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THE
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WESTERN AUSTRALIA

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Annual Report of the Council for the Year ending 30th June, 1983.

Membership

Membership of the Society stands at 297 Ordinary and Associate members, 16 Honorary members and 2 student members, a total of 315.

During the year there were 4 resignations and 13 Ordinary members were admitted to the Society.

Council

To conduct the business of the Society, ten Council meetings were held during the year.

Professor J. F. Loneragan, Past President, Dr. M. J. Mulcahy and Dr. P. R. Wycherley retired from Council at the end of the year. Dr. B. Dell and Mr. J. Backhouse joined Council.

Meetings

The Annual General Meeting was held on Monday, 19th July, 1982 at Murdoch University. Professor J. F. Loneragan delivered the Presidential address entitled "Curiosity and practicality in scientific research: Their roles in solving plant nutritional problems in Western Australia".

The Society was honoured to welcome the Hon. Sir Ronald Wilson K.B.E., C.M.G., who installed Dr. A. E. Cockbain as the incoming President of the Society.

JOURNAL
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VOLUME 66 1983-4

Contents

Parts 1 and 2

Publication date: 13 May 1983

Page

Part 3

Publication date: 8 December 1983

Part 4

Publication date: 6 June 1984

Ordinary meetings of the Society were held in:

September	"Advances in Dieback Research" Dr. S. R. Shea
November	"Biology and status of the Western Australian underground Orchid" Dr. K. Dixon.
December	Christmas meeting. Two films, "Forests Forever" and "Focus on an Estuary" were shown. A display was also mounted which included original illustration drawn by Dr. S. Tingay for the book "Common Animals of Kings Park", posters from the Environmental Protection Authority and rare books recently bound which are part of the Society's library.
March	"Project Aquarius" Dr. P. Cheney
June	"Principles of Reserve Management in Britain" Dr. T. Wells.

Library

The Society library continues to be held at the Western Australian Museum and administered by the Librarian Mrs H. Balme.

Journal

Volume 65, Parts 2, 3, 4 were published during the year. Volume 66, Parts 1 and 2 were combined to present a special issue titled "Research on Rottnest Island", to coincide with the ANZAAS conference held in Perth during May.

Council activities

A questionnaire was sent to members and most replies implied that they were satisfied with the current programme of activities and priorities of the Society.

National Trust

Dr. P. E. Playford has continued to represent the Royal Society on the Council of the National Trust (W.A.)

Acknowledgements

The Society thanks the Government Printer for cooperation in publishing the Journal. It is also indebted to the W.A. Museum for housing the Journal stocks.

The Board of Kings Park are also thanked for allowing the Society to hold meetings on the premises under their jurisdiction.

FOREWORD

Rottnest Island occupies a unique place in the mythology of West Australians: a place where one retreats to "get away from it all". Its rôle as a refugium from change also extends to the wildlife, and marsupial species such as the quokka now abound on Rottnest after being all but extinguished on the mainland in the 1930's along with the development of agriculture in the south-west.

The papers collected in this volume draw attention to the many facets of this singular environment: geological, biological and sociological, and summarize the research which has been done on Rottnest since 1959. The function of research is to extend knowledge and thereby bring about a better understanding of the environment and our place in it. The work reported here brings into focus current scientific knowledge of the plants, the animals, the soils and of the evolution of Rottnest Island as a distinctive habitat, and underlines the need for enlightened management in the face of ever-increasing pressure from people seeking the "Rottnest experience".

West Australians are fortunate in having an island so rich in natural beauty virtually on their doorsteps but, as with all assets, it needs protection from abuse. The papers presented at this Conference are not meant as a recipe for such, but they should provide guidelines for those who wish to preserve the uniqueness of this island habitat.

S. D. BRADSHAW
January, 1983.

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Macropod ecophysiology: a possible integration with ecological and evolutionary studies

by A. R. Main

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Abstract

The relevance of ecophysiological studies on macropod species is explored in the context of a Hutchinsonian model of the niche. Perturbations which bring about an equivalence between, or an approximation of the realized to the fundamental niche are shown to be associated with large-scale increases in population size due to the loss of normal stabilizing mechanisms such as predation and competition. These concepts are discussed in relation to the problem of conservation of insular species of macropods.

Introduction

When the late Harry Waring took up the post of Professor in Zoology at the University of Western Australia his professed goal was to initiate studies on marsupials. Shortly after his arrival he was introduced to the quokka and thereafter took this species to be the typical macropod upon which the study of marsupials was to be based.

In the first decade of Waring's work on the quokka he spent much of his time and energy inducing those with access to funds or other resources to support his dream of basing marsupial studies on this animal on Rottnest Island. I was present on a number of such occasions and invariably the response was: "Why support work here? You have only a single marsupial, and that not in a typical habitat." This comment was accompanied by the advice that what he should do was come to the East where there was a much greater variety of marsupials and a real study could be undertaken. The outcome of these encounters was usually that Waring gained some support and, as everyone knows, stayed to study and sponsor studies by others on the quokka.

Having this background in mind, it is useful now to see whether and how the original studies on the quokka have enabled an expansion to include other species, and particularly what generalisations might be made from such studies. The purpose of this paper is not to review what has been achieved but to indicate in broad outline where and in what manner marsupial studies might be related to developing ecological theory and ecology generally.

Aims of ecophysiological studies

The central question is to establish whether the implied criticism of the single-species approach was valid or whether the study did allow for predictions and generalisations to flow to other species and so lead to broadly interpretative concepts or relate such to concepts raised in connection with other situations. Of course such generalisations require that some theoretical basis be established from which testable predictions and generalisations can be made. Prediction is likely to be more successful in so far as one departs from a mere recital of species differences and similarities and develops an hypothesis bearing a relationship to common environmental conditions.

In this regard one of the ubiquitous events of the environment in Australia is and has been the progressive influence of desert and drought on the fauna. It is noteworthy that the environment of Rottnest Island is markedly different from the habitat occupied by the quokka on the mainland of Western Australia, and if one is interested in marsupials as a unique Australian biological entity or in the response of marsupials to drought, then the quokka on Rottnest is equally suitable regardless of whether it is the sole inhabitant of the island or not.

The early work carried out in the 1950's in Waring's laboratory was either related to reproductive physiology or physiological ecology (Bartholomew 1956, Bentley 1956, Moir *et al.* 1954, Moir *et al.* 1956). Subsequently a great many workers have used quokkas and a number of other species of macropods of various sizes as subjects of ecophysiological studies. Thus there is now a large body of information on the ecophysiological performance of a range of macropods. These studies fall broadly into one or the other of the following:

(i) The physiological responses of macropods to ecological or field-induced stresses, e.g. urine volumes, electrolytes and urea in urine and plasma under conditions of electrolyte loading or water or heat stress, or urea recycling under conditions of inadequate diet (Kinnear *et al.* 1968, Purohit 1971, Main 1970, Kinnear and Main 1975, Hume and Dunning 1979).

(ii) The physiological responses of macropods to stresses administered in the laboratory which are believed to be a realistic representation of field conditions. In the laboratory situation care is taken to see that the experimental animal is denied any opportunity to avoid the stressful situation by behavioural means. Such studies have encompassed regulation of body temperature under heat or cold stress, nitrogen balance with diets of various qualities or presented under conditions of heat or cold stress or water deprivation (Bartholomew 1956, Dawson and Bennet 1971, Brown 1969, Brown and Main 1967, Prince 1976).

(iii) The physiological mechanism of response to field conditions or laboratory conditions presented to mimic field situations, such as the rôle of endocrine glands in initiating and sustaining the animal's responses e.g. pituitary, adrenal and kidney responses to water deprivation or electrolyte loading or adrenal function in mobilizing tissue catabolism in starvation (Bradshaw *et. al.* 1975, McDonald 1977, McDonald and Bradshaw 1977, Miller and Bradshaw 1979).

Adaptation and persistence of macropods

While the studies have been progressing for a number of years in several laboratories, it is still true to say that relative to the total number of macropod marsupials, only a few species have been examined and none has been subjected to a complete ecophysiological analysis. We are thus left to ponder two questions. One is: are the species that have been accessible and amenable to study, the appropriate ones for making generalisations which are badly needed now that so many species require conservation and management in reservations? The second is: given that ecophysiological studies tell us what an animal can tolerate and how it does so in terms of physiological mechanisms, where do such studies fit in terms of ecological and evolutionary theory, i.e. what is their present function and how did they arise in the past? The possible answers to these questions are pursued below.

In many respects macropod marsupials appear to be in no way inferior to their herbivorous eutherian counterparts. On Rottnest Island the quokka occupies a habitat that would be quite unpredicted from its mainland occurrence, yet it and with few exceptions other marsupials have been unable to maintain their abundance in the face of agricultural and pastoral development on the mainland.

There is thus a paradox: on the one hand it is clear as the result of ecophysiological analysis that many species have well-developed physiological capacities to handle environmental stresses imposed by heat, water deprivation and low quality diet. In many cases the range of responses far exceeds what the animal may be called upon to perform for survivial in nature. In this sense they are well-adapted to the environment in which they live.

On the other hand a number of species have declined in range and abundance (Lundelius 1963, Baynes 1980) since the advent of European man in Australia. A test of being adapted is to survive as an individual and persist as a population; in this sense they are unadapted to the new circumstances or at least their adaptations are not relevant to the changed conditions.

This last point would infer that the expression of the evolved physiological adaptation in a survival situation is in some way dependent on the structure of the environment as it is this part of the Australian scene that has changed so markedly in the past century because of the presence of European man and his agricultural and pastoral practices. But it is possible to see the changes induced by man's activities as being merely the culmination of a long period of environmental change which commenced some time in the Pliocene. During this period the biological part of the environment has changed from forest or woodland to open woodland and shrub understorey to open scrub-grassland or hummock grassland. In this context it is appropriate to consider ecophysiological responses as the end product of a long evolution in response to aridity which has manifested itself principally in terms of water deficit accompanied by a simplification of the vegetational component of structure of the environment, i.e., the quokka on Rottnest Island is the analogue of what has happened over a longer period in the continent.

The fossil record suggests that as the floral composition and vegetational structure change, there appeared first a radiation of marsupials culminating in the evolution of very large species which in the recent past was terminated by widespread extinctions (Wells 1978). In view of the faunal reduction following these extinctions, one might ask whether adaptations of an ecophysiological nature have allowed persistence or whether other kinds of adaptation have been more important (Main and Bakker 1980).

Aspects of this problem have been discussed by Main (1978) in terms of how a species perceives the environment. The perception will be different for each species depending on its degree of adaptation. For example, a hot-arid climate may not be stressful to a species with a well-developed capacity to produce concentrated urine, which possesses a reflective coat or lives in a habitat which provides a heat refuge (e.g. *Macropus rufa* or *Macropus robustus*), but a similar environment would certainly be inadequate for any species which lacked such adaptive traits. In this way it is possible to see physiological performance as contributing to the ability to occupy specific habitats, but one needs to relate physiological capacity in a more general way to the field and the general ecology of a species. Thus one needs a bridge between ecophysiology and ecology and it seems that a conceptual framework is provided by the fundamental niche of Hutchinson (1957), conceived as a set of states of environmental variables permitting species to exist indefinitely.

The relevance of niche theory

In the context of ecophysiology we determine the states by laboratory or field measurement, and so may define the fundamental niche as an n-dimensional hypervolume or space which encloses all the environmental states that a species can tolerate and persist in indefinitely. In the presence of other species with which there are biological interactions, a species occupies a realized niche which differs from the fundamental niche. Kinnear and Main (1979) discussed these concepts with respect to nutrition.

In several papers (Main 1978, Kinnear and Main 1979, Main and Bakker 1980) it has been proposed that ecophysiological findings, when they establish limits of performance, really delimit boundaries of the n-dimensional hyperspace that is the Hutchinson fundamental niche. These measurements describe the conditions which would limit existence of each species if biological interactions (eg. competition) did not occur. In the absence of competition one might expect the fundamental niche to equate with the realized niche, i.e. the conditions under which the species is actually found e.g., the quokka on Rottnest. This is an unusual case and more realistically one might expect that biological interactions would lead to the occupancy of only part of the fundamental niche, i.e., the realized niche is less than the fundamental, e.g., the quokka in its mainland habitat.

It has already been mentioned that in Australia there has been considerable extinction in the recent geological past, and one might expect distribution of the survivors of this extinction to have ranges approximating to their fundamental niche because competition has been reduced. For example, the two species of grey kangaroo might have their ranges in the north-west and north-east determined by the fundamental niche of each species, but in the south-east *M. fuliginosus* may be restricted by competitive interactions with *M. giganteus* which is similarly limited on the south and west side of its range (Main 1978). Considering the significant answers which might be obtained by studying these species, we know surprisingly little of the ecophysiological responses of each.

In the field however, factors additional to physiological capacity appear to be important and in the face of a perceived stress an animal seems, to respond initially by committing the fewest resources to its relief generally by avoiding the stress in a behavioural way (Kitchener 1972). In the event that this is not successful, then progressively more and more resources are committed by way of physiological responses and then acclimation. The ultimate stage in the resource commitment is when part of the genotype is devoted to the heightened development of morphological and physiological attributes which permit existence in the continued presence of the stress, i.e. the organism adapts at the morphological and physiological levels. In the foregoing series, behavioural response are reversible at very little cost; physiological responses are more costly to reverse, for example, should evaporative cooling be used in temperature control when the replacement of water lost may be very difficult. On the other hand, once genetic resources are committed, change is in the order of generations and so is not likely to be rapid and reversibility is unlikely. Enhancement of physiological capacity to tolerate stress by genetic change is only likely to arise under a long-term régime of stress and selection.

Responses to aridity

In Australia, ecophysiologically stressful events are mostly associated with aridity. Earlier (Main 1973) I discussed how arid environments are a composite of favourable and unfavourable environments which may be dispersed in time and place. Periods of favourableness vary in duration and amplitude as do the periods of unfavourableness or drought. In such an environment persistence as a population is only possible if the favourable periods are exploited by restoring population size and the unfavourable periods withstood because of behavioural avoidance or physiological tolerance. Such a system ceases to work when favourable periods are too short or the unfavourable periods exceed the generation time or life span of a species. Thus an arid-adapted species has to adapt to two sorts of environment which are quite different and for which adaptations may conflict. For example, a lowered metabolic rate may conserve water during drought but it would also produce delayed growth and hence development to sexual maturity would be longer, a disadvantage when population size is to be restored during favourable periods of short duration; or kidneys which can excrete concentrated urine are advantageous during drought but when there is a surfeit of water in and on plants the kidney must be able to excrete the excess. The physiological adaptations which we see today result from long-term trends in aridity, the duration and amplitude of favourable and unfavourable periods, and the physiological and other compromises with which the species has responded to the periods of abundance and scarcity of resources.

The role of habitat

Southwood (1977) has discussed habitat in a general ecological context as the templet of ecological strategies and develops a matrix for assessing reproductive success in terms of breeding "now" or "later" and "here" or "elsewhere". He then proceeds to discuss in terms of quantitive characters the components of habitat, these being heterogeneity in time (favourable or unfavourable), predictability (predictable, unpredictable, ephemeral), heterogeneity in space (patch characteristics with respect to food gathering or migration, and patch characteristics with respect to patch size and interpatch space, i.e. isolation) (Southwood 1977, Figs 6-9).

If ecophysiological capacities require a structured environment for successful expression, then the suggestions of Southwood appear to provide the necessary framework within which to interpret reproductive tactics of currently-surviving macropods along with their phsyiological adaptations and their use of habitat. Thus it would appear that ecophysiological capacities and habitat resources can be linked in a way which is potentially useful for devising management strategies, particularly if we think of the aims of management as being analogous to evolutionary success as conceived by Slobodkin (1972).

Evolutionary success can be gauged in two ways, after some have failed to survive, i.e. retrospectively, or as Slobodkin (1972) has suggested, by assessing the probability of a population surviving in the future, those more likely to survive having the greater measure of evolutionary success. The probability of survival will depend on having some assessment of the stressful situations that are likely to arise in the near future (more likely when they occur in the same season every year or when changes follow a trend and are not irregular, intense or sudden), and when the organism has the behavioural, ecological and physiological adaptations to meet the problem. Slobodkin (*op. cit.*) also points out that "high abundance and high reproductive rate are of evolutionary value in themselves only in situations in which there is a high degree of unpredeictability expected in the environment." This is so because if physiological and behavioural adaptations fail, the organisms in a population can only ensure persistence by reproducing as rapidly as possible when conditions are favourable.

In the sense of the fundamental niche of Hutchinson, aspects of the sets of environmental states have been determined for macropods on five broad fields of study, namely, behaviour, nutrition, water and electrolyte balance, heat tolerance and reproduction. Within each of these fields of study there are numerous adaptive responses but none occurs in all surviving species so far analysed, nor are the adaptive responses of the same magnitude even in species apparently subject to the same environment, which poses the question. why is this so?

In terms of Slobodkin's concepts the surviving arid land macropods appear to have assessed the future in two ways: (1) with respect to shelter: (a) that vegetation will continue to provide cover—(agile wallaby, hare wallaby, grey kangaroo and tammar) (b) that vegetation will not continue to provide cover and so electing to shelter elsewhere, e.g. in rock shelter—(euro, rock wallaby,) or evolving a reflective coat—(red kangaroos); (2) with respect to food quality: (a) those assessing that quality will remain high and retaining a little-modified gut and eating moderate to good quality diet—(red kangaroo, agile wallaby,) and (b) those assessing quality as being low and fibrous and whose gut is highly modified morphologically for fermenting fibrous diets: these are capable of recycling urea—(euro, grey kangaroo, hare wallaby, tammar).

In terms of Southwood's concept all those macropods that breed continuously are breeding "here" and "now", and in terms of the quote from Slobodkin, cited above, are indicating that, to them, the environment is unpredictable, which fits with Southwood's concept of habitat being favourable or unfavourable in time as well as being predictable or unpredictable. Macropod species recognise heterogeneity in space in different ways. Some species, e.g. red kangaroos and to some extent grey kangaroos, leave unfavorauble patches and move to favourable ones. i.e. are nomadic, while other species, e.g. euro, hare wallaby, tammar, remain in their shelter sites in unfavourable times but may increase their foraging range. Those species depending upon structural vegetation for shelter will have their patches become progressively less favourable as successions proceed and the vegetation matures and dies or is replaced by plant less suitable as cover. In such cases the adults do not move but, during their occupancy of the patch, juveniles in excess of the carrying capacity of the patch have been produced and these act as explorers for and potential colonisers of unpopulated patches at the right stage for colonisation, e.g. mainland quokka (Christensen and Kimber 1975).

Environmental predictability

The question revolves around both the intensity of the unfavourable periods, i.e. the amplitude of the swing from favourable to unfavourable, and the periodicity of the recurrence of favourable or unfavourable. For example, annual summer drought has a fixed period of recurrence and so is predictable but may vary from year to year in intensity, i.e. amplitude. In arid regions generally, failure of rainfall and consequent absence of fresh plant growth may lead to long-term droughts which not only extend over several summer and winter seasons but may also persist for several years. In such cases the recurrence of drought can be regular or irregular and at intevals of several to many years. This is an aspect dealt with Slobodkin and Rapoport (1974) who classify perturbations as expected (e.g. seasonal heat or drought) or unexpected—the former being those within the animal's repertoire of responses and the latter outside them. In this sense expected perturbations can easily be accommodated within the evolved behavioural or physiological capacities of the animal. Unexpected perturbations are those for which there are no evolved responses; if they occur with some regularity, then selection will lead to evolved capacities to handle them.

These authors suggest that it is the periodicity, expressed in terms of the expected life span, of the same environmental perturbation which results in a spectrum of adaptive responses raging through behavioural, physiological, acclimation mechanism to morphological change. The extant macropod species are successful in one sense used earlier and it is of interest to see how their evolution and adaptations to unpredictable environments fit the above schema. In keeping with the ideas of Slobodkin & Rapoport (1974) on selective forces and responses we would expect seasonal perturbations to be experienced by all animals throughout their life span and they would respond with superficial behavioural or physiological adjustments. Droughts may or may not be experienced by all animals during their life span, yet when they are experienced they may call for a more intense and sustained response than is required to survive seasonal perturbations. Under such circumstances one might expect acclimation or enhanced physiological capacity such as metabolic depression, increased concentrating capacity of the kidney, an ability to recycle urea, and significant morphological modification might be selected. In this regard one would interpret the spectacled hare wallaby *Lagorchestes conspicillatus* and the euro *Macropus robustus* as being highly evolved.

