other fields, almost always without the full advantages of an interdisciplinary approach. Of the three standard histories of Western Australia, Kimberley (1897), Battye (1924), and Crowley (1960), Battye shows the least, and Crowley the most appreciation of the environmental and economic factors influencing the spread and character of settlement. All wrote before the rise of the current concern with ecology, and none shows the subtle environmental awareness of a recent work such as W. K. Hancock, *The Monaro* (1972). Consequently an essay in synthesis can attempt little more than to record the various contributions made by contemporary observers and later scholars, and to suggest an immediate and obvious need for future research.

The era of European contact may be divided into a period of pioneering, 1829-50, when the first appreciations and assessments of the terrain took place; a period of consolidation, 1850-90, following the stimulus of convict transportation and the spread and diversification of rural activity; and the modern period, since 1890, when growth reflected the multiplier effect of the gold-rushes.

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1829-50: Pioneering

There are as yet no authoritative surveys of the historical demography of Western Australia, although a major project is shortly to be initiated by Professor R. T. Appleyard, under whose supervision current work is in progress at the Department of Economic History at the University of Western Australia. Statham is engaged on a study of the first twenty years of settlement, as a result of which it may be possible to test Kimberley's assertion (*op. cit.*, p. 39) that 'Substantially, Western Australia had for its pioneers more highly educated men of good society than perhaps any other British dependency'. "Musters" or census returns were compiled regularly, from which it would appear that although over 4,000 settlers were attracted to the Swan River Colony by the too-optimistic estimates of Captain Stirling and others, only 1,132 remained in 1830 and 2,311 in 1840. Numbers improved to 5,886 in 1850, in which year convict transportation, rejected by other Australian colonies, was introduced as a stimulus to Western Australia's economy (Gertzel, 1949). Until then, it may be doubted if the white inhabitants of the south-west significantly outnumbered the Aborigines.

The spread of settlement was spasmodic and uneven. The first comers in 1829 sought land which was accessible to sea or river transport and which, so far as possible, met English criteria for desirable farming country. Along the Swan River above Guildford a number of estates still flourishing as vineyards were established before 1840. Much of the coastal sandplain was either alienated to absentees or unsuitable because of what was discovered much later to be deficiency in trace elements. The colony was too isolated and under-populated to generate economic growth (Staples, 1961). The pressure for land led to the early exploration and settlement of the Avon Valley during the 1830s and the Victoria Plains during the 1840s (Deacon, 1947; Erickson, 1971). Itinerant shepherds shifted their flocks frequently, following feed and surface water. Meanwhile Albany on King George's Sound, since December 1826 the site of a convict garrison, became after 1831 another nucleus for free settlement. The Bunbury and Vasse districts, sparsely settled from 1830, received some stimulus from the ill-fated 'Wakefieldian' settlement at Australind in 1840-42 (Shann, 1926; Staples, 1948). Geraldton, founded in 1848, became the base for the occupation of the Champion Bay district (Kelly, 1958). These four centres of settlement—Geraldton, Fremantle/Perth, Bunbury, and Albany—were linked by a coastal shipping service

whose shipwrecks were frequent. Land transport was inhibited by the tracts of dense timber and scrub, or of sandy soil, which separated each nucleus of settlement.

Shortages of capital, labour, and time made for a modest architecture. An authoritative survey is in progress for the early colonial period by Dr John White, Department of Architecture, University of Western Australia. Cameron (1968) following Irwin (1835) notes that a number of the 1829 settlers brought out prefabricated timber houses, which warped in the heat and excessively wet season of 1830. Most early houses were of wattle-and-daub—basketwork plastered with clay—or “ramjam”, a mixture of sand and clay rammed into consistency and bolted at intervals. More substantial buildings were later constructed of locally-made brick or (in the Fremantle area) of limestone. Jarrah and sheoak shingles gradually replaced thatch as a roofing material (Bunbury, 1930). Verandahs were not common inland, but were a feature of Perth and Fremantle houses (Ogle, 1839). Most public buildings retained a modified Georgian idiom until the 1850s, sometimes with unfortunate effects, as with the heavy Grecian portico of the first Anglican Church, more often with a simple elegance, such as the Old Court House of 1836, or the Chapel of the Children of Mary of 1846 (Oldham, 1961). The cities of Perth and Australind were both laid out on the formal, rectangular pattern preferred by early 19th century town planners (cf. Adelaide, Melbourne). Bold (1939) regretted that opportunity was not taken to lay out the city around the contours of the many swamps and lakes then existing north of the Swan, but Roe, the first Surveyor-General, seems to have considered that the uneven and dissected terrain presented sufficient difficulties without embarking on town-planning experiments (J. B. Roe, 1927).