In the Australian environment fire is unpredictable: also its effects exacerbate the deleterious effects of seasonal or more extended droughts. but its effects probably do not call forth any new responses. Of the macropod marsupials studied, the habitat of the hare wallaby *L. conspicillatus* is most seriously affected by fire because the *Triodia* tussocks used for shelter are very inflammable. Destruction of cover should exacerbate the effects of the irregular but prolonged droughts which occur over its range. The adaptive responses of the hare wallaby are consistent with those expected from the reasoning of Slobodkin and Rapoport (1974) in so far as the hare wallaby has the highest relative medullary thickness of kidney and the maximum urinary osmotic pressure of those macropods studied (Main and Bakker 1980).

The testing of the foregoing theoretical expectations and their application to macropod species generally is not possible with our present knowledge. Undoubtedly the integration of ecophysiological findings with other aspects of the ecology requires an attention to the quantitative aspects of the habitat (Southwood 1977). Moreover, in order to account for the different adaptive responses of different species to the same environmental perturbations it is necessary, following Slobodkin & Rapoport (1974), to relate the probability of encountering the perturbations to the expected life span of the species under study. Should such an ambitious goal be achieved, ecophysiological studies will become a significant and integrated part of ecological and evolutionary studies of populations. Moreover, such an integrated approach affords the opportunity for wide-ranging comparative studies for which the present ecophysiological and ecological knowledge is unfortunately inadequate. However, this inadequacy cannot be ignored because the development of strategies and tactics for the management of macropod species in conservation reserves of limited size depends on integrated laboratory and field studies somewhat on the lines of Prince (1976) but with attention to the components of habitat which contribute to amelioration of the stressful effects of drought such as shelter as a heat refuge or nitrogen status of plants or access to fermentable energy so that urea can be recycled.

Conclusion

It is apparent that many of the results arising from work on the quokka on Rottnest Island have given rise to interpretations which are applicable to and testable on macropods generally. The findings and interpretation show a congruence with the general theories proposed by Hutchinson (1957), Slobodkin and Rapoport (1974) and Southwood (1977), and can be readily interpreted within such a framework. Such a result is ample justification for the selection of the Rottnest Island quokka as the model macropod marsupial, as mentioned in the introduction. Moreover, it seems clear that in terms of usefulness as a model, the quokka has not been superseded.

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Geological research on Rottnest Island

by P. E. Playford

Geological Survey of Western Australia

Abstract

Rottnest Island forms part of a chain of limestone islands and reefs marking former Quaternary shorelines. It is composed of Pleistocene to Holocene dune limestone (Tamala Limestone), late Pleistocene coral-reef limestone (Rottnest Limestone), mid-Holocene shell beds (Herschell Limestone), and superficial Holocene deposits.

The Rottnest Limestone coral reef grew about 100 000 years ago when sea level was relatively at least 3 m higher than today. Separation of the island from the mainland occurred about 6 500 years ago as sea level rose near the end of the Holocene Flandrian transgression. This was followed by the extinction of most animal and plant species.

The Holocene transgression reached its peak about 2.6 m above present sea level some 5 500 to 5 000 years ago. Two earlier brief still-stands occurred successively about 0.5 m and 1.2 m above present sea level. The final regression to modern sea level may have been of tectonic (rather than eustatic) origin.

A lens of potable groundwater situated west of the salt lakes has been developed to service settlements on the island.

Introduction

The first detailed geological studies on Rottnest Island were carried out by Teichert (1950). His work dealt mainly with the eastern part of the island and the evidence displayed there of Quaternary sea-level changes. Hassell and Kneebone (1960) studied the island as a B.Sc. Honours project at the University of Western Australia, and their work was summarized by Glenister, Hassell, and Kneebone (1959).

Research by the Geological Survey of Western Australia at Rottnest began in 1976 as part of an investigation into the island's groundwater potential (Playford 1976, Playford and Leech 1977). This work further elucidated the Quaternary geology and geological history and succeeded in finding a source of potable groundwater. Since then work by the Geological Survey has continued, and this paper summarizes present knowledge of the geology of the island.

Geomorphology

Rottnest is the largest island in a chain of limestone islands and reefs on the continental shelf opposite Perth. They are composed of dune limestones marking former mainland shorelines which migrated as sea level rose and fell successively during interglacial and glacial periods of the Pleistocene.

Rottnest Island is characterized by alternating limestone headlands and bays with wide sandy beaches backed by Holocene sand dunes. The coast is fringed by shoreline platforms and offshore "reefs" formed by marine planation of Pleistocene dune limestone and encrusted with thin layers of coralline algae and corals. The Pleistocene dune limestone which underlies most of the island is prominently exposed on the headlands; in the interior it is mainly obscured by a veneer of residual or wind-blown sand.

Salt lakes occupy about 10% of the area of the island. They have elongate-ovoid to sub-circular shapes, and are believed to overlie dolines formed by rainwater solution of the limestone and subsequent collapse of cave systems during low sea levels of the Pleistocene. The dolines were subsequently largely filled with Holocene sediments. The prominent "blue holes" of the Houtman Abrolhos appear to have a similar origin (Playford and Leech 1977). Water levels in the lakes rise to about mean sea level in winter and fall more than a metre in summer. Some of the smaller lakes dry out completely at the end of summer, forming a salt crust, while the larger lakes commonly have late-summer salinities exceeding 150 000 mg/L.

Geology

Rottnest Island is composed of Pleistocene to middle Holocene dune limestone (Tamala Limestone), with a thin intercalation of Late Pleistocene coral-reef limestone (Rottnest Limestone), overlain by thin middle Holocene to modern deposits: shell beds (Herschell Limestone), dune sand, beach sand, swamp deposits, and lake deposits. The surface geology is illustrated on Figure 1.

Rock Units

The *Tamala Limestone* is a unit of eolian calcarenite composed of wind-blown shell fragments with variable amounts of quartz sand, and is characterized by large-scale eolian cross-bedding. Over most of the island the formation is mantled by residual quartz sand derived by weathering of weakly lithified sandy limestone.

The Tamala Limestone is known from coastal areas and islands extending from Shark Bay to the south coast, and it ranges from Pleistocene to Holocene in age. At Rottnest the oldest exposed part of the formation probably dates from the Riss Glaciation and the following transgression; the youngest is Holocene, laid down during the Flandrian transgression. The formation contains some prominent soil horizons marking interruptions in dune building. They are underlain by calcrete layers, often associated with abundant fossil root structures (rhizoliths).

Drilling suggests that the Tamala Limestone below Rottnest is about 115 m thick, extending to 70 m

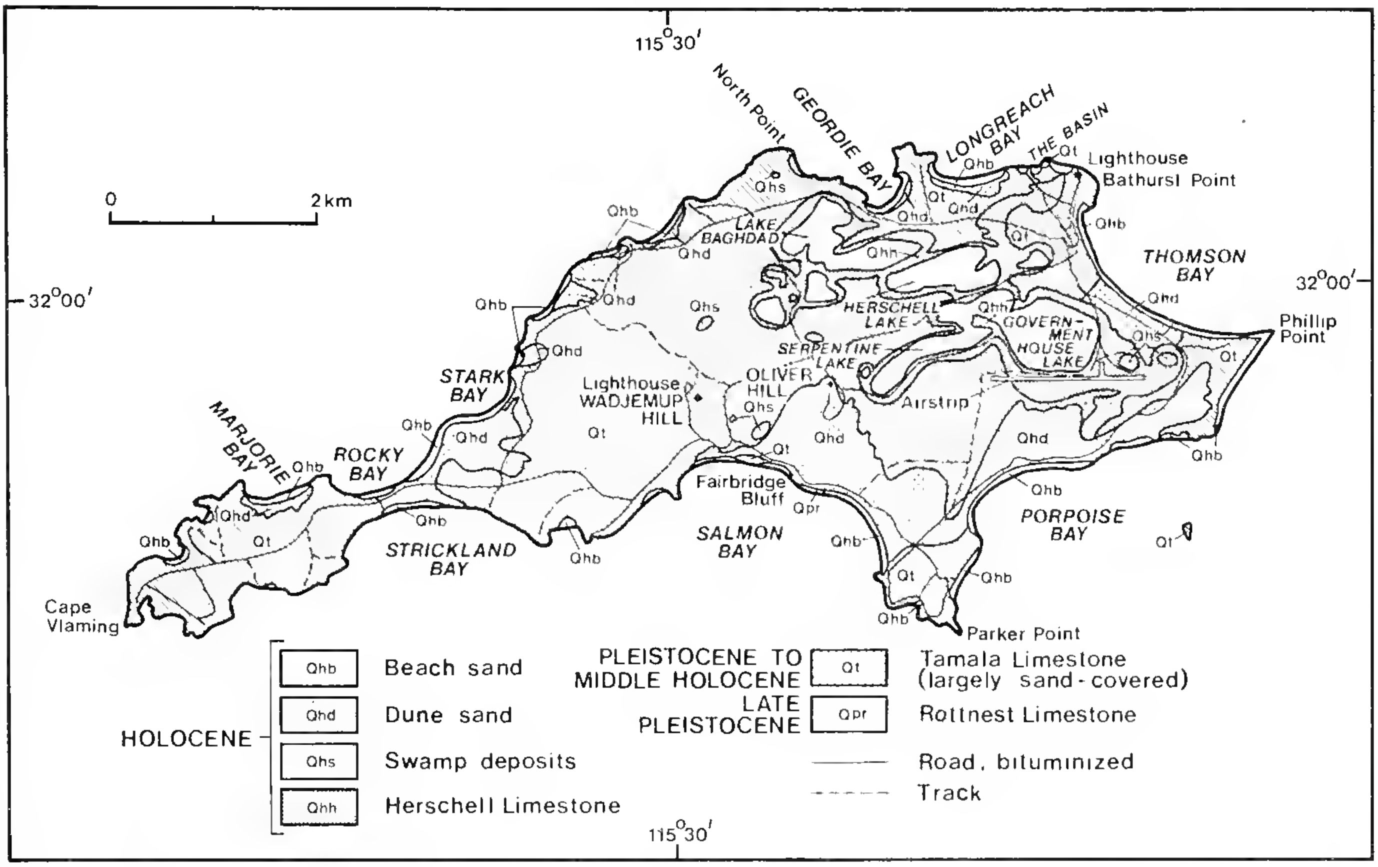

Figure 1.—Geological map of Rottnest Island.

below sea level, where it overlies older Pleistocene or Tertiary sands.

The *Rottnest Limestone* (Fairbridge 1953) is a Late Pleistocene unit of coral-reef limestone and associated shelly (gastropod-rich) limestone exposed at Fairbridge Bluff in Salmon Bay. The formation is overlain and underlain by Tamala Limestone and is believed to represent a marine tongue intercalated in that formation. The total exposed thickness of the Rottnest Limestone is 3 m.

The coral fauna is dominated by branching species of *Acropora*, a genus which today is not known further south than the Houtman Abrolhos, 350 km to the north. Its occurrence in the Rottnest Limestone thus indicates warmer-water conditions when the reef grew than those prevailing in the area at present. Coralline algae (*Lithothamnium*) also made substantial contributions to the reef framework.

The Rottnest Limestone has been dated by uranium-thorium methods as 100 000 ± 20 000 years old (Veeh 1966), and it thus dates from the last Pleistocene interglacial period.

The *Herschell Limestone* is a unit of Holocene shell beds with intercalated lime sand and marl which is exposed around the margins of the Rottnest salt lakes. It overlies and abuts the Tamala Limestone and is overlain by superficial Holocene deposits. The unit is at least 3 m thick, and it is believed to have been deposited in subtidal to intertidal environments.

The fauna of the formation is dominated by many species of bivalves and gastropods (Kendrick 1977). All are living species, but some no longer live in the Rottnest area.

Radiocarbon analysis of shells in the formation gives dates of around 5 500 to 5 000 years (Tamers *et al.* 1964, Deevey *et al.* 1959), with one anomalous date of about 3 800 years (Deevey *et al.* 1959), which is probably too low because of contamination by younger carbonate. Playford and Leech (1977) concluded that the Herschell Limestone was probably deposited about 5 500 to 5 000 years ago, at the peak of the Holocene transgression in this area.

Superficial deposits of Holocene age mantle most of the island. They consist of dune sand, beach sand, swamp deposits, lake deposits, and residual sand (largely derived from the Tamala Limestone).

The swamp deposits were laid down in a series of small fresh- and brackish-water swamps. They consist of thin layers of marl, lime sand, peat, and algal sediments. The palynology of these deposits was studied by Hassell and Kneebone (1960), who showed that pollen from tuart, jarrah, marri, white gum, sheoak, peppermint, banksia, and zamia palm occur at depths of a metre or more below the surface. This shows that the typical tuart-woodland association of the mainland occurred on Rottnest in the past, although none of the species occur there naturally today. Playford and Leech (1977) deduced that this floral association (characteristic of mainland coastal areas opposite Rottnest) probably disappeared soon after Rottnest separated from the mainland. At the peak of the Holocene transgression the land area was much smaller than that of the island today (Fig. 3) and the effects of salt spray (inimical to tuart woodland) were consequently more extensive.

The modern salt-lake deposits consist of algal and evaporitic sediments. In Government House Lake they include columnar algal stromatolites growing in water up to about 3 m deep.

Sea-level changes

The most notable feature of the surface geology of Rottnest Island is the excellent evidence there of Quaternary sea-level changes. This is in the form of (a) elevated marine deposits, (b) elevated shoreline platforms and notches, and (c) subaerial features which now extend below sea level.

The Department of Lands and Surveys has recently carried out levelling at Rottnest on behalf of the Geological Survey in order to better relate the various elevated features to their present-day equivalents. Although further levelling is desirable, some preliminary amendments are made in this paper to the approximate elevations assigned by Playford and Leech (1977) to the various emerged features.

The levels of modern shoreline platforms were determined at three localities adjoining the eastern half of the island; these are –0.402 m at The Basin –0.428 m at Fairbridge Bluff, and –0.480 at Thomson Bay (near the hotel). They average about 0.44 m below mean sea level (A.H.D.), which is 0.1 m below mean low water level, and would be exposed about 1% of the time each year (D. F. Wallace, pers. comm., 1982). Elevated shoreline platforms and associated notches, and the top of the fossil coral reef, have been related to this level in order to deduce the amount of emergence that has occurred.

Elevated marine deposits: The fossil coral reef of the Rottnest Limestone extends to 3.02 m above the adjoining shoreline platform. Consequently it is concluded that sea level relative to Rottnest during the last interglacial was at least this amount higher than it is today. However, this is a minimum figure, as the top of the coral reef could have grown in water several metres deep.

The highest marine shell beds of the mid-Holocene Herschell Limestone extend to about 2.15 m above mean sea-level or 2.6 m above the modern shoreline platforms. This is the same level as the highest of the emerged shoreline platforms, and both apparently formed at about the same time, some 5 500 to 5 000 years ago.

Elevated platforms and notches: Three levels of elevated shoreline platforms and notches are recognised at Rottnest Island: an upper level at about 2.6 m, an intermediate level at about 1.3 m, and a lower level at about 0.5 m above the modern shoreline platforms (Fig. 2). These are the '3 m, 1.5 m, and 0.7 m" levels of Playford and Leech (1977).

The upper (2.6 m) level is visible at many places around the coast, and especially around the salt lakes. The intermediate (1.3 m) and lower (0.5 m) levels are best preserved around the lakes, in the form of notches with weakly developed narrow platforms (Playford and Leech 1977. Figs. 15-17). The intermediate and lower levels are rarely preserved around the coast of the island, as there they are subject to modern wave attack.

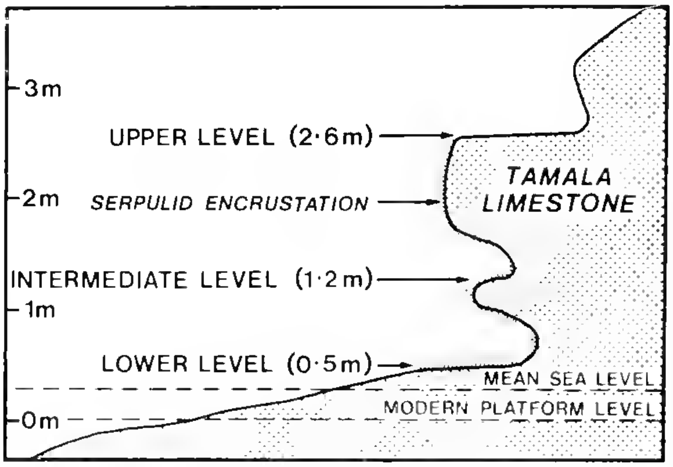

Figure 2.—Diagram illustrating elevated shoreline platforms and notches around the Rottnest salt lakes. The elevations of these features are related to the average elevation (0.44 m below mean sea level) of modern shoreline platforms around the island.

At many localities a layer of serpulid worm tubes is discontinuously preserved encrusting the two lower notches and platforms, and extending up to the upper-level platform (Fig. 2). The limestone on which the serpulids grew is commonly intensely bored by marine organisms. Some pockets of bivalves and gastropods (species also found in the Herschell Limestone) are associated with the serpulid layer, and there are also some encrustations of bryozoans and small solitary corals. These organisms grew under subaqueous marine conditions and once formed an essentially continuous crust over the surface below the upper-level platform. From this it is clear that the two lower notches and their associated platforms were already in existence when the transgression reached the upper (2.6 m) level. Each of the three levels is believed to represent a still-stand of no more than a few hundred years as relative sea level rose through three steps to its final peak about 5 500 to 5 000 years ago. The regression following this peak must have been abrupt; otherwise the relatively fragile serpulid crust would have been removed by marine erosion.

Subaerial features extending below sea level: Lithified dune limestone of the Tamala Limestone extends below sea level around the coast of Rottnest, and may reach depths of 70 m or more. Most of the formation is thought to have accumulated when sea level was considerably lower that it is today.

At several localities around the coast solution pipes in the Tamala and Rottnest Limestones can be seen extending below sea level, testifying to sea levels lower than at present when they formed. As previously mentioned, the salt lakes probably overlie major dolines formed by rainwater solution and collapse during the low sea-level stands of the glacial periods.

Origin of sea-level changes

The major changes of sea level affecting the Swan Coastal Plain and adjoining continental shelf during the Pleistocene resulted from eustatism associated with waxing and waning of the continental ice sheets (see discussions in Playford *et al.* 1976 and Playford and Leech 1977). However it is doubtful that the Holocene "high sea levels" evidenced at Rottnest and elsewhere along the Western Australian coast were truly eustatic (i.e. world-wide events), as had been postulated by Teichert (1950), Fairbridge (1958 and 1961), and Hassell and Kneebone (1960).

As pointed out earlier, there was apparently an abrupt fall in sea level at the close of the still-stand evidenced by the upper-level platform. This prompted Playford and Leech (1977) to suggest the possibility that it had a tectonic origin.

However, it still remains to be shown whether this relative fall in sea level during the mid Holocene was of regional or local extent. If it was regional, did it result from world-wide eustatism, epeirogenic uplift, global changes in the geoid, or some other cause? If the relative fall in sea level was of local extent, did it result from movement along a fault on or adjoining the continental shelf, possibly triggered by rapid loading of water during the Flandrian transgression, or was it associated with movement along the Darling Fault? The answers to these questions must await further precise work to correlate emerged platforms and other features at Rottnest with similar features in Western Australia and elsewhere in the world.

Quaternary geological history

The foundations of Rottnest Island may have been originally localized by a sand shoal, perhaps associated with an uplifted area in underlying Tertiary rocks. Calcareous sand dunes accumulated in the area during the Pleistocene to form the Tamala Limestone. This formation had a long history of dune building, soil development, and karstification during successive glacial and interglacial periods of the Pleistocene. The oldest dune limestones exposed on the island may date from the Riss Glaciation and the ensuing transgression, but older Pleistocene parts no doubt occur in the subsurface.

During the Riss-Wurm interglacial a coral reef grew on the dune ridge of Tamala Limestone. Sea level fell progressively during the Wurm glaciation, reaching its lowest level of about 130 m below its present level some 18 000 years ago. The coastline was then about 12 km west of Rottnest (Fig. 3), and the old dune and reef limestones stood as a

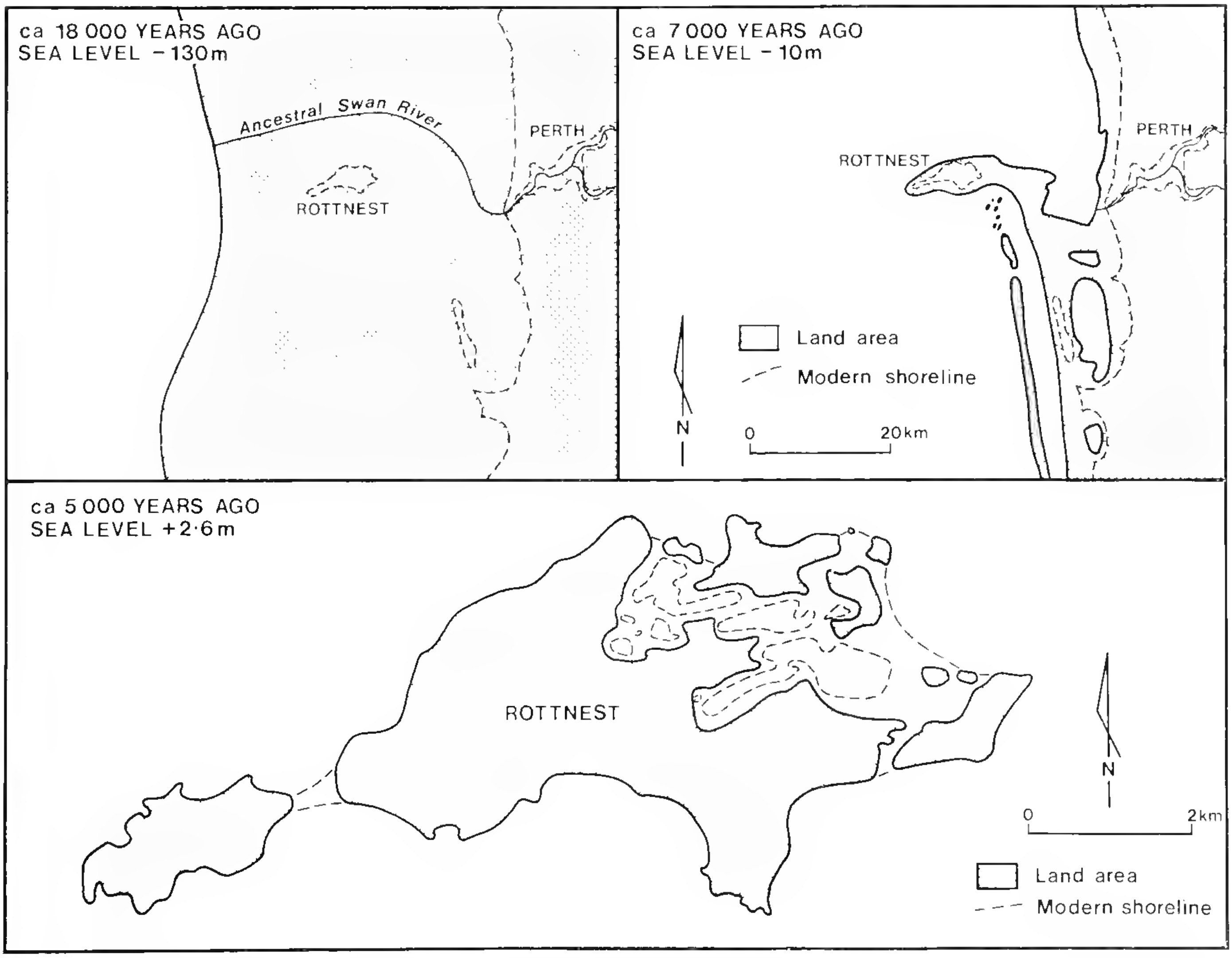

Figure 3.—Palaeogeographic maps illustrating shoreline changes in the Rottnest-Perth area during the late Pleistocene and Holocene.

conspicuous "mountain" high above the surrounding plain. The ancestral Swan River then flowed out to sea northwest of Rottnest, where it joined a submarine canyon (the Perth Canyon) incised into the continental slope. Strong karst solution proceeded in the limestones, with the formation of the large dolines that were afterwards to localize the modern salt lakes.

Sea level rose rapidly during the Holocene Flandrian transgression. Dune sands of the younger Tamala Limestone accumulated on the Rottnest platform as part of a belt extending through the present Carnac, Garden, and Penguin Islands. As the sea rose towards its present level, Rottnest remained in connection with the mainland along this belt of dunes (Fig. 3). The island probably separated about 6 500 years ago. Major changes in the land flora and fauna of the island followed this separation; only a few of the original plants and animals survived to the present day.

The maximum submergence at Rottnest, to about 2.6 m above present sea level, probably occurred some 5 500 to 5 000 years ago. The area of the present salt lakes then formed arms of the sea between more than 10 separate islands (Fig. 3). Prolific molluscan faunas lived in the warm shallow waters between these islands, and their close-packed shells now form much of the Herschell Limestone.

There were two brief intervals of still-stand, totalling no more than a few hundred years, at about 0.5 m and 1.2 m above present sea level, as the sea rose to its peak (2.6 m) level. Notches and narrow shoreline platforms were eroded at each of those levels.

There was an abrupt fall in sea level, or the Rottnest area was suddenly uplifted, about 5 000 years ago, when the sea attained its present level relative to the island. The area of the present salt lakes remained in connection with the sea for some time, but it was eventually cut off by the accumulation of beach ridges and sand dunes. Superficial deposits continued to accumulate after that time, but there have probably been no major changes in the configuration of the island for the past 2 000 or 3 000 years.

Hydrogeology

The supply of domestic water in sufficient quantities and at reasonable cost was a major problem at Rottnest for more than 60 years. After World War II most drinking water came from sealed catchment areas and (1961 to 1976) by barge from the mainland. However, when a decision was made in 1975 to build a second settlement at Longreach and Geordie Bays, it was clear that some new water source would have to be found, either

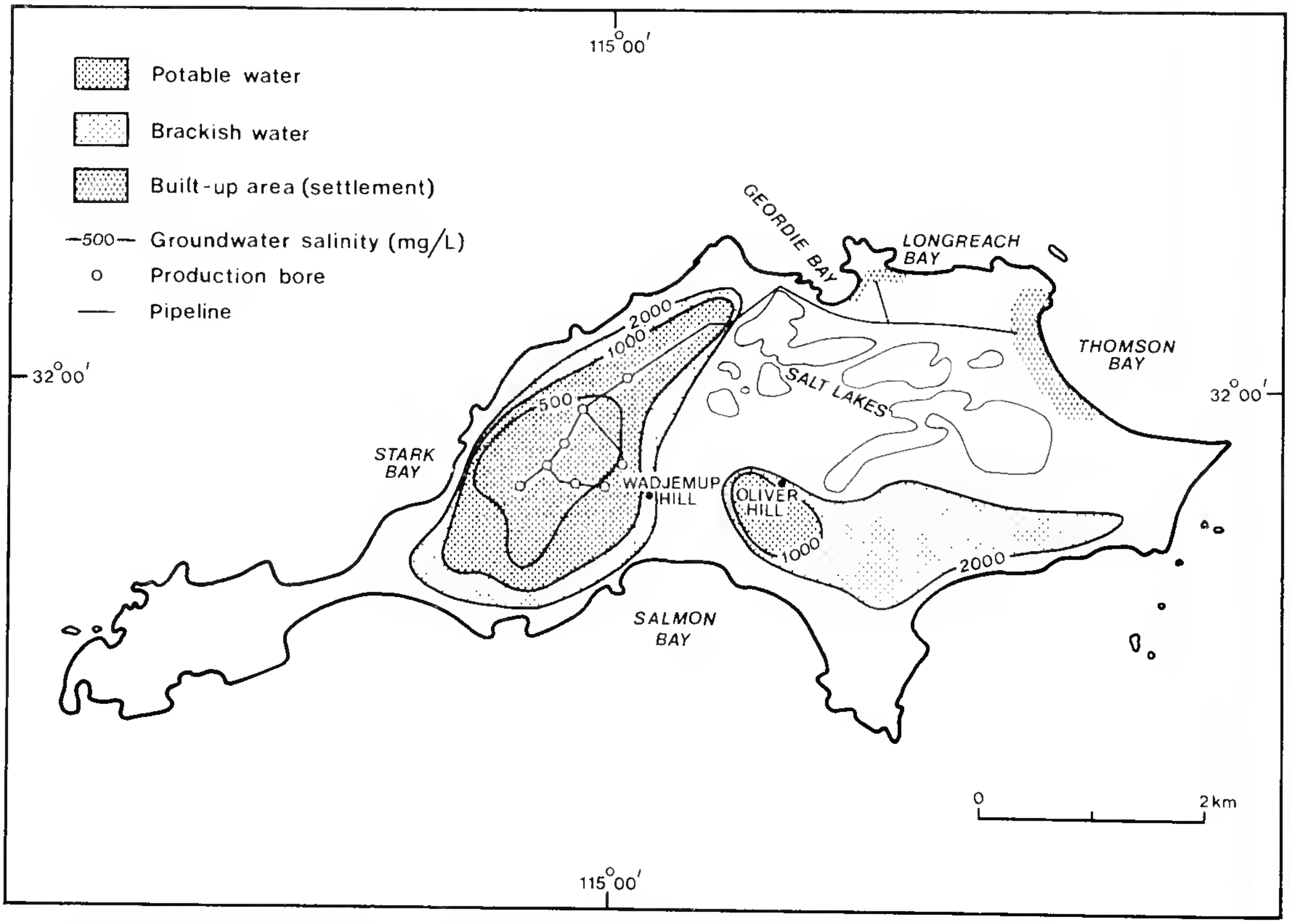

Figure 4.—Map showing the locations of fresh and brackish groundwater lenses below Rottnest Island.

from underground aquifers or by building an undersea pipeline from the mainland.

There had been a long-held belief that secure sources of potable groundwater could not be found at Rottnest. This was because in 1911-12 an artesian bore drilled on the island had recovered nothing but salt water, and shallow bores and wells around the Thomson Bay settlement yielded only brackish to very saline water. The Geological Survey's re-evaluation of the groundwater prospects in 1976 showed that the chances of finding potable artesian water were almost nil, but that the most prospective part of the island for shallow groundwater, situated below the high ground west and south of the salt lakes, had never been tested. It was suggested that these areas could yield significant volumes of domestic-quality groundwater, and that accordingly they should be drilled as soon as possible (Playford 1976). The prediction was proved correct; two lenses of fresh (less than 1 000 mg/L) to brackish (1 000 to 2 000 mg/L) water were defined in these areas (Fig. 4). The area west of Wadjemup Hill contained sufficient reserves of potable water in a lens up to 10 m thick in the Tamala Limestone to be developed for use in the settlements (Playford and Leech 1977). The necessary bores and a pipeline were completed within a few months, and production began in October 1976. Since then exploitation of the groundwater lens has proceeded without major problems, and it is estimated that abstraction in each year has averaged only 9% of the annual recharge from rainfall.

Supplies from this source together with those from existing sealed catchments should be sufficient to meet the essential potable water needs of the island for many years. The other lens, in the Oliver Hill area, contains mainly brackish water, but it has potential for development to improve the second-class water system (for ablution and sanitary purposes), which at present is supplied by saline wells in the settlement areas.

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Salmonella on Rottnest Island: Implications for public health and wildlife management

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Abstract

Salmonella infections of 40 serotypes have been studied in humans, a wild marsupial (the quokka, *Setonix brachyurus*), birds and the environment on Rottnest Island (W. Australia). The vegetation of the island is very disturbed and during the hot and dry summer the quokkas suffer starvation. Up to 100% of the quokkas are infected throughout the summer (median rate of excretion $10^{8.5}$/g of faeces) although there is no evidence of disease. There is widespread environmental contamination and consequent infection of birds and humans. The situation has been studied in detail in relation to public health and wildlife management.

A) Public health aspects

Introduction

The epidemiology of non-typhoidal salmonellosis and the emergence of the disease as an international public health and veterinary problem is inexorably linked with ecological changes affecting the behaviour of humans, domesticated animals and wildlife.

Fauna populations located on small islands close to densely-populated areas are particularly vulnerable to environmental changes, and public health problems may arise when man-induced changes in habitat and behaviour involve wildlife more closely in the epidemiology of human infections.

The discovery in 1972 of a major reservoir of salmonella infections in the quokka population (Iveson and Bradshaw 1973) was a finding of considerable public health and ecological significance. The popularity of the island as a recreational centre was rapidly increasing, and it was evident that additional bacteriological monitoring procedures covering water supplies, waste disposal facilities, effluents and island fauna, were necessary precautions in order to maintain health standards and minimise risks of infection to the public.

Salmonella infections

Salmonellosis in humans is usually acquired after ingestion of the pathogen in contaminated food or water. Close association with infected patients, carrier animals, contaminated soil or droppings exposes humans more directly to risks of infection. Symptoms of acute gastroenteritis usually commence 18-24 hours after exposure to infection, diarrhoea continues for a few days, but may continue for protracted periods and develop into a lengthy carrier state. Septicaemia, meningitis and other serious clinical manifestations may also occur as rare complications. The first laboratory confirmed human salmonella case traced to Rottnest Island occurred in April 1972 when a 14-month old infant developed symptoms of acute enteritis during an island vacation. *Salmonella javiana*, a serotype which had not previously been isolated from humans in Western Australia, was isolated on two occasions from the child's faeces.

A single isolation of *Salmonella javiana* had been recorded previously from a dugite *(Pseudonaja affinis)* captured on the island. The child became ill after playing in sand surrounding the holiday accommodation, which was copiously littered with quokka *(Setonix brachyurus)* and silver gull *(Larus novaehollandiae)* droppings. Several quokkas were domiciled under the hut and the parents had observed the child playing with fresh quokka droppings which were occasionally transferred from hand to mouth.

Subsequent investigations at the holiday site (Iveson and Bradshaw 1973), revealed that quokkas and their droppings were heavily infected with a wide range of serotypes, including *Salmonella javiana*. The extent of infections in quokkas was remarkable and in these first studies a total of 100 isolations comprising 92 *Salmonella* and 8 *Arizona* serotypes were recorded from 62 (71%) of 87 adult quokkas tested. Multiple infections were common and up to four serotypes were detected in individual quokkas. Since April 1972, a total of 22 laboratory-confirmed salmonella infections in humans has been traced directly to Rottnest Island. Of these, 17 infections have occurred in vacationers and 4 in residents. A further *Salmonella javiana* case occurred in a contact hospitalised on the mainland. To put these data in context : 3 582 isolations were reported on the mainland over the same period.

Water and sewage

Coliforms and occasionally salmonella have been isolated from the water supply usually in the wake of chlorination problems or post-chlorination contamination by wildlife gaining access to tanks. A total of 24 serotypes and 130 salmonella isolations have been recorded from water storage tanks or wells since monitoring was intensified in 1972. The major serotypes comprised *S. adelaide* 16, *S. anatum 12*, S. *chester 10*. S. *javiana 10*. S. *muenchen 26*, *S. newington* 16, *S. wandsbek* 11, and *S. waycross* 8.

The well waters piped to the sink of the Rottnest Biological Research Station kitchen were found, prior to upgrading, to be contaminated with faecal coliforms, *S. adelaide*, *S. waycross*, *S. barhenfeld*, *S. newington* and *S. muenchen*.

Well waters at the old Riding School were also heavily contaminated and multiple serotypes including *S. javiana* were also isolated from sick horses, and poultry supplied with water from the well.

The tapsites and drainage sumps located in the camping area are foci for people, silver gulls, crows, black swans and quokkas. Salmonella contamination is a constant feature of surface waters, soil and droppings around these sites.

Monitoring of sewage from both mains and coastal outfall sites has identified 19 salmonella sertoypes including *S. javiana*, in a total of 114 isolations.

Quokkas

Since May 1972 a total of 4 038 quokkas including a small number of recaptured animals has been examined for salmonella and 1 551 (38%) of these were positive. The major isolation are as follows:— *S. muenchen* 484, *S. newington* 291, *S. adelaide*, 239, *S. wandsbek* 125, *S. oranienburg* 93, *S. chester* 84, *S. orientalis* 79, *S. javiana* 76, *S. waycross* 77, *S. typhimurium* 75, *S. rottnest* 38, *S. bahrenfeld* 36 and *Arizona 26:26:25* 39.

Collection sites in this review of isolations have been broadly grouped in to less-disturbed areas in the central and western parts of the island and also the more disturbed eastern areas where the settlements and major recreation areas are situated. A summary of serotypes and isolation totals is presented in Table 1.

Epidemiology of *Salmonella javiana*

The geographical distribution and published evidence indicating the undoubted virulence of *S. javiana* to humans has been reviewed previously (Iveson and Bradshaw 1973). *Salmonella javiana* was first identified on Java (Edwards and Bruner 1942). The serotype is common in quokkas and droppings throughout the settlement area, but has not been isolated to date from the relatively-undisturbed fauna on the West End area of the Island.

The landing on Rottnest Island of Volkersen on March 9th, 1658, after sailing South from Batavia, provided the first of many opportunities for the

Table 1

Salmonella isolations from quokkas on Rottnest Island 1972–1982 inclusive

Salmonella serotypes	Least-disturbed areas				Disturbed areas			Totals
	West End	Central	South & east	Lake site	Tip site	Golf Course	Settlements	
S. adelaide	19	47	21	14	37	48	53	239
S. alsterdorf				1				1
S. anatum	2	3	4	2	1	6	3	21
S. bahrenfeld	1	29	5				1	36
S. bleadon	6	1						7
S. blukwa	1		1					2
S. bootle	3	1		3	1		1	9
S. bovis-morbificans				1	1	3	2	7
S. bunnik		1						1
S. chester	4	21	5	5	10	27	12	84
S. decatur		4		1		1	2	8
S. derby				1			1	2
S. fremantle	5					2		7
S. give	2							2
S. infantis					2			2
S. javiana		15	7	10	21	12	11	76
S. muenchen	49	213	49	47	50	39	37	484
S. newington	40	130	22	38	25	28	8	291
S. newport						1	3	4
S. orianienburg	5	29		3	33	15	8	93
S. orientalis	1	28	11	9	18	9	3	79
S. orion	2	11	4		3	1	5	26
S. potsdam				1				1
S. rottnest	9	9	10		3	7		38
S. saint-paul							1	1
S. singapore		1	1				1	3
S. typhimurium	5	18	6	10	16	3	17	75
S. wandsbek	10	50	7	12	21	17	7	125
S. waycross	2	20	2	9	7	19	18	77
S. 48:d:—	1							1
A. 9: 26:21	1	1		1				3
A. 9: 26:31		1						1
A. 9: 29:21	2	1					1	4
A. 16:23:25	3	6				1		10
A. 16:26:25					1			1
A. 20:29:21	1	2				1		4
A. 20:29:25	1	4		1				6
A. 26:23:21		2						2
A. 26:26:25	7	18	3	1	2	2	6	39
A. 28:32:28				1				1
Arizona spp.		4		1	1		8	14
Isolations	182	670	160	171	253	242	209	1 887
Serotypes	25	28	27	21	24	20	30	40
Quokkas	313	912	290	271	674	699	879	4 038
Quokkas +ve	140	511	141	130	234	203	192	1 551
% +ve	45%	56%	49%	48%	35%	29%	22%	38%

unnatural introduction of serotypes from other countries and continents and also a possible source of entry for *S. javiana*, which is absent from terrestrial wildlife and introduced livestock on the W.A. mainland. The exotic strain hypothesis for *S. javiana* is supported by the tracing of the origin of all human *S. javiana* cases occurring in Western Australia either to Rottnest Island or South-East Asia including Bali and Java Islands. The prevalence of *S. javiana* and *S. typhimurium* phage 202 in quokkas and humans on Rottnest Island and their absence from foodchains on the mainland, have led to routine precautionary quarantine procedures, for all quokkas and other fauna removed from the island (Iveson and Bradshaw 1977).