This raises the question of how the first settlers perceived their environment. Their first expectations were shaped by European experience. Cameron (1970) points out that as a naval man Stirling judged the potential of the Swan River in terms of trade, strategy, and anchorage:

He found difficulty in translating what he had seen into meaningful terms, and had resorted to comparisons of the Swan River with Virginia and the Plains of Lombardy. Both these comparisons no doubt raised entirely different ideas in the minds of his readers than he intended. Their frame of reference was somewhat different from his.

As the hinterland was penetrated some settlers viewed the new environment with nostalgia for the past, others with an appreciation of its differences. Following Dale's expedition of 1830 to the Avon Valley, Clarkson and Hardey named the district “Yorkshire” from a fancied resemblance to their native county (Deacon, 1947). On the contrary James Henty, on a separate expedition about the same time, saw the Australian bush as *sui generis*:

The grandeur of the scene among the valleys surrounded by increasingly tall white gums and the solemn silence prevailing in the bush, totally unaccompanied by any signs of civilization, imparts ideas that it is impossible to reflect on without awe and reverence and

which those who have not experienced it can scarcely appreciate (Bassett, 1954).

This sort of reaction was none too common. Most observers, even after a dozen years of settlement, still used the English landscape as a standard of comparison, while some such as Wollaston (1948) needed time to realize that appreciation of the Western Australian bush required the newcomer to divest himself of preconceptions. He found the trees stunted and sombre, and most praised those Australian trees such as the peppermint which reminded him of European foliage. Some, however, such as Georgiana Molloy, were captivated by the Western Australian wildflowers:

It is to be regretted that the flowers of this country are so uncommon in England, as were they imitated in that beautiful work of art, artificial flowers, they would create a great rage. They are so well calculated from their size for that work, also the brilliancy of colour could well be imitated in the manufacture of porcelain and china . . . (A. Hasluck, 1955)

Because there was no assured water supply and little labour, even the most nostalgic settlers could not hope to recreate an English landscape in Western Australia. An article in the *Perth Gazette* (9 March 1833) listed fruit-trees and bushes introduced and already “flourishing”. Most were Mediterranean or tropical: grape vines, two varieties of fig, peach, almond, several varieties of apple, pear, strawberries, aloes, several varieties of plum, four varieties of olive, mulberry, pineapple, plantain, sugar-cane, flax-lily and Cape gooseberries. Alfred Stone, builder of the first cottage in St. George's Terrace, planted a geometric layout of olives and vines behind his house and a selection of “natives” in front, including *Nuytsia floribunda* and various “mahogany” trees (Oldham, 1961). The Benedictines at Subiaco also planted olives. It is known that Norfolk Island pines and Moreton Bay fig were planted in Perth at this period, and the cypress was probably introduced before 1860.

In a recent Flinders University honours thesis Moon has appraised the attitudes to the rural environment of South Australian colonists. It is probable that a similar detailed study of the attitudes of Western Australian colonists would lead to the same general conclusions.

. . . . (the grasses and the trees) . . . were mostly utilized in their natural state, little attempt being made to improve, or conserve their value as a resource . . . the trees were generally tried, found wanting, and consequently cleared away as much as possible.

The early nineteenth century Englishman, reacting against the immediate horrors of industrialization, created the myth of a rural Eden which was certainly far from the reality of the pre-industrialized rural life. The early colonists would have found the strange Australian environment difficult enough to appreciate even if their attitudes had not been partly shaped by such a myth. Their attitude, as Moon has shown for the South Australians, was too often one which later generations would see as exploitative. It is an attitude which still persists amongst many. In any case, with so much virgin bush around them, the early settlers would not have seen any need for reserves. The

first reserves were set up under the Land Regulations of 1872 and 1887, though they lacked legislative security (Australian Academy of Science, 1962).

There can be little doubt that the Aborigines also exploited the environment beforehand and Merrilees (1968) and Hallam (1971) have discussed the significant effect of the use of fire by them. Hancock (1972) also discusses similar studies of the effect of fire in south-eastern Australia. However, there seems to have been too little research on the comparative effects of naturally-occurring fires, Aboriginal fires and the fires of the European settlers. Hallam draws attention to the relative infrequency of fire due to lightning strike. However, the Western Australian flora displays many adaptations to fire and these adaptations may have required a longer time span than that now suggested for Aboriginal occupation. Further research may reveal that this time span was in fact sufficient for man-made fire to be effective. Some of these adaptations may have evolved in response to increasing aridity, and it may be impossible to separate the effect of fire and climate. Gardner (1957) argues for the primacy of fire as a factor and suggests greater frequency of "natural fires" caused by lightning strike, but on more subjective evidence.

Man's use of fire may have affected principally the distribution of species, both of plants and animals. It would be interesting to know in more detail the different results of the varying practices of the European and the Aborigine. It is possible that the European use of fire has been more destructive, because of the altered pattern and greater frequency of burning, settlement in fixed locations, and because of the more intense pressure of a greater population. Hatch (1959) and Wallace (1966) have discussed the effect of post-settlement fires in the jarrah forests, while Gardner (1957) examined the effect of fire on the whole flora. It is hoped that current research by forestry scientists will greatly improve our appreciation of the role of fire in environmental management. It may be too late, however, to study in detail the relative effects of Aboriginal and European practices.

Fire is only one of the factors that changed significantly when the Europeans arrived. It appears that the grazing habits of sheep, for example, very quickly altered the distribution of native grasses. There appear to be fewer local contemporary observations than Hancock could draw on for his Monaro study. Cattle and goats have, in their own ways, been destructive of the environment, particularly in a region where fresh-water sources are relatively thinly distributed. Introduced animals have to concentrate near these sources, whereas the native animals have adapted to be independent, or less dependent, on direct water supplies.

Popularly the introduction of the fox and the rabbit have been recognized as environmental tragedies. However, except for a colony of rabbits on Carnac Island (Moore, 1931) neither was introduced into Western Australia before the 20th century. Because of sentiment there has

been far less popular recognition of the great impact of the cat and the dog on marsupial fauna. The descendants of European dogs "gone bush" were also probably more often responsible than dingoes for attacks on sheep. At the same time native species of animals and birds were assumed, sometimes quite falsely, to be vermin, and this led to unwarranted destruction.

Introduced pathogens are part of the total impact on the environment, although in the earlier years of the colony the long ocean voyage may have been an effective quarantine against the introduction of plant and animal disease. It has nevertheless been speculated, for example that 'jarrah die-back disease' may have been introduced with plants brought by the colonists (Newhook and Podger, 1972). Scab was intermittent among sheep from its first introduction from Van Diemen's Land in 1831 to its gradual eradication around 1900 (Deacon, 1950; Cranfield, 1959). Another early setback to pastoral settlement was the presence of native poison plants, leguminous pea-flowered bushes which to an unaccustomed European eye might look like good grazing. Drummond in 1840-41 identified the York Road poison (*Gastrolobium calycinum*), and other gastrolobia were later brought under suspicion (Erickson, 1959).

Farming practices were at first of necessity poor. Bunbury in 1837 censured the Avon Valley settlers for slovenly farming, deploring especially the habit of broadcasting seed among the old stubble of last year's crop. From an early period agricultural associations were formed at Perth and York to encourage improvement, and Hutchison is at present undertaking a study of 19th century farming techniques which should lead to a more accurate, and possibly more favourable, assessment of the performance of Western Australian settlers by contemporary standards.

1850-90: Consolidation

The coming of convict transportation in 1850 gave the expected stimulus to Western Australia's growth. From 5,886 the Anglo-Australian population rose to 25,084 in 1870 (Gertzel, 1949). With the ending of transportation a period of recession and near-stagnation followed, but from 1882 the growth of population again accelerated, to reach 48,502 by the attainment of self-government in 1890. Increased contact with the outside world brought to the colony diseases from which it appears to have been previously immune. Research now nearing completion by E. J. P. Joske should throw light on the first decades of the colony's medical history (M.A. thesis, Department of History, University of Western Australia). An outbreak of measles in 1860-61 attacked Aborigines and young children with particular severity as did another in 1883. Infant mortality was high throughout this period; between 1860 and 1870 nearly 45 per cent of all deaths were of children under five (Knight, 1871). Diphtheria, first reported in 1865, was prevalent thereafter. Typhoid was reported several times between 1872 and 1900,

though it was not until 1889 that the common 'colonial fever' was identified by Dr Adam Jameson as a form of typhoid (*Inquirer*, 3 April 1889). Sanitation was primitive; it was not until 1888 that even the city of Perth could boast a system of nightsoil collection, and though improvements followed fairly rapidly in the city, conditions were less good in country and gold-fields districts.