Reptiles and frogs

Previous studies in Western Australia (Iveson, Bamford and Mackay-Scollay 1969; Iveson 1971, 1977), have established that reptiles throughout Western Australia are natural carriers of numerous salmonella serotypes. Furthermore reptiles examined from the disturbed Rottnest and Carnac Island habitats carry many indigenous infections as well as exotic serotypes common to the introduced urban and agricultural ecosystems on the mainland. The predominance of *S. derby* for example in king skinks (*Egernia kingii*), tiger snakes (*Notechis scutatus*) sea lions (*Neophoca cinerea*) and silver gulls (*Larus novaehollandiae*) on Carnac Island, which is exposed directly through seagull vectors to *S. derby* and other exotic strains in mainland abattoir and sewage effluents, is a good example of exotic infections being transmitted to wildlife as a result of human disturbance (Iveson 1979). A total of 30 salmonella serotypes and 102 isolations have been recorded from reptiles examined on Rottnest Island. Infection rates have averaged 66%, and in one lizard (*Tiliqua rugosa*) 9 serotypes were detected during multiple sampling. Salmonella have been isolated from reptiles frequenting picnic areas, campsites, army barracks, sewerage facilities, water catchment areas and

Table 2

Salmonella isolations from reptiles, birds and domestic animals on Rottnest Island 1972 1982 (inclusive)
(Figures in brackets are isolations from bird droppings)

Salmonella serotypes	Lizards	Snakes	Birds	Domestic animals	Totals
S. adelaide	5	....	1 (8)	22	36
S. anatum	.	....	.... (3)	17	20
S. alsterdorf	4	....	....	....	4
S. bahrenfeld	2	1	....	....	3
S. blukwa	3	..	....	....	3
S. bootle	3	...	....	....	3
S. bovis-morbificans	....	....	.... (1)	....	1
S. bunnik	5	2	....	....	7
S. chester	5	.	1 (2)	15	23
S. decatur	2	..	1	1	4
S. derby	...	....	1	....	1
S. give	1	. .	....	....	1
S. havana	. .	....	1	....	1
S. houten	....	2	....	1	3
S. javiana	....	1	.. (2)	15	18
S. muenchen	3	3	1 (8)	12	27
S. newington	4	1	1 (2)	32	40
S. oranienburg	2	...	....	3	5
S. orientalis	3	...	... (1)	8	12
S. orion	2	.	....	2	4
S. rottnest	2	1	.	.	3
S. typhimurium	1	1	2 (6)	8	18
S. wandsbek	5		1 (1)	9	16
S. waycross	2	..	...	10	12
S. 53:d:z42	2	....	..	....	2
A. 16:23:25		6	..	....	6
A. 20:29:25	.	2	..	....	2
A. 26:23:21	.	1	....	. .	1
A. 26:26:25	4	4	... (1)	...	9
A. 28:32:28	1	6	... (1)	. .	8
A. 29:26:28		1	....	....	1
A. 29:29:25	2	2	...	....	4
A. 1, 33:23:21		2	...	....	2
A 26:23·25		2	....	....	2
Isolations	63	38	10 (36)	155	302
Animals	58	18	417	45	538
Animals + ve	36	14	10	40	100

the inside of water storage tanks. Salmonella serotypes and isolation totals from reptiles, birds and domesticated animals are detailed in Table 2. *S. decatur* was isolated from a frog (*Litoria moorei*) sampled in the settlement area.

Birds

Salmonella carrier rates among birds are low, averaging 2.4%. The majority of isolations have been from cloacal swabs or fresh droppings collected from silver gulls, and 8% of 105 gulls examined yielded salmonella comprising 15 serotypes. Isolations were also recorded from mountain duck (*Tadorna tadornoides*), black swans (*Cygnus atratus*), and welcome swallows (*Hirundo neoxena*). No salmonella were detected in wedge-tailed shearwaters (*Puffinus pacificus*), kestrels (*Falco cenchroides*), ospreys (*Pandeon holiaetus*), crested terns (*Sterna bergeii*) or droppings from introduced senegal doves (*Streptopelia senegalensis*), pheasants (*Phasianus colchicus*), and peacocks (*Pavo cristatus*).

Swallows and silver gulls were implicated in water storage contamination problems. Silver gulls were also present in large numbers at open air drinking and eating venues.

Domestic animals

Multiple recurring salmonella infections including *S. javiana* were detected in horses and a donkey used for public hire. It was evident that equines made a significant contribution to contamination problems on the island and were a potential source of infection to the public. Horse dung was also detected in swallow nests inside water storage tanks (Iveson and Bradshaw 1977).

Discussion

The epidemiological studies and on-going monitoring programmes, have revealed both active and latent reservoirs of infection on the island with foci in quokkas, birds, reptiles and domesticated animals. The majority of human cases has been caused by *S. javiana* which is not found on the mainland. Sewage monitoring has also provided evidence of latent human infections.

Significant contamination of water storage facilities, the settlement environment and occasionally waters used for bathing and fishing have been documented.

However, regular maintenance and upgrading of water and sewage facilities have maintained public health standards and reduced high risks of exposure to infection.

Since 1972 a small number of salmonella cases has been traced to contact with infected animals or their droppings, however the total of 22 cases recorded to date represents only 0.6% of the 3 582 cases which have occurred over the corresponding period in the Perth Metropolitan Region. All patients have made an uneventful recovery, however the public health importance of the overall findings emphasises the continuing need for adequate preventative measures including regular bacteriological monitoring of waters, animals and environment particularly at peak summer vacation periods.

Increased public usage of the island facilities, and further increases in levels of interaction between humans and animals will require careful management if problems are to be avoided particularly in settlement areas (Iveson and Bradshaw 1977). Quokkas and scavenging birds will continue to be attracted to these areas as long as access to supplementary food and water is freely available. Furthermore public feeding practices interfere with the natural processes of population regulation and amplifies naturally occurring cycles of infection. Combined public health and wildlife management strategies are essential ingredients in preventing further involvement of wildlife in the epidemiology of human infections.

B) Salmonella in the Rottnest Quokka—a wildlife management problem

Introduction

The first record of a *Salmonella* from a quokka (*Setonix brachyurus*) was of *S. newport* made from the pouch of a captive Rottnest animal (Yadav, Stanley and Waring 1972). However Iveson and Bradshaw (1973) first drew attention to the abundance of enteric infections in Rottnest quokkas.

Recent studies have focused attention on the opportunistic nature of the salmonella and it is now known that a wide range of environmental stresses can convert a latent and harmless infection into an active infection and possibly a disease state. These stresses include food and water deprivation, handling stress, disease and environmental discomfort (Hart 1980). The vast majority of infections are now believed to be non-disease states. This dependence on host-related factors suggests that the salmonella may be useful indicators of such stresses. The Rottnest quokka appeared to provide a convenient case study of this phenomenon, since it is known to suffer a severe seasonal stress (Main, Shield and Waring 1959).

The patterns of infection

The frequency of salmonella infections was found to be markedly seasonal (Hart 1980). In most areas of the island the infection rate (percentage of animals positive by rectal swab) was 0-30% in the winter (June-Oct) and 70-100% in the summer (Nov-May). The change-over between these levels was very abrupt and probably occurred in a matter of a few weeks. In several areas on the island this pattern did not occur. In the settlement (and surrounding areas) and at the tip site the infection rate was always low (0-30%). These patterns were related to the well-being of the animals by using the body weight-based Condition Index of Bakker and Main (1980). In all cases where there was a seasonal cycle of infection rate there was also a marked seasonal cycle of condition. The animals reached maximum weight as late as December, declined slowly until about February and then showed a dramatic decline until May. During the winter they showed a slow recovery which accelerated in the spring. Conversely in the areas where there was no change in infection rate there was no change in condition and the animals remained in good condition in all seasons.

Relationship between infections and nutrition

Although it was clear that the salmonella infections and poor condition were related in that both or neither occurred in any one population it was also clear that poor condition was not the cause of the infections since the infections precede this in time. The relationship of the infections to nutrition was examined firstly by quantitative study of the timing and course of infections over the summer period and secondly by feeding animals in the field (Hart 1980).

Using animals sacrificed over the critical spring to summer period it was found that up to 10^3 salmonella cells per ml of stomach fluid could be recovered as early as the end of October. Furthermore there was a significant correlation between the numbers of *Salmonella* cells in the stomach and in the faeces. By the end of summer virtually all animals were excreting Salmonella at a rate of greater than 10^3 *Salmonella* cells per gram of faeces. In the settlement area the rate of faecal excretion of salmonella showed only a small rise in late April.

In the second study a population was divided in two and one half received a complete food and water supplement. This was done in the field so that the animals were otherwise exposed to all normal stresses, and the feeding commenced just before the critical spring-summer change. The animals which received the food supplement did not show the abrupt proliferation of salmonella infections until immediately after the food was withdrawn five weeks later. After another three weeks the test and control groups were indistinguishable. Again the animals did not reach their maximum weight until as late as December, **after** the experiment had ended.

In a further analysis of the quantitative results (Hart 1980) it was found that there was a significant correlation between the incidence of infections and the weather. The median rate of faecal excretion began to rise as soon as the rains ended (the temperature is of course strongly and inversely correlated with rainfall) and fell abruptly with the return of the rains in autumn.

Salmonella in the Rottnest environment

Hart, Iveson and Bradshaw (unpub.) studied the behaviour of some 40 serotypes of *Salmonella* which occur on Rottnest. By examining the spatial and temporal distribution of 1 754 isolations from 3 751 quokkas it was found that there were significant variations in the distribution of some serotypes in some locations. In examining two of these locations, evidence was found that the variations were due to amplification of a serotype in another host. These were *S. javiana* in the welcome swallow *(Hirundo neoxena)* and *S. typhimurium* phage-type 202 in the silver gull *(Larus novaehollandiae,)* both in the settlement area.

A major object of this study was to document differences between the group of native serotypes and the introduced serotypes described by Iveson (1977). It was found that these groups did not behave coherently and each serotype had to be examined separately. The only apparent distinction was that relatively more of the rare native serotypes occurred on West End (the most isolated segment of the island) and relatively more of the rare introduced serotypes in the settlement. These differences show the failure of many introduced serotypes to invade West End, and document the presence in the settlement of recently-arrived serotypes which have not yet dispersed. There is thus strong evidence that new serotypes are still becoming established on Rottnest.

An important finding of this study was that the range of serotypes present on Rottnest showed marked differences to that of the adjacent mainland, and there appears to be little interchange.

Discussion

Hart (1980) suggested that the *Salmonella* are able to proliferate in the Rottnest quokka because the normally hostile stomach contents are altered as the diet of the animals changes abruptly at the end and beginning of the winter rains. The most likely mechanism for this is a drop in volatile fatty acid production which would raise the pH. In this way the *Salmonella* infections precede the effects of the subsequent starvation. Although infections are established in this way there is no necessary consequence of a disease state. The levels of *Salmonella* excretion reported by Hart (1980) are too low to represent disease. This supports the finding of Shield (1959) that disease does not appear to be a factor in the summer decline of the animals. The animals in the settlement and tip site are able to avoid this situation by receiving a food supplement in the form of hand-outs and garbage.

Despite some three decades of work there is still no general agreement on the precise nature of the summer decline of the Rottnest quokka (reviewed by Miller & Bradshaw 1979) however the *Salmonella* appear to be an indicator of the presence of environmental stress, and more particularly of the precise beginning and end of the period over which the stress operates. The present difficulties of the Rottnest quokka are believed to be due to recent human-related changes in the vegetation (mostly by burning and overgrazing) which have altered the vegetation from a dense woodland and shrubland to an open steppe dominated by species less palatable to the quokka and annual weeds (Storr 1963, Pen and Green, this volume). However the results of a study of quokkas living on Bald Island (Hart 1980) suggest that the Rottnest quokka may already have suffered a severe summer starvation before European settlement. Before this time only native serotypes could have been involved in the annual proliferation.

At present the annual proliferation of *Salmonella* in the Rottnest quokka represents a significant reservoir of infection and this situation results from the degraded environment afforded the Rottnest quokka. The annual proliferation will go on until seasonal starvation is removed as the dominant feature of the biology of the Rottnest quokka. The feeding experiment described by Hart (1980) suggests that this could be achieved, by restoring the vegetation and controlling the population so that suitable forage was available. A more difficult problem is the transfer of serotypes between Rottnest and the mainland. New introduced serotypes on Rottnest can only exacerbate the problems, while the transfer of *S. javiana* to the mainland could have serious consequences (see Iveson and Bradshaw 1973).

Hart (1980) has discussed the more general application of *Salmonella* infections as indicators of environmental stress on wild animals. He has proposed that while any large concentration of *salmonella* suggests such stress, the presence of introduced serotypes indicates either heavy input from another source (as has been described by Iveson 1979, for Carnac Island by silver gulls) or that the host has been rendered susceptible to infection and has amplified a small input (as has happened on Rottnest Island and particularly Bald Island). These ideas may find application in the management of natural ecosystems.

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Botanical exploration and vegetational changes on Rottnest Island

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Abstract

The former, extensive cover of low closed forest and closed scrub, characterised by *Callitris preissii*, *Melaleuca lanceolata* and species of *Acacia*, has declined in area from perhaps 1 000 ha in 1919 to less than 150 ha today, and has largely been replaced by low shrubland dominated by *Acanthocarpus preissii*. These changes, which have not been quantitatively documented, appear to be related to wood-cutting, fire, coastal erosion and grazing by the native marsupial *Setonix brachyurus* (quokka). There is fossil evidence of the prehistoric occurrence of *Eucalyptus gomphocephala* (tuart) woodland.

Brief history of botanical investigation

The first opportunity for a scientific examination of the vegetation of Rottnest Island came in the early nineteenth century when, on 14 January 1822, a party including the botanist Allan Cunningham, from the brig Bathurst under the command of Lieut. P. P. King, landed at Thomson Bay. Cunningham made a detailed description of the flora he saw but, as he visited only the Thomson Bay area for a few hours, his observations on abundance need to be interpreted carefully (Marchant 1977).

In 1838 Ludwig Preiss, a Prussian botanist, arrived in Western Australia to collect natural history specimens apparently with the financial support of the Russian and Prussian governments. His extensive biological collections, made over a period of about three years, from December 1838, included 58 plant species belonging to 36 families, collected from Rottnest Island; these are recorded in Lehmann's "Plantae Preissianae" (Hamburg, 1844-1848).

After Preiss's visit a period of more than a hundred years passed before any further scientific work on the vegetation of Rottnest Island was undertaken. Somerville (1949) touched only briefly on the natural vegetation of the island, being mainly concerned with the planting of exotic species. In 1952 W. M. McArthur, in studying the plant ecology of the coastal islands near Fremantle, examined the plant communities of Rottnest Island in some detail (McArthur 1957.) In dividing the vegetation into four associations and three communities, McArthur's was the first attempt at a formal vegetation classification: it was to stand for some 17 years, later classifications differing from it mainly in the further subdivision of the littoral and succulent communities. McArthur's classification is compared with others in Table 1. He included in his publication a list of 75 native and 21 introduced plant species.

An extensive fire on the island, in February 1955, provided the stimulus for the first detailed botanical study of Rottnest Island. A study of the flora and vegetation of the island was carried out in 1955 and 1956 by R. D. Royce and J. W. Green of the State Herbarium. They made extensive plant collections, monitored post-fire regeneration, set up sampling plots and transects, and compiled a vegetation map. After a time they were joined by G. M. Storr whose interest in the vegetation began in relation to the diet of the quokka, and D. M. Churchill who had discovered plant microfossils and macrofossils in the lake sediments.

A simplified description of the vegetation was given by Storr, Green and Churchill (1959) who made no attempt at a formal classification but recognized five elements in the present vegetation: supralittoral, coastal dune, interdunal, limestone ridge and swamp including salt-lake vegetation. An important finding having a bearing on vegetation changes was reported in that paper: fossil evidence was found indicating the occurrence on Rottnest Island, in Pleistocene times, of a woodland community of *Eucalyptus gomphocephala* (tuart), similar in species composition to present occurrences on the mainland. An annotated checklist of plant species was published by Storr (1962), consisting of 118 native and 62 introduced plant species. Storr's thesis (Storr 1957) also led to a further article dealing with vegetation change (Storr 1963). Besides the above publications, some information from the 1955-1956 study has been preserved in the archives of the Western Australian Herbarium, including a species list, a general account of the vegetation communities and a map showing the distribution of the associations, consociations and other communities then recognised.

In 1974 B. J. White and R. J. Edmiston of the Western Australian Forests Department reported an investigation aimed at prescribing a management programme for the maintenance and rehabilitation of the island's vegetation. Their report contained a classification of the vegetation into 9 associations and two communities, with descriptive notes on each, while in an appendix was a map taken from 1941 aerial photographs showing the distribution of low closed and low open forest (*Melaleuca lanceolata* and *Acacia rostellifera*), which they estimated as covering 400 ha.

Table 1

Plant Communities of Rottnest Island as recognized in published and unpublished reports

Name of Association (a), Consociation (ca), Community (c) or Vegetation (v)	Royce & Green (1956, unpub.)	McArthur (1957)	White & Edmiston (1974, unpub.)	O Connor *et al.* (1977)
Olearia—Westringia (= Littoral or mobile dune)	a	v	a	c
Westringia—Acacia littorea—Scaevola (= Stable dune low dense heath)	a		a	c
Acanthocarpus—Stipa flavescens	a	c	a	c
Stipa flavescens	ca		.	....
Acacia littorea	a	a	a	c
Acacia rostellifera	a	a	a	c
Melaleuca lanceolata	a	a	a	c
Melaleuca lanceolata—Acacia rostellifera			a	
Templetonia retusa	ca	a	a	c
Templetonia—Pittosporum	c			
Pittosporum phillyraeoides	ca			
Sclerostegia arbuscula (= Halophytic, salt marsh)	a	c	c	c
Carpobrotus aequilaterus—Mesembryanthum crystallinum (= Mixed succulent mat)	a		a	c
Nitraria billardieri			a	c
Lavatera plebeia				c
Gahnia trifida	a			
Callitris preissii	a			

More recently O'Connor *et al.* (1977) studied the vegetation and flora as part of a National Estate survey of Rottnest Island. Here the methods included quadrats, estimates of area and cover for each plant community, and the compilation of an inventory of both observed and previously-known plant species. Their species list, though based largely on Storr (1962), contained a number of new records, bringing the known flora for the island to 122 native and 57 introduced species.

Vegetation change

Early observations

Seven thousand years ago Rottnest Island probably supported a *Eucalyptus gomphocephala* woodland (Churchill 1959). This had become extinct by the time the first written accounts of the vegetation were made in the mid-seventeenth century. The first, by Volkersen who visited the island in 1658 (Appleyard and Manford 1979), noted the presence of numerous woods and thickets, as did Freyeinet in 1801 and Cunningham in 1822. The latter author was particularly struck by *Callitris*, which he said "is found abundantly over the island" and, later, was "covering the surface of the island" to the point of monotony, except where "occasionally relieved by . . . melaleuca . . . and the more elegant pittosporum". Though these accounts have sometimes been taken to indicate a dense cover of trees or tall shrubs over the whole island, this was not the impression given by Wilson (1835), referred to by Marchant and Abbott (1981), who spoke about hummocks and sandhills devoid of vegetation. Wilson was probably describing the western part of the island, whereas the earlier visitors had probably seen only the environs of the anchorage in the north-east.

Settlement to 1930

Permanent settlement began on Rottnest in 1838 with the establishment of a prison. In order for the community to become self-supporting, forest was cleared to make way for farmland, roads and building sites. In addition cypress pine was felled to provide timber for construction purposes. Pigs, sheep, horses and cattle were introduced. All this activity afforded an excellent opportunity for many exotic plant species to become established on the island. The spread of these palatable plants may have caused quokka populations to increase, by increasing the island's food reserves, particularly in winter.

A dramatic change in the vegetation then began with the advent of a greater frequency of fire caused by man. Aboriginal prisoners were allowed to hunt quokkas for food; to make this easier they used their traditional method of firing the vegetation. Similarly European settlers, when hunting quokkas, deliberately lit fires to disclose their prey (Somerville 1949). Accidental fires further increased fire frequency. Both *Callitris preissii* and *Melaleuca lanceolata* are relatively fire-sensitive, regenerating after fire from seed only (Storr 1963).

It is easy to understand how a devastating fire, followed by others at close intervals, could have destroyed seedlings and depleted the soil seed bank, leading to the elimination of fire-sensitive species over much of the island. *Acacia rostellifera*, on the other hand, which is relatively fire-tolerant, owing to its ability to produce numerous suckers after burning (Marchant 1977), formed dense thickets in place of *Callitris* and *Melaleuca*. Though *Acacia rostellifera* is a very palatable plant, and thus vulnerable to quokka damage, continued hunting is thought to have kept the quokka population too low to prevent regeneration of *Acacia* (White and Edmiston 1974).

By the early 1900s *Acacia* scrub was the predominant plant community in the east of Rottnest Island, having replaced *Callitris preissii* and *Melaleuca lanceolata* in all but a few areas. R. E. Weir, a stock inspector, quoted by Storr (1963), estimated that in 1919 *Acacia* scrub covered two thirds of the island. Similarly, Glauert (1929) noted that: "much of the island is clothed with dense wattle scrub tangled with creepers and undergrowth".

1930s to the present

The success of *Acacia rostellifera* on Rottnest Island was short-lived. By the late 1930s the almost-continuous scrub began to fragment into scattered thickets. Storr (1963) believed this to be caused by the interaction of fire and quokka grazing. In the late 1920s quokkas were protected, leading in the early 1930s to a sudden increase in their numbers. No longer was *Acacia rostellifera* regeneration to proceed relatively unhampered. The species had now to contend with heavy quokka grazing, which probably resulted in the observed sharp decline in the distribution of *Acacia* scrub over the coming decades. An estimate of the rate of decline of *Acacia rostellifera* between 1919 and 1941 may be made by assuming that Weir's estimate of two thirds *Acacia* scrub is equivalent to some 1 000 ha: by 1941, judging from contemporary air photos, the total area of forest or scrub of any kind was only 400 ha (White and Edmiston 1974, see also Figure 1). This represents a decline of some 600 ha over 22 years or about 27 ha per annum.

In February 1955, fire devastated about 730 ha in the central western part of the island (Storr 1963). To investigate the effect of quokka grazing on regeneration, exclosures were erected and they and neighbouring areas were visited frequently throughout 1955 and 1956. The exercise confirmed a decline in the palatable *Acacia rostellifera* community and a corresponding increase in the less palatable *Acanthocarpus-Stipa* low dense heath in areas prone to heavy quokka grazing (Storr 1957).

The extent of forest and scrub communities was about 320 ha in 1956, ascertained from an unpublished vegetation map compiled in 1956 and preserved in the Western Australian Herbarium (redrawn in simplified form in Figure 2). These communities have continued to become reduced, largely in favour of *Acanthocarpus-Stipa* low dense heath. Since 1956 the area of *Melaleuca lanceolata* has been greatly reduced, mostly in the central areas of the island; today it is mainly restricted to the eastern end, Parker Point, and areas surrounding the lakes. Furthermore there is evidence that *Acacia rostellifera* thickets are not long-lived on Rottnest Island (White and Edmiston 1974). A stand located 60 metres south of Lake Vincent, which was seen in 1976 aerial photographs to have had a full canopy, was observed by one of us (L.J.P.) to be almost entirely dead in October 1982.

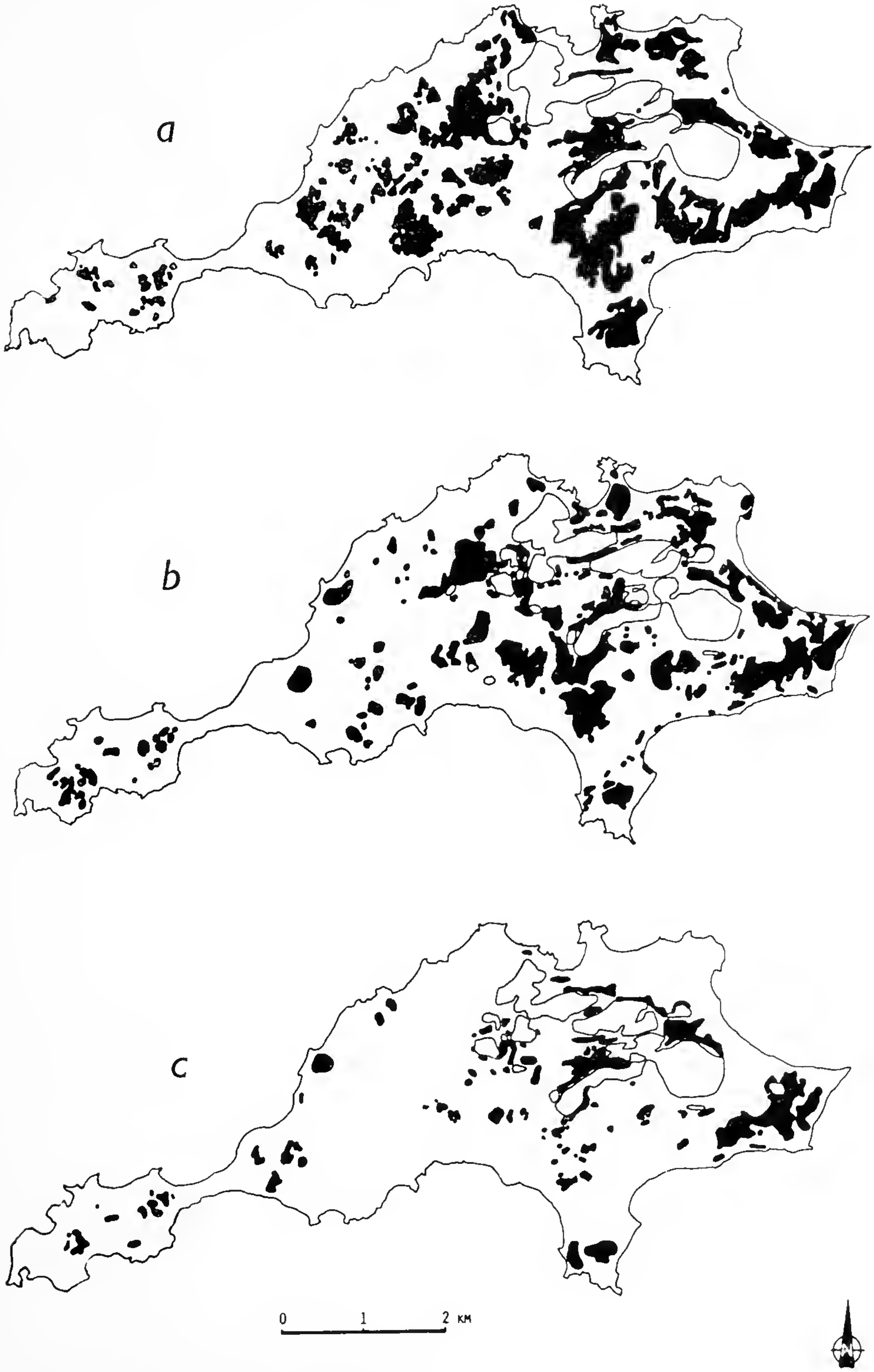

Figure 1.—Forest and scrub vegetation cover of Rottnest Island.

a. Interpretation of 1941 aerial photographs, after White and Edmiston (1974). Shading represents Low Open Forest and Low Closed Forest or Scrub communities, both comprising chiefly *Acacia rostellifera* or *Melaleuca lanceolata* as dominants.

b. From an unpublished map prepared by R. D. Royce and J. W. Green in 1956, based on 1955 aerial photographs and ground survey. Shading represents three associations: *Acacia rostellifera, Melaleuca lanceolata* and *Pittosporum —Templetonia.*

c. Based on current interpretation of 1978 aerial photographs and 1982 ground survey. Shading represents the same communities as in Figure 1b.

By 1974 only 130 ha of forest and scrub remained (White and Edmiston 1974). A slightly smaller area remains today, forming mostly scattered relic stands (Figure 3) of the communities which once predominated over much of the island. On the other hand, there is evidence of a limited recovery of *Acacia rostellifera* over the last 30 years, south of Stark Bay, northeast of Wilson Bay and within protective exclosures.

Coastal erosion was recognised by Storr (1965) and White and Edmiston (1974) as a factor inducing vegetation change. In the short term, erosion favours some species associated with the mobile dune environments, and this can lead to an increasingly larger area of the island being exposed to salt spray. Several large blowouts occur on Rottnest Island, the largest of which, Barnett's Gully, has increased substantially in size over the decades (White and Edmiston 1974) while others have fluctuated only slightly.

Despite the fragmentary nature of early accounts, and the qualitative nature of many observations since, a number of clear trends are evident, mostly related to the severe effects of man's interference with the island ecology:

1. Large tree and shrub species, such as *Callitris*, *Melaleuca* and *Acacia*, are declining and mostly failing to regenerate.
2. Some communities dominated by large or small shrubs seem capable of natural regeneration, though they are not vigorously expanding. These include *Templetonia*, *Pittosporum*, *Spyridium* and *Leucopogon*. Given reasonable protection, such plants may be encouraged to extend their areas.
3. *Acanthocarpus*, *Olearia*, *Westringia* and *Trachyandra* are highly successful colonisers of niches left by the destruction of sensitive species.

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Marine biological studies on Rottnest Island

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Abstract

Recent studies on marine invertebrates at Rottnest Island have revealed four main features about animals living on the rock platforms. First, large components of the fauna and patterns of reproduction of individual species are characteristic of more tropical conditions. Secondly, quantitative analyses of observations on natural history and experimental manipulations involving different behaviours, morphologies or microhabitats disclosed the significance of particular traits. Thirdly, biological interactions were powerful determinants of the use of food and space among a group of grazers. Finally, analyses of the genetical structure of populations demonstrated responses to environmental heterogeneities and a previously unappreciated prevalence of asexual modes of reproduction.

Introduction

The Rottnest Island Biological Research Station in the last three decades has been the base for studies on the invertebrate animals living on the rock platforms which surround the island. These studies follow four themes described in the following sections. In combination, these four approaches have revealed a great deal, not only about the benthic marine invertebrates on Rottnest Island, but also about general ecological processes influencing and involving benthic marine animals.

Descriptive biology

The most extensive work has been on individual species of molluscs: basic patterns of growth and/or reproduction are established for the gastropods *Dicathais orbita* (Phillips 1969; Phillips and Campbell 1968, 1970; Phillips *et al.* 1973), *Turbo intercostalis* and *T. torquata* (Joll 1975, 1980, pers comm), and for the sea urchin *Echinometra mathaei* (Pearse and Phillips 1968; Ebert 1982). On the other hand, descriptions of particular faunas are available for isopods on rocky islets (Bunn and Green 1983), for decapod crustaceans inhabiting the coral *Pocillopora damicornis* (Black and Prince 1983) and for fishes (Hutchins 1979).

A striking pattern emerges from these studies: large components of the fauna, and patterns of timing reproduction of individual species are characteristic of the tropics, despite the temperate latitude of Rottnest Island. For example, there are 90 species of tropical fish. As well, local diversity of animals living in *Pocillopora damicornis*, as measured by number of species per unit volume of coral, is as high at Rottnest Island as at some tropical sites. Furthermore, both species of *Turbo* and *Echinometra mathaei* all have continuous rather than seasonal reproduction.

Analyses of ecological processes

These studies involve pairs of interacting species (Black 1978; Chalmer 1974*, Clarke 1975*), analyses of intraspecific morphological differences (Black, *et al.* 1982; Bowen *et al.* 1982*), and analysis of nutrient fluxes (Vink 1982*).

The multi-armed starfish, *Coscinasterias calamaria*, is a generalist predator which feeds on the most abundant species of prey available. When prey density is low, grouped starfish consume a lower number and proportion of prey than when density of prey is high. This behaviour would tend to stabilise the abundance of prey (Clarke 1975*).

The predatory gastropod, *Dicathais orbita* is a major agent of mortality for the limpet, *Patelloida alticostata*. Some 41% of the shells of recently-dead limpets were drilled by this predator. Its tactics, as revealed by the location of the drill holes, are to drill into the gonad and digestive gland, and into segments of the shell where the aperture of the predator's shell fits evenly onto the limpet's shell. This complicated handling of prey provides access to energy-rich tissues and probably prevents dislodgement of the predator (Black 1978).

The ovoviviparous cap limpet, *Hipponix conicus*, lives on other gastropods such as *Turbo intercostalis* and *Campanile symbolicum*. The positioning of the limpet relative to the aperture of the host's shell is critical because the cap limpet consumes the faeces and mucus of the host. Chalmer's (1974*) ingenious experiments demonstrate that limpets adjacent to the aperture of living hosts grow faster and produce more offspring than limpets far from the aperture or on shells without living hosts.

The sea urchin, *Echinometra mathaei*, displays variation in the relative size of components of its skeleton. Black *et al.* (1982) discovered that the size of the food-gathering apparatus, Aristotle's lantern, relative to the diameter of the test, differed between sites with apparently different amounts of food, and among locations with different densities of urchins. These differences suggest that relative or absolute shortages of food are associated with relatively larger Aristotle's lanterns. Experiments by Bowen *et al.* (1982*), clearly showed the adaptive significance of relatively larger lanterns, because these animals consumed more food than urchins with relatively smaller lanterns.

Finally, in a more general approach to ecosystems, Vink (1982*) found that for benthic marine animals the universal application of the Redfield planktonic composition ratio (106 C: 16 N: 1 P) used in the estimation of nutrient fluxes and production, is probably in error, because her analysis of simultaneous CO_2 respiration and excretion of phosphorus gave a C : P ratio of 300 : 1, intermediate between the compositional ratios of plankton and benthic plants.

Distribution and abundance on a steep intertidal gradient

As anticipated by Hodgkin (1960), an extensive series of studies has attempted to discover the causal factors responsible for the observed patterns of zonation of animals on Rottnest Island shores. The emphasis has been on a group of grazing animals living on the 2 metre-high vertical rock walls which form the landward termination of the horizontal rock platforms and which experience steep gradients in both physical and biological conditions (Black *et al.* 1979). The distribution of each of the 11 species overlaps with several others, so there is potential for inter- as well as intraspecific interactions.

Although tolerances to physical conditions on the steep intertidal gradient undoubtedly mould the overall pattern of distribution, biological interactions within and among the species influence the details of this pattern. All three of the mobile grazing gastropods, *Littorina unifasciata*, *L. australis*, and *Nerita atramentosa*, responded to experimental increases in the density of conspecifics by occupying larger vertical ranges on the shore (Prideau 1976*) This feature too was evident among natural differences in the abundances of conspecifics for *Littorina australis*, *Nerita atramentosa*, *Collisella onychitis*, *Clavarizona hirtosa*, and *Patelloida alticostata* (Ayre *et al.* 1977*). Intraspecific interactions apparently determine the vertical range of distribution of these animals.

Interspecific interactions also affect the patterns of distribution. A summary of results of comparative analyses and manipulative experiments is that *Nerita atramentosa* restricts the vertical extent of distribution of *Littorina australis* (Prideaux 1976*), *Collisella onychitis*, and *Patelloida alticostata* (Ayre *et. al.* 1977*), and *Collisella onychitis* reduces the abundance of *Siphonaria kurracheensis* at mid-shore (Black 1979).

The mechanisms of these interactions among the sedentary, adult stages of these species revolve around both behavioural and morphological features. All the sedentary gastropods occupy home scars and return unfailingly to these scars after excursions for grazing (Ayre *et al.* 1977*; Threlfall 1977*; Black 1977; Austin *et al.* 1979*). This behaviour

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* Indicates unpublished Honours thesis, Department of Zoology, University of Western Australia.

means that individuals can interact only with their most immediate neighbours. In fact, detailed observations of movements of these animals disclosed a very low rate of contacts among neighbours, even though the areas grazed did overlap. The mechanisms of interspecific competition are probably by exploitation rather than by interference, since the items of diet overlap (Turner 1978*), growth rate decreases with increased density of conspecifics (Black 1977, Turner 1978*), and the relationship between average size and density is inverse (Stoddart 1975*, Black 1977).

The basis for the exploitation competition appears to be the structure of the radula. There is great variability in the length of the longest active cusp which scrapes against the rock to remove algae, and these differences do not follow a pattern consistent with the average body size of the species. However, there is a significant positive relationship between the length of the radular teeth and the rate of excretion of inorganic material in the faeces (Ayre *et al.* 1977*, Black, Lymbery and Hill unpublished). The interpretation is that the larger teeth allow grazing not only of the superficial algae but also of the top layer of rock surface, which is impregnated with filaments of algae. For the pairs of species for which the outcome of competitive interactions is known, the species with the larger teeth and greater rate of producion of inorganic material in faeces is the superior competitor. This analysis therefore provides predictions for the outcomes of competitive interactions between pairs of these species not yet experimentally examined, and suggests an approach for analysing interactions among other grazers.

In combination, these studies on distribution and abundance of grazers on the vertical rocky shore demonstrate that biological interactions are powerful organizers of the use of the resources of food and space among members of this guild. Although these interactions involving the sedentary animals seem to have predictable outcomes, a great deal of unpredictability is imposed upon these grazers through extreme variability in recruitment to these populations. Records of recruitment of four species of limpets over 9 seasons show average abundances differing by 2 orders of magnitude from year to year, and even complete failure of recruitment in some years at some localities (Black unpublished). To some extent particular localities are consistently good for recruits in each year, explaining some of the between-habitat differences in the abundances of adults. These data on recruitment emphasize that the essential events of recruitment in these sedentary marine animals are extremely sporadic or patchy in time and space.

Population genetics

Genetic studies of marine animals at Rottnest can be viewed in two contexts. First, the heterogeneity of the marine littoral environment provides a useful situation for the study of localized genetic differentiation. Secondly, population genetics can reveal much about the breeding structure of populations. Electrophoresis of enzymes has allowed detection of genetic polymorphisms in nearly all species examined, allowing a genetic approach to a variety of problems.

The first such study at Rottnest was a comparison of the blue and orange "morphs" of the rock crab *Leptograpsus variegatus*. Earlier work had shown ecological differences between the blue and orange *Leptograpsus* (Shield 1959). Mahon's (1974) electrophoretic study demonstrated the absence of gene flow between these colour forms, indicating that they are in fact separate species.

More recent, and continuing, genetic studies at Rottnest are focussed on the genetic structure of local populations of several species, considering the effects of localized selection and the nature of recruitment. Studies of enzyme polymorphisms indicate that the source of recruits can have a large effect on the genetic mosaicism of local populations.

The vertical rocky shores at Rottnest are dominated by limpets, and two species of the pumonate genus *Siphonaria* have been studied. These limpets produce planktonic larvae which develop into sedentary adults. This common pattern among marine invertebrates poses a conflict between genetic mixing due to planktonic dispersal and genetic differentiation due to localized selection after settlement. Extending Black's (1979) demonstration of bimodal vertical distributions of *Siphonaria kurracheensis*, a study of 5 polymorphic enzymes revealed no differences between high-shore and low-shore populations (Black and Johnson 1981). Contrasting with this absence of a detectable genetic response to the steep environmental gradients in the intertidal zone, there were genetic differences among sites and between adults and recruits. A similar result was obtained for a second, undescribed, species of *Siphonaria*: depending upon the genetic locus examined, genetic differences were found among sites along 50 m of shore, between high and low portions of the shore within sites, between adults and recruits, and between recruits in successive years (Johnson and Black 1982).