European penetration inland was extensive but very sparse during the period between 1850 and 1890. The activities of sandalwood cutters from about 1845 resulted in the pioneering of a number of tracks which almost certainly followed Aboriginal routes, and would in turn be followed and developed during the great period of goldrush expansion in the 1890's. Improving wool prices and the availability of convict shepherds encouraged the eastward thrust of the pastoral frontier, and by the mid-1860's much of the present wheat-belt was held under grazing leasehold; but because of impermanent water and transport difficulties, very few improvements resulted. From the 1860s pastoral expansion was directed to the Gascoyne, north-west, and Kimberleys. One effect of this spread of settlement was the destruction of habitat and near-extinction of some local fauna. The noisy scrub-bird was believed extinct after 1889, but has recently been located at Two People Bay, east of Albany.

Rowley (1942) and Mouritz (1964) have discerned four major regions of closer settlement in the period between 1860 and 1890. The Irwin-Greenough district and the Avon Valley were the habitat of the "yeomanry", grain farmers on small acreages. The Swan coastal plain was mainly devoted to "kitchen gardens" and vineyards. In the fertile valleys of the south-west, such as the Preston, the Capel, and the Blackwood, the "bush grazing" of sheep and cattle was supplemented by occasional fruit-growing for local markets. Meanwhile from about 1850 a demand for local hardwoods, "Western Australian mahogany", led to the clearing of some stands of jarrah in the south-west (Stewart, 1948; Robertson, 1958).

At first sight, the effect of these developments on the Western Australian environment seems meagre. Only 132,000 acres were cleared by 1890, understandably in view of the density of the timber in much of the south-west. The typical homestead was sited in a clear patch of land surrounded by a huge area of bush. Fencing was slow to spread. Although some paddocks were enclosed in the Toodyay area as early as the 1850s, fences were not common in the Williams district until after the establishment of a road board in 1877; while in the impoverished Irwin-Greenough district even after fencing became compulsory by the Land Act of 1887 the usual expedient was wattle fencing which rotted quickly, as there was no money for any other (Erickson, unpublished; Chate, 1953; McAleer, 1956). In the Hay River district sheep were folded in hurdles: "Their stay in one fold position was largely determined by the deposit of manure within and the condition

of grazing without' (Sten, 1943). In the Harvey district problems of soil and water led to a cycle of grazing between coastal homesteads and out-stations towards the Darling scarp (Staples, 1947). There is indirect but suggestive evidence that grazing practices during the 19th century led to environmental deterioration. Deacon (1950) noted the belief of farmers in the Manjimup district that frequent fires had promoted the growth of scrub and undergrowth. Giles (1950) noted the presence of severe soil erosion and evidence of over-cropping in the long-settled districts of the Avon Valley. Sten cites a Hay River property occupied by one pioneering family for 72 years after 1855, during which time no more than 160 acres were cleared. By 1927 the native grasses were largely eaten out; attempts to introduce prairie grass, timothy, white clover, and other exotics had largely failed; the land was neither rested, ploughed, nor fertilized. Of the owner for much of this period Sten wrote: 'He makes no claim to have improved his property outside the homestead and the dividing fences; he even possibly feels a little contemptuous of those who have expended so much capital and have perhaps less ready cash than himself. His aim was to acquire land free of debt . . .'. It is probable that such an attitude towards investment was common. Reliance was placed on hard work and the recuperative properties of the land. Economic necessity fostered this attitude. One pioneer family in the Kojonup district began farming in 1851 with five sons, two daughters, '17 6 in cash after our journey, two mares, one cart and three dogs on which we depended to catch kangaroos for our own use and the skins to provide us with what else we required. We also had two spades, three grub hoes and two sickles' (Bignell, 1971).