Transplant experiments are under-way to determine if these genetic differences are due to localized selective mortality. Such selection is unlikely to provide a simple explanation, however, because the genetic heterogeneity does not follow a simple, consistent pattern, but forms a shifting, ephemeral genetic patchiness. This patchiness results at least in part from temporal variation in recruitment. Over a 2-year period, monthly samples of recruits of the undescribed species of *Siphonaria* were collected from 11 sites around the island (Johnson and Black unpublished). Genetic differences were found among recruits settling at different times. Combined with temporal variation in the distribution and abundance of recruits, this genetic variation gives rise to genetic differences among sites.

These studies of *Siphonaria* indicate that planktonic dispersal, although causing uniformity on a large scale, can give rise to fine-scale genetic patchiness. Large-scale uniformity for the undescribed species of *Siphonaria* has been documented by a study of geographic variation: variation among sites at Rottnest is nearly as great as that among sites from Kalbarri, Western Australia to Port Robe, South Australia. Thus, temporal variation in recruits at Rottnest is not due to differences in source populations. Instead, the variation is correlated with environmental conditions at the time of settlement, implying selective mortality. Since genetic differentiation among areas is often used to delineate stocks of commercial importance, these results for *Siphonaria* are important in demonstrating that the source of such differentiation need not be isolation of populations.

In contrast with the sexually-reproducing *Siphonaria* species, there are many species which utilize asexual reproduction. Genetic studies at Rottnest have been useful in both the detection of asexual reproduction and the assessment of its effects on local populations.

The cherry anemone, *Actinia tenebrosa*, broods young, which subsequently settle near their brood parents. Electrophoretic studies have showed that the young are genetically identical to their brood parents, even when they are heterozygous (Black and Johnson 1979). This absence of segregation indicates asexual reproduction. Similarly, the brooded planula larvae of the coral, *Pocillopora damicornis*, are produced asexually (Stoddart unpublished). This is a startling result, as the production of planulae has always been assumed to be through sexual means.

The effects of this clonal reproduction on the genetic structure of these populations are striking. For both *Actinia tenebrosa* (Black and Johnson 1979, Ayre 1983) and *Pocillopora damicornis* (Stoddart unpublished), there are 1) large departures from Hardy-Weinberg genotypic frequencies, 2) low local diversities of genotypes, as a few clones predominate, and 3) large genetic differences between populations less than 100 m apart. A similar pattern was found for the starfish *Coscinasterias calamaria*, which reproduces by fission (Threlfall 1977*). For *Actinia tenebrosa*, Ayre (1982, 1983) has shown that fine-scale clustering of genetically-identical individuals is facilitated by interclonal aggression, as clones compete for available space.

Each of these species combines sexual and asexual reproduction, as indicated by histological and population genetic studies. Sexual reproduction is apparently used for long-distance dispersal, and is the source of genetic diversity within sites, whereas asexual reproduction contributes to local recruitment. These contrasting modes of reproduction are of interest in two respects. First, there is the theoretically important question of the significance of sexual reproduction; is genetic diversity of offspring beneficial in the colonization of unknown areas? If so, each clone should be selectively favoured in the areas of its establishment. Transplant experiments with *Actinia tenebrosa* have been established, and preliminary results indicate that clones do differ in life history traits, so that the clonal composition in each area may not be simply the result of a planktonic lottery (Ayre unpublished).

The second context in which modes of reproduction are of interest is in the assessment of the importance of local recruitment. The clonal structure of the populations of *Actinia tenebrosa* and *Pocillopora damicornis* at Rottnest indicates the locally asexually produced recruits account for the maintenance of the populations, and that sexually produced recruits only rarely contribute.

Discussion

The research on benthic marine invertebrates at Rottnest Island can be considered from at least two points of view. The first is the development of our knowledge of the fauna of Rottnest Island, and the physical and biological processes which interact to produce the events and patterns we observe on these seashores. This development has been successful for two reasons. First, the studies have been of conspicuous, relatively large, sedentary or slow-moving animals. This approach allowed detailed and repeated observations on the same individuals as well as complete censuses of the adult populations. The second reason for success is that the studies at Rottnest Island have been quantitative and increasingly addressed to testing specified hypotheses for which particular kinds of information are purposely collected. The second point of view on marine biological studies at Rottnest Island depends on the descriptive background provided by the first, and also on a quantitative, hypothesis-testing approach, but is one of fundamental processes and general ideas in population and community biology, rather than the particular details of animals at Rottnest Island and communities.

In conclusion, or perhaps as a preface to the next phase of marine biological studies on Rottnest Island, there is an emerging pattern of environmental heterogeneity both in the processes involving sedentary adult animals on the shore, which can be studied directly, and in the processes involving the planktonic larval stages of these animals, which can only be studied indirectly. Even if processes both on the shore and in the plankton are deterministic, their interaction may lead to apparent chaos, in which the effect of environmental heterogeneity on the structure of populations and communities seems unpredictable. Predictability will come only from the study of this interation between processes.

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Immunological studies on the quokka

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[This paper is dedicated to the late Harry Waring and our PhD students.]

Abstract

A major advantage of studying marsupial immunology is that the marsupial pouch-young, at birth, are at a much earlier stage of development than eutherian young. Much of the work cited in this review concerns the cellular and humoral responses of marsupials from which the cervical and thoracic thymus glands had been surgically removed shortly after birth. Specific emphasis on the quokkas developed as they are representative of a property unique to the Phalangeroidea—the possession of two sets of thymus glands. A concept of the immunological recovery following total thymectomy is presented and it is concluded that marsupial and eutherian immunology are essentially similar and that the mammalian immune system must have been fully developed prior to marsupial and eutherian divergence.

Introduction

"The immune system is a diffuse organ assigned to monitor the identity of the body. Its basic constituents are lymphocytes and antibody molecules, both of which recognise foreign molecules and one anoher."[1]

After 20 years' study, 40 publications and four doctoral theses, the only general statements I am prepared to make are:

1. marsupial and eutherian immunology are essentially similar in all major aspects; and
2. the mammalian immune system must have been fully developed prior to marsupial and eutherian divergence.

Peripheral to and supporting the generalizations is a large body of data comprising interesting technical and conceptual studies initiated 20 years ago when the discipline of immunology was at an early stage of development. Today we have developed techniques of exquisite specificity and sensitivity that reveal function and activity not possible to visualize when we started in 1963. Rather than disregard the sound observations of the past, it is more useful to recognise imaginative and skilful work as it comes into perspective.

This short review pays tribute to many contributors, particularly the late Harry Waring. As I recall, the initial stimulus came from Sir MacFarlane Burnet when he suggested that "Waring and Stanley do something about that quokka thymus". We did. The first presentation of our quokka immunology research was made in 1966 at an international CIBA Foundation Symposium on the "Thymus—experimental and clinical studies" in honour of Burnet and coinciding with the 50th anniversary of the founding of the Hall Institute of Medical Research (Stanley *et al.* 1966). Reproduced here are the original figures showing the development of the cervical and thoracic thymus glands and their location.

The potential of marsupials as experimental models for immunological function was not fully appreciated until Miller (1962) demonstrated the critical role of the thymus gland in maturation of some immune responses in the mouse. From this initial observation there have developed the classical studies on T and

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[1] After Jerne, N. K. (1973).—*The Immune System*, pp. 49-57. Freeman, San Francisco.

B lymphocytes and a vast battery of tests involving cell function, immunoglobulin structure and function and ontogeny, evolution and genetics of the immune response. Without doubt, one of the major advantages of studying the immunology of marsupials is that their young are at a much earlier stage of development than eutherian young. This permits study of ontogenetic processes which may clarify aspects of physiological maturation which take place *in utero*, and thus are not easily accessible in eutherian mammals.

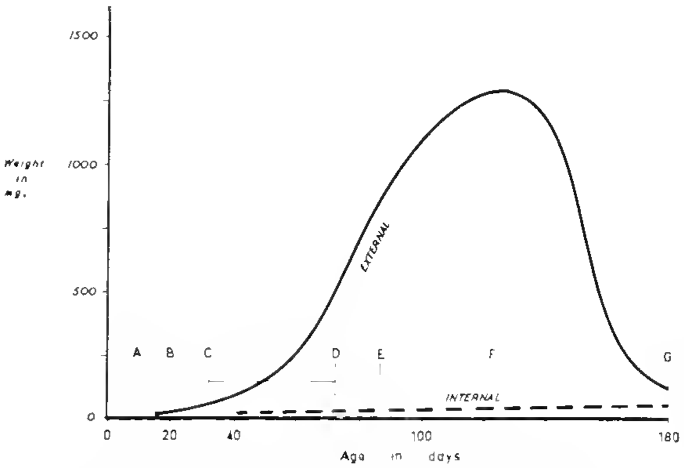
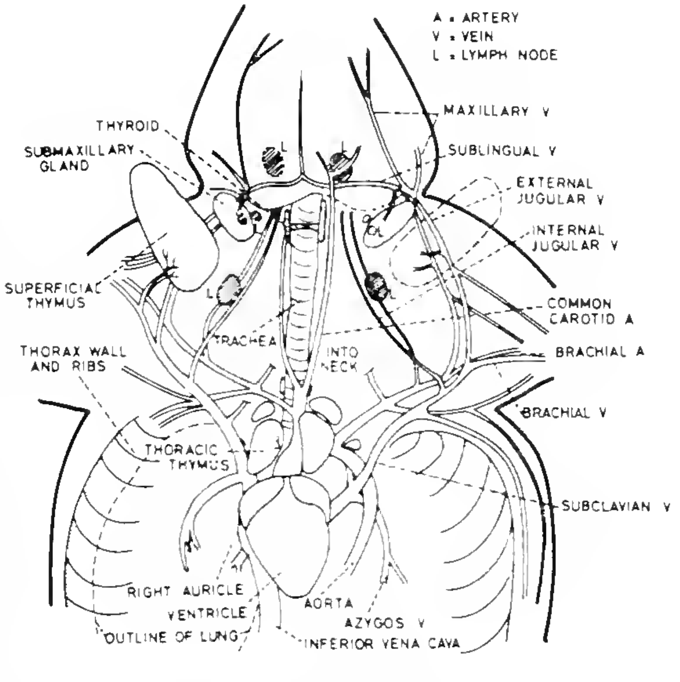


Figure 1.—Weight of internal and external thymus glands of quokka during pouch life.

A. Small lymphocytes apparent (both glands).
B. Cortex and medulla commence to differentiate (superficial).
C and D. Densely compact small lymphocytes in cortex (both glands). Hassall's corpuscles located.
E. Large increase in lobules of external thymus.
F. Stands erect, underhair first apparent.
G. Joey leaves pouch.

With permission of the CIBA Foundation (see Stanley *et al.*, 1966, p. 209).



QUOKKA (150 DAYS OLD)

Figure 2.—Drawing of dissection to show location and blood supply of the superficial and thoracic thymus glands of the quokka.

With permission of the Australian Journal of Experimental Biology and Medical Science (see Yadav *et al.*, 1972a, p. 350).

For convenience the original work will be viewed from two separate but related areas (1) the thymus glands and cellular aspects, and (2) humoral (immunoglobulin) studies, followed by discussion of the findings in presenting the overall immunological picture—still far from being understood.

The thymus gland

Of 93 marsupial species examined by Yadav (1973), histologically-classical cervical thymus glands occur in only one superfamily, the Phalangeroidea. The question this observation poses is the evolutionary advantage that this extra thymus tissue confers—hence one of our initial interests was comparison of immune responses of *Setonix brachyurus*, which possesses both cervical and thoracic thymic tissue, with those of *Didelphis* marsupials which have only thoracic thymus tissue (Block 1964, Stanley *et al.* 1966, Yadav and Papadimitriou 1969, Ashman *et al.* 1971, Yadav *et al.* 1972 a and b, Stanley *et al.* 1972, Ashman *et al.* 1978).

Large lymphocytes appear in the cervical thymus of the quokka at 2-3 days and in the thoracic thymus at 5 days (Yadav *et al.* 1972 a, Lightowlers 1979). Much of the study of immune response consequently concerned the reactions of quokkas whose thymus glands had been removed surgically at different times and then tested for response to various immunological stimuli. Briefly the following categories of quokkas were studied in detail:

Intact and sham-thymectomised
Superficial thymus only removed
  before lymphocytes appear
  after lymphocytes appear
Superficial and thoracic thymus removed } Total thymectomy
  before lymphocytes appear
  after lymphocytes appear

Table 1, shows the comparative development of lymphoid tissue and peripheral blood lymphocytes in *Setonix* and *Didelphis*.

The main antigens used in studying both marsupials were sheep red blood cells (SRBC), Φ X 174 bacteriophage, *Salmonella adelaide* flagellin, Bovine serum albumin (BSA), Dinitrophenyl-bovine serum albumin (DNP-BSA), rye grass pollen allergen (RPA), ovalbumin (OA), dinitro-phenyl-haemocyonin (DNP-Hc), and various mitogens and skin-grafts.

Although the cervical thymus becomes functional about 30 days before the thoracic thymus, there is no evidence to show that the glands have different functions (Stanley *et al.* 1972). A very large amount of the experimental surgical work involved "standard" total thymectomy—that is, cervical thymectomy before day 10 and thoracic thymectomy before day 20. This treatment delayed the first appearance of transplantation immunity until about 100 days of age. It was only in the latter years of our experiment, that it became technically possible to remove both sets of thymus glands prior to lymphocytopoiesis

Table 1

Comparative development of the lymphoid tissue and peripheral blood lymphocytes in the quokka (*Setonix brachyurus*) and the opossum (*Didelphis virginiana*). [Data from Block 1964, Yadav 1969, 1972, Ashman and Papadimitriou 1975].

Tissue	Lymphoid development	Age (days after birth) of first appearance of lymphoid development	
		Quokka	Opossum
Cervical thymus	Large and medium lymphocytes	1–2	
	Small lymphocytes	3	
	Hassall's corpuscles	14	
	Cortex/medulla differentiation	21	
Thoracic thymus	Large and medium lymphocytes	4	1
	Small lymphocytes	5	5–6
	Hassell's corpuscles ...	60	7
	Cortex/medulla differentiation	60	12
Lymph nodes	Small lymphocytes	5	6
	Large lymphocytes ...	35	60–80
	Cortex/medulla differentiation	14	10–12
	Plasma cells ...	60–90	60–80
Spleen	Medium and small lymphocytes	7–14	17–20
	Large lymphocytes ...	7	65–100
Peyer's Patches	Medium and small lymphocytes	42	60
Blood	Medium lymphocytes	5	7
	Small lymphocytes	10	11

(Lightowlers 1979). These experiments enabled us to determine unequivocally whether the mammalian thymus is uniquely responsible for those immune responses classically described as thymus-dependent.

Prelymphocytopoieisis thymectomy did not affect growth, development and survival. Blood lymphocyte numbers were depressed and specific areas of lymph nodes and spleens showed marked lymphocytic depletion. E-rosette forming cells were absent for 130 days and SRBC antibody response not detectable until after 150 days. Juveniles, after leaving the mother's pouch developed these two responses and allogeneic skin grafts developed as rigorously as those of intact quokkas. In addition, the prelymphocytopoiesis-thymectomised juveniles responded to mitogenic stimulation by both phytohaemagglutinin (PHA) and concanavalin A (Con A).

It appears then that these responses, although delayed, are not uniquely dependent on thymus function in the quokka. There must therefore be an extra-thymic pathway for the development of the alleged classical thymus-dependent immunity. This could well be common to mammals.

Immunoglobulin studies

Following the initial responses of intact and thymectomised quokkas to SRBC, *S. adelaide* flagellin and x 174 bacteriophage antigens, the humoral responses were developed and extended by the staff of the Clinical Immunology Unit at the Princess Margaret Hospital under the direction of Kevin Turner. In a series of interesting papers, the following picture emerged. Unlike poikilothermic vertebrates which usually have only one class of immunoglobulin, the quokka has at least four immunoglobulin classes comparable to the IgG, IgM, IgA and IgE classes of eutherians.

The three antigens (SRBC, X 174, and flagellin originally used by Stanley *et al.*, (1972) to study the effects of thymectomy in the quokka were used by others to develop further the immunological picture. Yadav (1971) and Yadav and Eadie (1973) showed that maternal immunoglobulin (IgG) to these antigens appeared in the milk of immunized mothers and crossed the gut into the serum of pouch young. Bell *et al.* (1974) isolated IgG2, IgG1 and IgM in pure forms which differed in their electrophoretic mobility, molecular size, carbohydrate content and in the antigenic determinants of their heavy chains. Subclasses almost certainly exist with IgG2 and IgG1. This complexity is therefore comparable with eutherian mammals. Studies by Lynch and Turner (1974 a,b,c,) suggested an antigenic cross-reactivity between human IgE and the quokka homocytotropic antibody (HCA). This antibody elicited passive cutaneous anaphylactic reactions. If this is substantiated, it is further evidence suggesting that the immediate hypersensitivity system was developed prior to evolutionary divergence of marsupials and eutherians. However, the quokka HCA was indistinguishable from the IgG1 class which suggested to Turner and his colleagues that the extent IgG and IgE classes evolved from a primitive cytotropic chain. The IgA of the quokka has biological and physiochemical properties analogous to those of eutherian IgA (Bell *et al.* 1974).

Discussion

The thymus gland, cellular and humoral immune responses of the quokka so briefly outlined are only a small part of the complex immunological picture. Cockson and McNeice (1980) were aware of this when they reported on "survival in the pouch" and showed large numbers of alveolar macrophages present and both the macrophages and leucocytes in the milk filled stomachs of neonatal quokkas. Macrophages were also present in the milk and colostrum of lactating quokkas. These cells must surely be of significance to the immunologically incompetent embryo as it migrates from the birth canal along its path to the microbe-filled pouch in search of the teat. A study of the pouch microbial flora appears elsewhere (Charlick *et al.* 1981).

Much remains to be done with marsupials which are convenient models in immunological studies. In particular, studies with infective agents and carcinogens may well be productive, although we have not confirmed the observation of Jurgelski *et al.* (1976) who produced tumours in *Didelphis* with diethylnitrosourea (Stanley unpublished observations). The immunological recovery from neonatal thymectomy of the quokka has not been satisfactorily explained. Lightowlers (1979) suggested that the population of thymic-independent lymphocytes associated with the return to immunological competence is the result of the appearance of "Q cells" from an extra-thymic pathway and that this is a phenomenon "common to mammalian immunology". On the basis of his E-rosette forming cells he suggests the foetal liver be examined as a potential source. This speculation is interesting in the light of earlier comments by Ashman *et al.* (1978) on this particular problem when we stated "Although it is possible that another organ may take over the functions of the thymus in neonatally-thymectomized quokkas, it is difficult to see why this should function only early in life. Perhaps the thymus acts primarily as a biological amplification system, by providing a favourable environment for the proliferation of precursors migrating in from another source. In the absence of the thymus, these precursors may undergo spontaneous differentiation into clones of immunocompetent cells."

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Microbiology studies on Rottnest Island

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Abstract

Studies of four different groups of viruses, the bacterial flora of the pouch, and the ecology and pathogenesis of quokka filariasis, comprise the items of this review. The presence of reoviruses and arboviruses confirm the ubiquity of two major virus groups spread by entirely different means. The epidermal papillomata of the tails and feet of quokkas have been shown to be associated with a 'new' poxvirus. The Gram-negative bacterial flora of the pouch was dramatically reduced prior to birth. The life-cycle and immunobiology of quokka filariasis have been defined for the first time. Influenza A virus studies of birds have led to the isolation of a virus with a novel antigenic configuration.

Introduction

Microbiological (virology, bacteriology, parasitology, serology) studies on Rottnest Island were initiated for several reasons, the main one being the immunological immaturity of the quokka pouch-young in the first few days of pouch life. The relative isolation of the island quokkas for several thousand years, their constant association with sea-birds and arthropods, and their more recent association with man, has led to the studies briefly referred to here.