Such small beginnings offered little protection against adversity. In the Harvey district the absence of good communications obliged farmers to resort mostly to subsistence agriculture. There was little margin of resilience against natural hazards. Thus in the Irwin-Greenough district a promising settlement of small farmers on tillage blocks was severely checked by outbreaks of rust in wheat from 1865. Contemporary observers (e.g. Trollope, 1873; the Venn Commission, 1887-90) criticized the backwardness of these farmers, but in fact most were in debt to the Geraldton merchants and storekeepers who would make no advances for improvements. Fallowing was not practised because of wind erosion. Technology improved slowly. Reapers and binders were not commonly in use until the 1890s, and in many parts of the colony flails and scythes were still in use (McAleer, 1956; Kelly, 1958; Cranfield, 1959). Although from the 1870s guano deposits off the Western Australian coast were systematically exploited, local farmers did not consider it highly as a fertilizer, and made little attempt to seek out alternatives. Water conservation was not extensively practised, so that in the York district in the dry season of 1877, farmers had to cart water up to fifteen miles, though the severity of that drought and of others during the late 19th century has

been subsequently exaggerated. Some landholders such as Bishop Salvado practised extensive well-sinking (Dom William, 1961), at times exploiting earlier Aboriginal watering-places. In assessing the "conservative" performance of Western Australian farmers, it should be remembered that farmers in England were also very slow to adopt new machinery, even though they had readier access to manufacturers. Many colonists had not built up enough cash capital, and the scale of operation of many farms may not have been large enough to warrant mechanization. This question requires closer research.

The modest circumstances of most farmers limited the possibilities of vernacular architecture. Many settlers began with a bark hut, graduating later to either a white-washed abode house, "with mud walls a foot thick", or to a pit-sawn timber cottage. Roofing materials were either rush thatch or jarrah shingles. Verandahs became relatively common (Hillman and Norrish, 1938). A significant change came in 1879 with the introduction of galvanized iron. Its use for housing and roofing followed almost immediately in the Perth-Fremantle area. Little opportunity existed for planned landscaping, though mention must be made of the enlightened policies of Maitland Brown, resident magistrate of Geraldton in the early 1870s, who confronted by the encroachment of sandhills on the town area, employed the out-of-work Greenough farmers in a systematic and extensive plantation of native trees all round the outskirts of Geraldton (Farrelly and Maley, 1927). Meanwhile public buildings were erected on a more opulent scale, especially during the period of convict transportation. In Fremantle the use of limestone and an occasional hint of Cape Dutch influence gave individual character to such buildings as the Asylum (now the Fremantle Museum). In Perth the favoured medium was a brick provincial Gothic, often reflecting a strong Tudor or 'Flemish' influence, as with the Perth Town Hall, Wesley Church, and the Cloisters (Oldham, 1961). Private housing also reflected the growing opulence of some citizens, not only among the town residences of notables along Adelaide Terrace and Mount Street, but even in one or two country houses, such as Faversham House at York, where an attempt was made to reproduce the idiom of the English villa.

The diffusion of English culture and the stimulation of the Western Australian economy both depended on improved communications. Convict road-building gave Perth an adequate link with the Avon Valley and Albany, but railways were essential. The first public line from Geraldton to the base-metal centre of Northampton, was not opened until 1879. During the 1880s Fremantle and Perth were linked to the Avon Valley towns. Private entrepreneurs working on the land-grant principle were able to plan more boldly, building a line to Albany by 1889 and projecting another to Geraldton (Bolton, 1958; Manford, Ph.D. thesis, submitted 1973). The coming of the railway would provide primary producers with access to markets and

facilitate the introduction of wire fencing, galvanized iron, fertilizer, and other products which would transform the face of the Western Australian landscape.

1890-1973: Modern period

Western Australia was transformed by a series of gold discoveries beginning in a small way in 1885 and culminating in the Coolgardie-Kalgoorlie-Boulder finds of 1892-93. Demographically the "ancient colonists" were swamped by newcomers, mainly from Victoria and South Australia. These men and their families accounted for most of the increase from 48,500 in 1890 to 180,000 in 1900. Because of the consequent natural increase, reinforced by British migration, the population went on rising to 331,000 in 1920 and 432,000 in 1930. Depression and war then checked the rate of increase, but in 1946 the figure stood at half a million, and by 1973 exceeded a million—a more rapid growth than that of the rest of post-war Australia, though stimulated by the same ambitious programme of European migration.

During the whole of this 20th century increase it was remarkable that the area under white settlement in Western Australia did not expand significantly, and in some areas contracted somewhat. Gold pushed the eastward frontier of settlement forward during the 1890s to a line east of Sandstone, Kurnalpi, and Esperance, but except for the Kalgoorlie-Boulder regional metropolis and a few outposts such as Norseman, Menzies, Leonora and Laverton, the continuity of settlement depended on other industries: wool (sparsely), agriculture (to the 10-inch isohyet) and, more recently, base metals such as iron ore and nickel. It was nevertheless the gold-rush of the 1890s which prompted a bold policy of public works. The Coolgardie pipeline completed in 1903 brought an assured water supply to the Eastern Goldfields and the intervening farming districts. The railways linking the newly settled districts to Perth provided access to markets and to imports from outside Western Australia. The completion of Fremantle Harbour in 1897 encouraged regular shipping services, and the advent of a federated Commonwealth in 1901 ensured that Perth, open to outside competition, would produce few of the manufactures required for its own hinterland. Thus the pattern was established under which Western Australia's role was seen mainly as that of an exporter of primary produce, industrially backward and technologically dependent on outside skills.

Between 1900 and 1930 the three major rural areas were (1) the timber and dairying districts of the lower south-west (2) the mixed farming districts of the Avon Valley and the upper Great Southern and (3) the wheat-belt. It was the wheat-belt that dominated the planning of the Western Australian economy. The introduction of "dry" wheat facilitated the occupation of the 200 miles east of the Avon Valley. The "wheat-belt" extended from within five miles of the Murchison south-east to Southern Cross, then south to Hyden and Gnowangerup, for much of

its length paralleling the 10-inch isohyet and the rabbit-proof fences erected in the early years of the century to stem the invasion from the Eastern States. Light railways and the ready availability of public finance stimulated agricultural settlement, even though the lack of surface water and of dams exacerbated the drought seasons of 1911 and 1914. Between 1900 and 1930 the area cleared of timber increased from 3.440,000 to 11.8 million acres, and the area under crop from 201,000 to 4.8 million acres. In 1930-31 the wheat harvest reached 53 million bushels, a figure unsurpassed for thirty years. Despite the establishment of a Department of Agriculture in 1898, this growth was largely without scientific foundations. Most settlers identified soil types by the characteristic vegetation, e.g. morrell gum soil, heavy gimlet soil, York and jam soil (Schapper, 1955). Soil erosion was discerned as a problem in the Geraldton coastal districts as early as 1901. The planting of rye grass was recommended as a palliative, but no mention was made of altered farming methods as a means of preventing erosion (*Jour. Dept. of Agric.* 1901). Scientific soil analysis was first attempted by Teakle in 1929 in an attempt to solve the problem of poor crop yields in the Salmon Gums area, but his findings of excess salinity were at first disputed by "practical" farmers and politicians. It was only with the collapse of wheat prices in the depression of the early 1930s, followed by the extensive abandonment of marginal farms, that value came to be placed on the research of agricultural scientists. The same applied to the dairying industry of the lower south-west where the group settlement scheme of the 1920s was based on the fallacious assumption that country supporting tall timber must be capable of pasturing dairy cattle tended by recently-arrived British migrants. Here too the failure rate was high (Hunt, 1958).

The 1930s saw the first break-throughs in the scientific appreciation of Western Australia's agricultural potential. Underwood (1935; 1972) showed that the 'Denmark wasting disease' in cattle, and other symptoms of wastage and infertility in livestock pastured in the coastal districts, were due to a deficiency in trace elements such as cobalt. Copper deficiency was found to cause neonatal ataxia in lambs (Bennetts, 1937). Teakle (1938) published the first comprehensive soil survey of agricultural regions in Western Australia, and Gardner (1942) definitely identified the three main vegetative forms of the wheat-belt: sand-heath, savannah woodland (York and jam gum country), and eastern sclerophyllous woodland (mallee and salmon-gum country). Meanwhile in an early study of farming practices Roberts (1942) showed that attempts at mechanization—specifically through the use of tractors—often failed because operation was neither efficient nor economically planned. This lay some stress on the quality of farm management, a factor to which greater attention would be devoted after the Second World War.

The years from 1930 to 1945 laid great burdens on the farmers. Apart from the depression, followed by the shortages of labour and materials in the Second World War, there were natural hazards: plagues of emus in 1927-29 and 1932, grasshoppers for several years in the mid-1930s, dry seasons in 1936, 1938, and especially 1940. Though unwelcome, the spread of foxes was thought to check the incursions of rabbits. Quarantine measures mostly prevented the introduction of exotic stock diseases, such as the tick fever common in the Kimberleys, but in 1923-24 there was a short-lived outbreak of rinderpest near Fremantle. However 'toxic paralysis', a form of botulism in sheep first reported in 1927, was responsible for the deaths of 10,000 sheep in the summer of 1932-3. The introduction of subterranean clover was hailed in the 1920s as an important contribution to pasture improvements. However it came under suspicion during the late 1930s and early 1940s as responsible for a serious fall in lambing percentages. This was later shown to be due to the oestrogenic action of the plant (Bennetts, Underwood, and Shier, 1946; Bull, 1972). All these problems were identified and countered by agricultural scientists, but they were not always made use of by the farmers, who with their bitter experiences of debt were naturally wary about investment in improvements, or even about departure from established practice.