This review comprises studies of the following:

A. Epidemiology of reovirus infections, arbovirus infections and avian influenza.
B. Quokkapox—a 'new' poxvirus.
C. The bacterial flora of the marsupial pouch.
D. Filariasis in the quokka.

A.1 Epidemiology of reovirus infections

Reoviruses are double-stranded RNA viruses of great ubiquity but little potential to produce diseases in man or animal (Stanley 1974, 1977, 1981). Antibodies to the three antigenic types have been found in all terrestrial vertebrates tested (Stanley *et al.* 1964, Stanley 1967). Studies on the Rottnest Island quokka have shown that quokkas in continuous contact with man manifest higher levels of antibody conversion than those with little human contact (Stanley and Leak 1963) (see Table 1). These observations led us to suggest that reoviruses infecting man could be transmitted to animals in contact with man: since that observation we have obtained evidence which does not support this hypothesis, by isolating reoviruses and demonstrating antibodies to them on Bald Island quokkas.

A.2 Epidemiology of arbovirus infections

Approximately 450 arboviruses have been described, of which about one-quarter produce disease in man and animals. All have the ability to replicate in both the arthropod vector and the vertebrate host reservoir and the majority are spread by mosquitoes, ticks and culicoides. They include serious pathogens of man, such as Australian encephalitis, yellow fever and dengue, and of animals, such as bluetongue and bovine ephemeral fever. One way of detecting the presence of these viruses is by searching for antibodies to them in the serum of vertebrates.

Table 1

Percentages of quokkas with detectable H-1 antibody (>1/10) against reovirus types 1, 2 and 3

Locality	No. of animals	Percentage positive against reovirus type			Contact with man
		1	2	3	
West End, Rottnest Island	35	17	34	28	rare
Lakes-Settlement, Rottnest Island	27	67	89	93	frequent
Mainland	10	70	100	100	continuous

After Stanley and Leak (1963)

In our studies of Australian encephalitis (Stanley 1975, 1980), we examined sera from many vertebrates throughout the State, including the Rottnest Island quokka. Sixty-five per cent of 87 sera tested in 1975 showed the presence of antibodies to flaviviruses—a group of arboviruses containing the pathogens Murray Valley encephalitis and Japanese B encephalitis. The identity of the virus has not been determined. Similar tests on Garden Island tammars were negative.

A.3 Epidemiology of avian influenza

As part of the WHO's International Expanded Programme on the Ecology of Influenza A viruses, over 6 000 wild birds have been examined for the presence of influenza throughout Western Australia, including 234 birds of Rottnest Island (Mackenzie, Edwards, Holmes and Britten, unpublished results). Of these, 166 cloacal swabs were obtained from *Puffinus pacificus* (wedge-tailed shearwater), 10 swabs from *Larus novaehollandiae* (silver gull), 15 swabs from *Sterna bergii* (crested tern), and 43 swabs from *Tadorna tadornoides* (Australian shelduck). Three strains of avian influenza have been isolated, all from the shelduck, and have been subtyped by Dr Hinshaw, International Reference Laboratory for Animal Influenza, Memphis, U.S.A., as H? N2, Hsw1 Nav6 and H? Nav6. The latter two viruses are of particular interest: the Hsw1 Nav6 isolate represents a novel antigenic combination which has not been found previously anywhere in the world; and the H? Nav6 isolate appears to have a haemagglutnin which does not react with any reference antisera, and may represent a new, as yet undescribed, haemagglutinin. If this is indeed the case, the possible surface antigens of influenza A will be extended to 14 haemagglutinin types and 9 neuraminidase subtypes (Hinshaw, Webster and Rodriguez, 1979). The third isolate, H? N2, has not yet been fully subtyped. No isolates of Newcastle disease virus were found.

B. Quokkapox—a "new" poxvirus

A pox-like virus has been implicated as the aetiological agent of epidermal papillomata commonly found on the tails of quokkas, and more rarely on other extremities such as nose, ears and feet. The papillomata usually occur on the dorsum of the distal end of the tail as single, but sometimes multiple, wart-like lesions varying in size from a few mm to 5-6 cm. Electron microscopic examination revealed virus particles morphologically resembling mature and immature poxviruses in the cytoplasm of cells of the stratum granulosum (Papadimitriou and Ashman 1972).

Extensive attempts have recently been made to cultivate the virus from homogenates of papillomata (Lalor, Mackenzie and Stanley, unpublished results), including inoculation onto chorioallantoic membrane of 8-, 10-, 12- and 14-day embryonated chicken eggs, into brains of suckling mice, and in tissue cultures of avian (chick embryo fibroblasts), eutherian (BHK-21 cells, vero cells and mouse L-cells) and marsupial (quokka kidney, lung, skin and brain; *Sminthopsis crassicaudata* and *Wallabia bicolor* pouch-young cell lines) origin, but no evidence of virus replication or cytopathic effect was observed in any culture over four consecutive passages.

Co-cultivation experiments were also unsuccessful. Nevertheless, quokkapox virus in papillomata homogenates was able to reactivate heat-inactivated vaccinia virus on the chorioallantoic membrane and in vero cells, which would indicate that the virus was able to enter cells and replicate to a limited extent. The property of reactivation is characteristic of poxviruses, regardless of their subgrouping (Joklik 1966), and thus confirms the morphological identification by electron microscopy that the virus belongs to the poxvirus family.

Attempts to subgroup quokkapox serologically within the poxvirus family have been hindered by the lack of a purified antigen and of a specific, high titre, antiserum. However, in preliminary experiments using a crude antigen preparation from papillomata homogenates, a slight cross-reaction was observed between quokkapox and fowlpox in a complement-fixation test, but not between quokkapox and vaccinia. The level of cross-reaction, which was similar to that found between fowlpox and Western Australian wild bird poxviruses (Annuar and Mackenzie, unpublished results), suggests that quokkapox may be a member of the avipox subgroup, but further experiments are required to substatiate this classification.

C. The bacterial flora of the marsupial pouch

The bacterial flora of the gut of the pouch-young and the pouch of the quokka were initially studied by Yadav *et al.* (1972) in an endeavour to determine the nature of the microbial environment presented to the immunodeficient embryo at birth. The bacterial flora was abundant and complex in all animals tested except a pregnant mother just prior to birth. This observation posed some interesting questions of possible hormonal control of bacteria in the pouch. Further and more exacting studies by Charlick *et al.* (1981) defined quantitative and qualitative differences in the pouch flora in different stages of the oestrous cycle. Oestrus was characterized by high numbers of Gram-negative bacilli, and during non-lactating anoestrus, a predominantly Gram-positive flora was found. A marked selective decrease in Gram-negative flora occurred during the gestation period until they were virtually non-existent in the pouch prior to birth. This interesting and dramatic phenomenon awaits explanation.

D. Filariasis in the quokka

Breinlia macropi, the peritoneal filaria of the quokka, has hitherto been known largely by its adult morphology: nothing of its life-cycle or immunobiology in its host has been established. Scanning election microscopy (SEM) revealed certain features of adult *B. macropi* morphology which previously were not discernible under light microscopy. The cuticular ornamentation, for instance, differs from that of a closely-related species, thus auguring a diagnotisc potential among *Breinlia* species. Similarly, SEM has detailed the precise, diagnostic topography of the caudal extremity of the infective larva.

Our studies (Yen 1982) have shown that *Aedes camptorhynchus* is the natural vector of *B. macropi*, the larvae of which develop within the fat-body of this mosquito. Although other mosquito species are susceptible to the parasite's infection, only *Ae. camptorhynchus*, with a natural infection rate peaking at 22%, is capable of transmitting *B. macropi* infection among the quokkas on Rottnest Island. Transmission of the parasite on the island is limited to between June to October, coinciding with the transient availability of brackish water for *Ae. camptorhynchus* to breed. Despite this, 95 of 203 (46.8%) of quokkas from the island were microfilaraemic, with males having significantly higher microfilarial rate than females. Although this difference in infection rate between the sexes was not apparent by fluorescent antibody (IgG) detection, this serological method detected 93% infection in the 203 animals examined. Both the parasitological and the serological data correlate well with the detection of circulating antigens as determined by the ELISA and counter-immunoelectrophoresis methods.

Peripheral blood leucocytes from normal, microfilaraemic and amicrofilaraemic quokkas proliferated equally well in dose-dependent pattern to PHA and CON A *in vitro*. No amount of soluble microfilarial, adult worm or secretory-excretory antigens, however, could elicit a significant response from these leucocytes. This was despite exhaustive serum or cell treatment.

By contrast, peritoneal macrophages from normal, amicrofilaraemic or microfilaraemic quokkas were equally efficient in adherence and cytotoxicity to *B. macropi* microfilariae *in vitro* in the presence of infected (microfilaraemic and amicrofilaraemic) sera. The prerequisite heat-labile serum factor probably resides in the reaginic antibody of the quokka. This factor, present only in the infected sera, seems to be cytophilic and specifically sensitized the macrophages to initiate adherence and cytotoxicity. As apparent from SEM, TEM, and time-lapse video recording, the death of the microfilariae is preceded by macrophages flatteninig themselves onto the microfilariae, encircling them and secreting material onto their surface. This killing process is effected by at least two types of macrophages distinguishable by size and ruffling of their membranes. The killing is also accompanied by inter-digitation of macrophage membranes of adjacent cells which jointly encircle the microfilariae as a cylinder of cells. The presence of multinucleate cells has also been noted in this study.

Conclusion

The microbiological studies cited show that the Rottnest Island quokka is not microbiologically unique, but that selected studies of an island-marsupial ecology can provide meaningful data which add significantly to our understanding of host-parasite relations. This is seen with the remarkable reduction in the bacterial flora of the pouch prior to birth, the clear demonstration of the cycle of filaria, *Ae. camptorhynchus* and the quokka, and the demonstration of a 'new' poxvirus.

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The Rottnest experience

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Abstract

This paper attempts to elucidate some of the diverse meanings that Rottnest has had for Western Australians. The psychological function of myth has always been to tell stories that establish exemplary models of behaviour and give dramatic substance to values, aspirations and conventions. Behaviour on Rottnest has many quasi-ritualistic elements, and the stories people tell about it are full of mythic overtones. Rottnest has played a significant part in sustaining Western Australians' self-image as a society that is friendly, gregarious, simple, unpretentious, physically oriented, pleasure loving and egalitarian. The paper explores some of these myths and their dependence on the physical characteristics of a particular place—the island of Rottnest.

Chronicle and myth

The history of Rottnest can be told in two ways. One is to give a chronicle of events. That has been done often for Rottnest. The broad outlines are very well known—the accounts of the early voyages of discovery, the settlement of Swan River Colony in 1829 and the plan for the township of Kingstown on the island in 1831 (from which the name of the Army settlement, Kingstown Barracks, is derived); the arrival of Constable Welch to take charge of Aboriginal prisoners in 1838 and the long subsequent history as a prison. An alternative use was foreshadowed by the increasing popularity of the island as a summer resort with successive Governors of the colony. Governor Fitzgerald (1848-1855) commandeered the original superintendent's cottage. Kennedy authorised the building of a new Government House on Rottnest and:

> 'a design was prepared by the Royal Engineers' Office in Perth and drawings were signed by Richard Roach Jewell, the Clerk of Public Works' (Commission for the National Estate, 1977, Book I, p. 29).

The building was completed in 1864—although not precisely to these drawings—and first occupied by Governor Hampton.

Thus began the recreational use of Rottnest—at first for viceregal shooting parties, but in 1903 the prison was closed, the pilot station transferred to Fremantle, and the island proclaimed for public use in March 1907 by his Excellency Admiral Sir Frederick Bedford. The present and future primary use was then established. In the last half century a secondary use of the island has evolved as a laboratory for scientific research. This is not always compatible with unrestricted large scale recreational pressures, although of course science has a special rôle in monitoring the effects of such pressures.

The second and more difficult approach to the history of Rottnest is to attempt to elucidate its meaning. It undoubtedly has meaning. The island seems to hold a very special place in the minds and imaginations of Western Australians. It is treasured with a fierce affection that calls for explanation, which must form a significant element in any serious attempt at a cultural history of Western Australia. The complex of attitudes towards Rottnest appears to encapsulate many deep-lying aspirations about the good life, the nature of society, the proper relations of man with man and of man with the environment, but the difficulty in writing about them is that they are hard to pin down, and those who attempt to do so generally turn quickly to purple prose eulogising that special 'Rottnest experience'. Despite the difficulties, this 'experience' is nevertheless the heart of the matter, and in considering the future of Rottnest, the conservation of 'the Rottnest experience' has to be the prime concern. The two National Estate reports (1977) tend to take a narrower view of conservation. One volume gives a very professional and necessary account of the history, present conditions and conservation needs of the built environment, and the second volume of the natural environment, but neither gives an adequate account of the experiential environment, although both are conscious of it.

Critics of literature over the last few decades have revived the word 'myth' to describe a form that deals in heightened experience similar to that commonly ascribed to Rottnest. Thus Northrop Frye says that 'myth is the imitation of actions near or at the conceivable limits of desire' (1957, p. 136). In popular speech, a myth is a commonly held belief that is not well founded, but truth or falsity are not applicable to the word as used by Frye, because myth is not intended as factual narrative. This is also true of the more recent extension of the word to some paintings—for example, Sidney Nolan's Kelly series is often described as having a mythic quality. Kelly is larger than life, both tougher and yet also more vulnerable, which accentuates the sense of courage and doom, further heightened by the bare, burning, harsh, beautiful background landscape. In this sense Rottnest too has a mythic quality as a simpler, better, truer world than the one we usually tread. The quality of Nolan's paintings would not be negated if historical research were to suggest aspects of Kelly that are not consonant with the myth, and the same holds for the myth of Rottnest. The important question is not to ask if it is 'true', but to ask how it is generated.

Islands and attitudes

Before looking at Rottnest in detail, it may be useful to consider the place of islands in our culture, because the mythic quality I attribute to Rottnest is part of a common response to islands. A current American television series bears the title *Fantasy Island*, in which the object of the host and management is to fulfill the fantasies of the guests—in short, to offer, if only for a brief moment, experience 'at or near the conceivable limits of desire'. It is not a very good television series, but it is skilful in identifying one of the things that people may want from islands. *Bali Hai* was of the same genre, with overtones of Paradise Regained thrown in. A number of films about the Tahitian islands have been more explicitly paradisal, offering innocent sensuality, with all the pleasures of the flesh but none of the guilts, nor the various consequences of overindulgence. The 'Noble Savages' of the French philosophes of the 18th Century are prominent in the cast of such films, and one of the intellectual antecedents of this set of attitudes towards islands is clearly revealed.

The promise of easy sex without penalty is also a conspicuous part of advertising in Australia for the tropical islands of the Great Barrier Reef, and an unwritten expectation of the very popular Club Mediterranée resorts, many of which are sited on islands. Wine flowing free like a fountain of eternal youth is a further attraction. Islands are intoxicating, but since all elements of myth can be interpreted at the level of the individual—Ariel or Caliban—for many, islands are a great place for a 'booze-up'. Those floating islands, the cruise ships, also promise similar delights.

Why do islands seem to encourage such behaviour? Because in some odd way, islands are perceived to be 'outside the law'. Some islands are literally exempted from some laws—for example, those who live on Norfolk Island, or the Isle of Man and the Channel Islands off the coast of Britain, pay no income tax. Norfolk Island is also 'duty-free', and most of the great duty-free ports, notably Hong Kong and Singapore, are islands. The perception of islands as being in some sense 'outside the law' is reinforced by the complex attitudes that have built up the tradition of 'holiday'. Holidays are today secularised, merely a period free from our regular work, but we nevertheless have special expectations of them. In earlier societies there was much variation—the holidays of Imperial Rome were different from those of the Middle Ages or Tudor England, but they also had some features in common. They were so exceptional in a life dominated by unremitting hard work, limited resources, ill-health and generally oppressive authority, that an inversion of order was not uncommon—the Feast of Fools in which anyone could be king for a day, and Bottom the Weaver adored by Titania, Queen of Fairies. The inversion of order was sometimes characteristic of special places, of which Prospero's island of *The Tempest* and the Forest of Arden in Shakespeare's plays are perhaps the best examples in English literature. The Forest of Arden, the scene of *As you Like it* and *A Midsummer Night's Dream* is not literally an island, but it has the characteristics of one, excised sharply from the cloth of the mundane.

An island such as Rottnest is not in reality outside the law at all. It is subject to the same laws as Floreat Park or Applecross, with regulations of its own as well. But the expectation of some release from the restraints of the mainland is strong, and this creates special problems of management, which must try to create a sense of freedom that is not socially or physically destructive. If people are not *given* liberties (such as the beautiful freedom from concerns generated by the dangerous motor vehicles of the mainland, and the tyranny of parking them), they will *take* liberties, for example by drinking too much and then going on destructive 'souvenir' hunts. Skilled management consists in walking this tightrope.

Because of the special place islands hold in our imagination, the way in which we reach them is very important to some people. In making a recent short visit to Rottnest in the course of preparing this paper, I told several old friends that I would use the air service, since time was short. The reaction was one of shock. 'Oh, no: you must go to Rottnest by ferry', thus observing due rites of passage between one mode of being and another. Arnold van Gennep (1908), a French sociologist, coined this phrase to describe the transitional rituals accompanying changes of place, stage, social position or age in a culture. The rites have three phases: separation from the habitual social structure, detaching the subjects from their old places in society; a transitional phase; and finally, installation in a new context. The 'betwixt and between' phase corresponds to the ferry ride; van Gennep claims that in this phase, when people are liberated from their 'place' in the world, a spontaneous sense of community or comradeship may spring up. On the Rottnest ferry ride it is helped along if there is a shared experience, such as a fairly rough crossing. The trip is too short for the sense of community to grow very strong, although it may continue to expand on the island itself, of which more later. It is obviously one of the attractions of cruise ships and long bus tours, although attempts at artificial stimulation of this mood tend to be counterproductive, and inhibit its spontaneous generation. The importance attached to handling this transitional phase emphasises the ritualistic character of a visit to Rottnest for those who make it a cult; it illuminates the ceremonious vestiges in our concept of holiday. The ferry is traditional, and thus begins 'the Rottnest experience' at the jetty, slowing the clock and allowing sociability under transformed circumstances. It also includes an element of simplification and a rejection of high technology—already noted in respect of the automobile. Ferries are 'good', aeroplanes are 'bad', because aeroplanes are a contemporary technology, and therefore obtrusive. This attitude is neither logical nor consistent—the same people are usually happy to use the telephone on Rottnest, but then the technology of the telephone is invisible (it works by putting twenty cents in the slot). Regardless of consistency, the attitude is powerful and real.

Another important feature of islands is their legibility. Elisabeth Riddell speaks in a poem of the sailor who wanted an island that he could hold in his hand like a green apple. The 'best' islands are perhaps those that you can walk right round in a few days. If you can do it in less than a day, too small: if more than a week, as Kangaroo Island, too big—although you can explore Kangaroo Island by car in a few days, and perhaps that will do. There is a special attraction, probably atavistic, in beating the bounds and knowing the territory, which islands can satisfy beautifully by being so well-defined.

But the legibility of islands is not only physical; it is also social. As I have noted elsewhere (Seddon, 1972, p. 219), some functions are on public display on Rottnest and other islands of similar size that are hidden discreetly from view on the mainland. For example, the baker bakes bread, and you can see him do it, smell it, and buy it warm, a satisfying transaction. Arrivals and departures on islands are generally very public. On Thursday Island in Torres Strait, everyone who comes or leaves can be seen quite clearly from the bar of the most popular hotel. Air transport is less public, but most people still come and go to Rottnest by ferry, and are seen to come and go by half the population at the jetty, since this is an event. All of the island water supply and its power generating plant could be seen at a glance until a few years ago, but such facilities are too complex to comprehend so easily in the metropolitan society a few miles to the east.