Among those farmers who survived, these pressures led to changing policies. Wheat gave way partially or wholly to sheep in some districts. Farms were enlarged and amalgamated. With returning prosperity after 1945 these larger units were better able to make effective use of tractors, combine harvesters, and other forms of mechanization. In the drier wheatgrowing districts (e.g. Burracoppin) the average size of farms doubled between 1940 and 1960 to from 1,500 to 3,000 acres. Productivity was established to be lower on smaller holdings. The rotation of crops was modified so that cropping for wheat tended to occur less frequently on any one piece of land. Despite improved farming practices wheat yields failed to increase significantly, and while controlled experiments failed to produce irrefutable proof of declining soil fertility, the circumstantial evidence was increasingly strong. Soil erosion was identified in long-settled districts such as the Avon Valley. Nevertheless in this and in other regions of higher rainfall a concerted policy of pasture improvement was followed to intensify sheep grazing under the stimulus of buoyant wool prices in the late 1940s and early 1950s (Schapper, 1955; Mouritz, 1964).

One response to improving conditions was the renewed expansion of rural settlement. During the 1950s and 1960s the previously unexploited "light lands" to the east and south of the old wheat belt were brought under cultivation. Official policy aimed at the yearly alienation of a million new acres for agriculture—usually at the expense of the pastoralists—and stimulated clearing by the incentive of tax concessions. The area under wheat reached a maximum of

7.3 million acres in 1968-69, and the harvest of that year attained a record of 112.4 million bushels. A rural recession in 1969-70 provoked some doubts about the continuing wisdom of these trends. 'The time is fast approaching when the only virgin bush left in Western Australia will be that which has been deliberately reserved for conservation' (Ride, 1968). Hogstrom (1968) estimated that in 1965 there remained 11.5 million acres of land in Western Australia suitable for allocation to agriculture—an area sufficient only to meet the estimated demand from families already settled in Western Australia. Despite this growth, many rural towns were stagnant or decaying after 1945. As motor transport replaced the old pattern of railways largely fed by horse-drawn traffic, the need passed for towns as service centres at intervals of every 15 or 20 miles. Instead, growth tended to concentrate in a few ports or railway junctions, such as Geraldton, Bunbury, Albany, Northam, Narrogin and Merredin. There was a slight corrective to this trend because of modern mining developments in the south-west. The extensive working of bauxite in the Darling Range after 1959 led to the choice of Pinjarra as the site for an alumina refinery, and the working of mineral sands in the south-west during the same period fed the secondary industry of Bunbury. Both these developments, however, gave concern to conservationists because of their influence on the environment, and neither had any major effect on the prevailing trend of population. Following a common Australian experience, the bulk of Western Australians concentrated in the towns, and especially in the Perth-Fremantle metropolitan area.

In the city of Perth the sprawl of suburban growth had been facilitated since the 1890s by the easy availability of timber weatherboards and machine-made bricks for house construction. Like Sydney, but unlike Brisbane and Hobart, brick was more highly esteemed as a building material in Perth. Iron roofing was common in workingclass suburbs, but its tendency to rust led the better off to prefer tiles, at first imported from Marseilles, after the First World War manufactured locally. Streets were planned almost entirely as straight lines or rectangles, although in the eastern suburbs the lines often ran diagonally on a north-west south-east axis following the boundaries of the original Swan River land grants devised to afford as many settlers as possible a river frontage. Curved crescents were introduced between 1911 and 1914 as an innovation in the laying out of Dalkeith and the Mount Lawley Number 3 Estate, but were not widely imitated outside the "prestige areas" (Hope, 1968). The "silvertails" congregated in Peppermint Grove, West Perth, and subsequently Dalkeith Nedlands, suburbs commanding access to Melville Water, King's Park, and similar amenities, while the sandy eastern suburbs, further removed from the ocean and the sea breezes, and in general somewhat flatter than the region between Perth and Fremantle, became predominantly low-cost working-class

residential areas. The provision of suburban railways was totally neglected, except where existing main lines were used to provide a local service; however during the 1890s light lines were built from Midland to serve the orchards and the timber-leases of the Darling Range, and this was a great stimulus to picknicking. The beaches, an alternative source of recreation, were only developed in the Cottesloe-Leighton area served by the suburban railways, until after the First World War the acceptance of mixed bathing and the growing supply of motor-cars and buses facilitated the opening of City Beach, Scarborough, and North Beach.

More than anything else, the provision of an adequate piped water supply transformed the Perth environment. Seddon (1970 and 1972) has shown how nearly all suburban householders eradicated the local flora when they built houses, and instead used their hoses to cultivate trim lawns flanked by beds of largely imported annuals, rose-bushes, frangipani, hibiscus, and other non-natives. Even King's Park, so often extolled as "a thousand acres of natural bush near the heart of the city" remained in that condition only because the trustees, such as Sir John Forrest, lacked the financial means to redeem such a large area from "the drab monotony of the Australian bush" (private communication from Dr P. R. Wycherly)*; and in any case it soon ceased to be a sample of the pristine flora of the coastal sandplain. It was not until well into the post-World War II period that public taste, perhaps in response to occasional summer water shortages, came to favour the encouragement of native trees and bushes in the suburban environment: just as it was not until then that variants on the conventional red-brick and tile were sometimes voluntarily chosen as acceptable building materials. One noticeable side-effect of Perth's domestic architecture was its influence on the planning of country farm-houses. With return of prosperity after the Second World War farmers who could afford to rebuild their homesteads forsook the old vernacular architecture, with its overtones of makeshift, and built houses in the bush undistinguishable from the ordinary suburban bungalow.

Rapid post-war metropolitan growth provoked a concern for environmental planning. Although Perth had been under a Town Planning Act since 1928 some factors affecting living conditions were little understood. Few foresaw that the establishment of an industrial complex at Kwinana after 1952 might affect the atmosphere of suburbs dependent on the south-westerly sea breeze for summer relief. Transport policy, despite the integration of bus services under the Metropolitan Transport Trust in 1958, failed to solve two major problems. These were the increasing use of private cars and the deliberate concentration during the 1960s and early 1970s of the administrative headquarters of almost the entire business and financial world, together with most State and federal government offices, along one over-crowded mile of

* King's Park and Botanic Garden, Perth.

high-rise blocks around Saint George's Terrace. A closely controlled policy of land zoning checked inordinate suburban sprawl, but only at the cost of high land prices. Differentiation between the status of suburbs continued to grow, the highest value being placed on those commanding views and access to the river or the sea.

Conscious nevertheless that by most world standards Western Australia was a favoured environment, the community took remedial action. At the official level the destruction of some native fauna was mitigated by the Game Acts of 1874, 1892, 1900 and 1912, and the Land Act of 1898 specifically provided for the creation of reserves for the protection of indigenous fauna and flora: but these early initiatives were not adequately followed up. At the voluntary level some studies of the effect of man on the environment came to be made by such societies as the Royal Society of Western Australia and the Naturalists Club, which although founded as early as 1914 and 1924 respectively, came to shift the focus of their interests in the postwar period (Australian Academy of Science, 1962). In 1959 a concern for the State's early buildings led, none too soon, to the foundation of the National Trust, which carried out useful work in classifying those deserving of preservation. In the same year the State Government took a new initiative by setting up the Swan River Conservation Board, an authority with overriding powers to control the problem of river pollution which had first been noted as far back as 1870. In 1970 the State's legislators agreed to create a Department of Environmental Protection, and in 1971 went further with an Act creating two statutory authorities, the Environmental Protection Authority and Council, with power to report on the implications of proposed new industrial and commercial developments. Controversy was aroused in 1972 when the Authority reported against a proposal to site the Pacminex alumina refinery in the upper Swan, but as alternatives proved to be available, it was hard to argue that the community lost through a concern with environmental factors.

The problems remained formidable. Western Australia—or at least its south-west—consisted of a hinterland increasingly seen as a "big man's" agricultural frontier in which closer settlement, if it came at all, would result only from the chances of mining development or from the deliberately subsidized transplantation of selected industries. The inhabitants of its main centre of population would continue overwhelmingly to seek work and recreation on a narrow coastal sand-plain with a delicate ecology; yet on this basis most experts forecast a population of one million by 1990, and the Lord Mayor of Perth (on evidence as yet unpublished) considered the optimum population to be between 2 and 2.5 million. It would not be easy to reconcile the demands of economic growth with a retention of the quality of life which made Perth, despite its isolation, a fine city to live in.

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