In being legible and fully comprehensible, islands may offer deeper satisfactions than those I have touched on so far. There is a dream of self-sufficiency that found its richest fulfilment for me as a child in the children's novel, *The Swiss Family Robinson*, and with darker overtones, in *Robinson Crusoe*. In both, the individual is able to make a world with his own hands. No island that functions as a holiday resort is self-sufficient in this way, but in being simpler and more comprehensible, may still satisfy this urge in part. On Rottnest, for example, most people most of the time are self-sufficient at least in their transport, by either walking or riding a bicycle, and this is a key element in the Rottnest experience.

The dream of self-sufficiency is the extreme of antisocial individualism, and is therefore often linked with the myth of 'the desert isle', which, ideally, is lush and tropical; not arid, but deserted of people. We would now say; 'uninhabited'. The wish to cut free from social links at least for a time is strong in some people, and it can be met on many islands around the Australian coast, although such islands are, almost by definition, difficult of access. It may be hard to have a whole island to yourself, but there are many islands around Australia where it is quite easy to have a beach to yourself. Even on Rottnest it is still possible to get away from the crowds fairly quickly, although perfect isolation can no longer be guaranteed. (Both 'isolate' and 'insulate' are derived from the Latin 'insula', an island.)

The legibility, completeness and clear boundedness or definition of islands has much to do with one of their major conceptual rôles in European cultural history, which is to serve as a locus for models of the ideal society. The *Utopia* of Sir Thomas More was an island; so was Bacon's *Atlantis* and, of course, Aldous Huxley's *Island*. Antithetically, they have also modelled dystopia, the corrupt or evil society, both in fact and fancy. Devils Island (Isle du Diable) the French penal colony off French Guiana; Alcatraz; Norfolk Island; all have a terrible history. Swift used islands for satirical ends in *Gulliver's Travels*. During the centuries of European exploration and discovery, islands (and those who lived in them) such as the Bermudas or the Pacific islands were seen as idyllic or barbarous, playing out a moral drama that is central to our culture:

> 'Both these attitudes to primitive man are deeply rooted in the past; and both found support in the behaviour of the natives, which was, as a rule, very amiable at first—as Caliban's was with Prospero and Stephano—but under provocation, and sometimes spontaneously, treacherous later. Behind all these observations are the two opposing versions of the natural; on the one hand, that which man corrupts, and on the other, that which is defective and must be mended by cultivation—the less than human, which calls forth man's authoritative power to correct and rule. This latter is the view which suits best the conscience of the colonist'
> (Kermode, 1966, pxxxvi)

It is symbolic that Rottnest, like Norfolk and Maria Islands and The Boys' Island at Port Arthur, should have been both light and dark, holiday paradise and aboriginal prison. In *Lord of the flies*, William Golding concentrates the conflict between the civilised and the primitive by showing both elements at war within a single society, a group of school children transformed by island life cut off from the familiar.

Islands have such a weight of symbolic meaning in our culture that the experience of them resonates in the mind and imagination, and in this lies much of their power.

Finally, islands may appeal to primitive survival instincts. Behavioural psychologists interested in recreation have long observed that there is a preference for 'edges'—that we choose for picnic spots or holidays a place that offers a transition between two environments, and that the strongest transition is that between land and water, whether it be that of river, lake or sea. To an ecologist, such edges are always especially rich, in that there is not only the flora and fauna of each zone, but those of the transition as well. Where forest meets pasture or meadow, for example, there are the birds of the forest, birds of the cleared land and, in addition, many birds that feed in the cleared land and roost and breed in the forest. The birds of the lakes and tidal zone are a similar example, and those of Rottnest are exceptionally rich. Even to those who are barely aware of their ecological surroundings, there may still be some dim perception of the richness.

The Rottnest experience

How much of the above is applicable to Rottnest? It is certainly seen to be 'outside the law' by many. Young people may described its principal attraction as 'getting away from home and parents'. Many people drink more, and this can be a problem for management, but if people must occasionally drink too much, Rottnest is a good place to do it, in that no one drives home, the drinking is usually sociable, and the sea restorative next day. Freedom of dress is complete, and although Perth dresses more casually than any place I know, people still enjoy the further freedom of going barefoot or in shorts and thongs. As noted above, freedom from motorised traffic is enormously important. Ten years ago, there were few roads and fewer vehicles. Mothers were free of the worry that their children might be hit by a car. Pedestrians and bicyclists scarcely looked behind them. There as still no private cars, but the Board and its licensees have a fleet of vehicles, and they are sometimes driven fast, especially in the remoter parts of the island, which should be the safest, so that this freedom may diminish as management tasks become more complex with increasing tourist numbers.

If Rottnest is 'outside the law', it is also 'outside time'; the clock runs more slowly. On holiday islands, time stands still, and this is always given as one of the attractions of our metropolitan islands. The 'slower pace of life' is perhaps most valued on Kangaroo and Phillip Islands, both of which have an indigenous farming and commercial life of their own, but one which moves more slowly than that of their mainland counterparts. Rottnest is too patently artificial to generate that response—it is too leisured to be leisurely, but people do go there to 'unwind' (a clockwork metaphor).

Since people go to Rottnest on holiday, the cultural expectations of 'holiday' discussed above apply, to some extent in a way that is unique to Rottnest. Although authority is not inverted, Rottnest is imagined as a great leveller, and this is important to Western Australians, who aspire to an egalitarian society, despite the marked differentiation in income and other resources on the mainland. Money won't buy all that much on Rottnest. The best and most expensive accommodation is not much better than the cheapest (even the new units at Geordie Bay have only marginally widened the gap); beer at the Quokka Arms is the same price for everyone, and the clear blue water of the Basin is free, as are most of the 'events', like watching the ferry come in, or walking up to Vlaming Lookout to see the sun set. This is an important component of the Rottnest experience, deeply valued, and one that should be maintained in future planning. Communal ablution blocks are cheaper, simpler and more egalitarian than units with en suite bathrooms, and part of the Rottnest style. The egalitarian 'feel' of Rottnest has complex origins. In a sociological analysis of the role of pilgrimage in the history of Western Society, Victor Turner (1978) surveys ritualised journeys—in both Mediaeval Europe and contemporary Mexico—with marginal notes on the secular pilgrimages of American society (to the Civil War sites, for example). He notes that pilgrimage has some of the characteristics of the transitional phase of the 'rites of passage': 'release from mundane structures; homogenisation of status; simplicity of dress and behaviour;' (p253), a sense of community or comradeship both on the journey and as a characteristic of the goal, which is itself a source of fellowship, healing and renewal. These characteristics have some application, not only to the journey to Rottnest, but to the experience of Rottnest itself (Rottnest as tourist Mecca?). The lack of defined status has much to do with the spontaneous friendliness so often encountered in unlikely places, such as the queue at the bike shop. One must add, however, that the claims to equality on Rottnest are in part specious and self-deceiving. Some years ago on Rottnest a friend pointed out to me the then Premier of Western Australia, Sir David Brand, padding down to the store in shorts and thongs. My friend glowed with pride, as if to say: 'There you are, he is just like you and me; there are no privilges of office here'—just as they had said forty years earlier of Sir James Mitchell, first Premier, then Lieutenant-Governor and finally full Governor (in 1948) as he took his daily stroll down St. George's Terrace and greeted his cronies (Bolton, 1972, p265); just as they said of Sir John Forrest's dedication of Kings Park in 1890 as a 'people's park'. Kings Park was open to all, but those who used it often in those early decades were those who could walk there from Mount Street, Malcolm Street and King's Park Road; the workmen and lower middle class of Victoria Park might get there once or twice a year as a special event. Similarly, few builders' labourers rent a cottage at Rottnest every year, although they are free to do so. The egalitarianism is in fact among equals, the professional and managerial class. The real distinction is between them and the day trippers.

Although it offers some freedoms, Rottnest also offers some structure, in a very pleasant informal way. Organised holiday camps, cruises and tours have a daily schedule of activities, often difficult to escape. So does Rottnest, but they are all informal and wholly optional, although with some regulars they are almost ritualistic. A swim at the

Basin before breakfast; the arrival and departure of the ferries; the arrival of the daily newspaper at the store, and of bread at the bakery; the 'sessions' at the 'Quokka Arms'; the several walks, as to the Lakes; the bicycle ride to the West End, and so on, all provide definite things to do, so that the sudden release from the timetable of the working week is not too unnerving.

Within this structure and its prescribed but informal activities there is excellent opportunity for casual encounter, and this is undoubtedly a major component of the Rottnest experience—'meeting people'. You can either meet people you know already, or meet new ones. The former is probably the more important, in that regular visitors are likely to be professional people, University students or Higher School Certificate students from the more affluent suburbs. Thus young doctors or lawyers or architects can run into their ex-classmates at the Quokka Arms, or in the queue at the Board Offices or bike shop or jetty or walking back from The Basin, and 'catch up on the news'. Meeting new people is largely an extension of this, in that in each of two small groups there will be a few who know each other, and a few who don't, who are then introduced, and who thus begin their relationship in an atmosphere of relaxed intimacy, perhaps the ideal context for striking up new friendships.

That Rottnest is legible, both physically and socially, has been noted already. Many people know the island intimately, recite the place names—Little Geordie, Parakeet Bay, Lady Edeline Beach, Lake Baghdad—like a litany, and are fiercely proprietorial in their attitude to the island. It is socially comprehensible because of its small size, the compactness of the Thomson Bay settlement, and the visibility of many public functions. The Manager, his staff, and the permanent residents are few in number, visible, and well-known to many people. The relative simplicity of the society is a satisfying contrast with that of the mainland.

The dream of self-sufficiency, on the other hand, is not nourished by Rottnest. It is not a lush tropical paradise, and it could not possibly support its holiday population without supplies from the mainland. The ecological diversity of Rottnest is not great in comparison with, for example, Fraser Island in Queensland, or Wilsons Promontory in Victoria (an island joined to the mainland by a sandspit), both of which are ecologically diverse, ranging from rainforest to heathland. Nevertheless, the richness in bird life, the quokka, the remants of low closed forest with its dense canopy of *Melaleuca* and *Callitris*, the attractive salt lakes, the complex indentations of the coastline and the abundant life of the offshore reefs are all part of the meaning of Rottnest for some people, and add to the density of the experience it offers. This is reinforced by the charm of the early buildings and their setting of great Moreton Bay figs and the sense of a long and varied history, including the wrecks around its coast, very well displayed by a 'Wrecks Trail'. The dark shadow still cast by the earlier use of the island as an aboriginal prison is also a part of the experience. So are the pedestrian scale, the compactness of the settlement, and the sharp definition between the world of man and the world of nature, although this is becoming blurred as 'development' goes on.

Rottnest as a metropolitan island

In serving as a playground for Perth, Rottnest is a special kind of island—a metropolitan island—but it is not unique in this. Each of the Australian capital cities has one or more islands to play with, and their history, character, land-use and management throw into relief some of the characteristics of Rottnest. Brisbane has Fraser Island and the islands of Moreton Bay, especially Stradbroke, Moreton and Bribie Islands. There are nine islands in Port Jackson, and more in Pittwater and the Hawkesbury. Melbourne has Phillip Island, and Wilsons Promontory, in effect, an island. Hobart has beautiful Maria and Bruny Islands; Adelaide has Kangaroo island.

Rottnest is perhaps the most accessible of all the metropolitan islands, only 18 km from Fremantle, an hour by ferry, half an hour by hydrofoil, 15 minutes by air. All of the other islands listed here require a substantial drive before the ferry ride. With Rottnest, the car is left behind almost at the beginning of the journey, since the Barrack Street and Fremantle jetties are within 20 minutes by car from most of middle-class Perth. Because it is so close, it is also the most visible; from all the suburban beaches, also very accessible to most of middle-class Perth, Rottnest lies clear and beckoning on the horizon, a continuing reassurance that escape is easy. The return view is perhaps more complex: the metropolitan coastline is equally visible from Thomson Bay, especially at night, when the lights aid identification of individual metropolitan segments and features. Thus escape is easy, but therefore not complete. Contact is maintained, a point emphasised by the telephone system: Rottnest-Perth is a local call. Nevertheless, the water barrier gives a comfortable separation, and the city can be regarded with impregnable detachment. Perceptually, there is a great sheet of bullet-proof glass between island and mainland.

Like Maria Island (discovered and named by Tasman in 1642), but unlike the others, Rottnest has a relatively long history, and a treasury of old buildings. Only Norfolk Island and Port Arthur have greater architectural interest, but neither is metropolitan and Port Arthur is a peninsula rather than an island. These two, Maria Island, St Helena Island in Moreton Bay, Dunwich on Stradbroke Island, and Rottnest, all have a history as penal settlements. Rottnest was the only aboriginal prison, however; Rottnest and St Helena are the only islands in which most of the prison buildings are still in use, and Rottnest is almost unique in Australia in that the accommodation is all publicly owned and managed. The Chalet at Mt Buffalo, managed—improbably—by the Victorian Railways, and limited cabin and lodge accommodation at Tidal River on Wilsons Promontory are the only parallels that come to mind, although good publicly owned accommodation is common in the National Parks of North America, South Africa, Malaysia, Thailand and many other countries. Portugal and some other European countries also offer State-run hostels in historic buildings.

Land tenure is also distinctive, in that there is no freehold land on Rottnest, and almost all the island is managed by a single Government agency, the Rottnest Island Board (the exception being a pocket of Army land at Bickley Bay). Wilsons Promontory and Maria Island are also in public ownership, and run by National park authorities, as is Flinders Chase on Kangaroo Island and the northern end of Fraser Island.

In scenic beauty and in ecological diversity, Rottnest ranks comparatively low. The most dramatically beautiful are Maria and Bruny Islands, Bribie and Fraser Islands in southern Queensland, and Wilsons Promontory. All of these also have an interesting and relatively rich fauna and considerable ecological diversity, much greater than Rottnest. Both Wilsons Promontory and Fraser Island range from coastal heath to rainforest. Nevertheless, Rottnest is at least their equal as a base for scientific research, and it has a very significant research record, although all of the islands have been attractive to ecologists and other field scientists.

Success in the conservation of the natural environment of Rottnest must rank very low, especially in comparison with Flinders Chase on Kangaroo Island, Wilsons Promontory, Maria and Bribie Islands. Most of the damage has been done in the past by fire and quokka grazing and browsing. Vigorous efforts to control the quokkas and to reforest the island over the last few years have met with some success, but much of it still has the appearance of an arid steppe, botanically impoverished and visually monotonous. Its limestone headlands, clear white beaches and the turquoise and aquamarine waters around the island are its best asset. The lack of naturally occurring fresh water streams—available on most of the eastern islands—rules out the possibility of informal camping in natural areas. Rottnest is tied inescapably to a serviced settlement acting as a base for exploration by foot or bicycle for one day only—unless, of course you have the use of a mobile, floating minisettlement (or boat). It is not an arcadian landscape in any but the most superficial sense, and could never evoke a passage like the following from the Italian patriot Garibaldi, who landed on Three Hummock Island off the northwest tip of Tasmania in December 1852. Here he found a deserted farm with a rough but comfortable cottage and garden—

> 'a most useful discovery, as it enabled us to take on board an abundant supply of fresh potatoes and other vegetables.
>
> How often has that lonely island in Bass's Strait deliciously excited my imagination, when, sick of this civilised society so well supplied with priests and police-agents, I returned in thought to that pleasant bay, where my first landing startled a fine covey of partridges, and where, amid lofty trees of a century's growth, murmured the clearest, the most poetical of brooks, where we quenched our thirst with delight, and found an abundant supply of water for the voyage.'
>
> (*The Age 'Monthly Review'*, Vol. 2, No. 7, November 1982)

Rottnest imports its support systems along with its tourists.

Rottnest and change

Vlaming wrote in 1697 of the 'odorus woods' of Rottnest, and all early visitors to the sheltered eastern end of the island describe it as heavily wooded. The botanist Alan Cunningham, who visited Rottnest in 1822, was impressed with the abundance of cypress (*Callitris preissii*), whose dominance over the island was only occasionally broken by *Melaleuca lanceolata* and *Pittosporum phylliraeoides*. These three 'constituted the timber of the island', and *Acacia* seems to have been relatively uncommon. The island had been protected from aboriginal 'fire-stick farming' for 6 000 years or so, and it had evolved on its neutral soils a dense closed forest of cypress and moonah with a heavy, nearly continuous canopy and a forest floor of needles or a mat of fallen leaflets. Quokkas grazed on limited open ground such as the margins of the lakes. With settlement, cutting and clearing for timber and the deliberate and accidental use of fire rapidly reduced the fire sensitive *Callitris, Melaleuca and Pittosporum*. *Acacia rostellifera*, which regenerates well after fire, became common. Clearing and introduced herbs greatly increased the food available to the quokkas, which were kept in check by hunting until the 1920s; after protection, they began to expand rapidly. The vegetation of Rottnest now consists primarily of a heath made up of fire-tolerant plants unpalatable to the quokka (primarily *Acanthocarpus preissii* and *Stipa flavescens*), except in areas from which they have been excluded by fencing. Reforestation has been attempted since Somerville's day, with variable success. Tuart (*Eucalyptus gomphocephala*) is not indigenous to the island, although pollen recovered from bores and peat samples shows that it once was. It has been planted quite widely, and although it survives, the trees do not thrive. They are ugly and mis-shapen, and detract from the landscape. Plantings of moonah (*Melaleuca lanceolata*) have been successful silviculturally, and some plantations will soon make an important contribution to the landscape, but they are only partly successful as the recreation of a natural environment, in that the regularity of boundaries and internal spacing are too evident. *Callitris preissii*, a tree of great beauty, especially when fully mature, is less easy to regenerate, in that planted specimens commonly die in about their seventh year. The small groves of mature cypress at Woodman Point and Coogee on the mainland show the beauty that Rottnest has lost. Recent plantings of non-indigenous plant material at Geordie Bay seem to me ill-advised. *Eucalyptus platypus* and *Melaleuca nesophila* for example, appear to be growing successfully, but they come from the south coast, and have no place in the Rottnest landscape. The Thomson Bay settlement has many exotics, including the great Moreton Bay figs. They are culturally appropriate to the 19th century character of the settlement, and enhance that setting, but they should not be extended beyond it. In an eighteenth century treatise, the Reverend William Mason gave the following good advice to landscape designers:

> 'Great Nature scorns control: she will not bear
> One beauty foreign to the spot or soil
> She gives thee to adorn; 'tis thine alone
> To mend, not change her features.'
>
> (Mason, 1778, Book 1, pp. 4-5)

His advice is very appropriate to Rottnest.

Conservation of the built environment at Rottnest is now of a very high standard, and appropriate design principles seem well understood. This is apparent in the restoration of old buildings such as the barn built by Henry Vincent about 1857-1859 and now used as a museum; the chapel and old school house, built around 1862; by the design of new buildings, such as the villas at Thomsons Bay and the new units at Geordie Bay and Longreach, which still look a little raw, but show high standards of design; and from attention to detail, as in the removal of the verandah infilling at the Quokka Arms, and the dramatic improvement of the new cottages southeast of the hotel. (For a photograph of these cottages in 1970 see Seddon 1972, p222.) The face brick has been washed with Rottnest yellow, the tubular steel verandah posts replaced with masonry pillars, the wire fencing with masonry walls, and the offensive power lines relocated. The honorary architect to the Board, R. J. Ferguson, has served it well.

Perhaps the two most significant dates in the history of the island are 1839, when all land grants made on the island were resumed: and 1976, when a limited amount of good fresh water was found (in a catchment northeast of the lighthouse) after hundreds of unsuccessful bores had been put down. This supplements water collected from a bituminised catchment—an eyesore visible from the Longreach-Geordie Bay Road—and replaces the carting of water from the mainland. The proposal to connect Rottnest to the metropolitan water supply (e.g. see Martin and Associates, 1973) now seems most unlikely to be implemented, and thus planning for Rottnest for the next 20 years or so must take place within the water locally available to it. A sewerage system has been installed using sea water; a dual supply system has been installed at Geordie Bay; and there will clearly be no water for golf greens or lawns and gardens at Thomsons Bay. This is a blessing.

The future will depend partly on numbers and partly on management decisions. The number of tourist accommodation units has grown from 58 in 1960 to 290 in 1982. Visitors to the island numbered around 85 000 in 1968/69, and 242 000 in 1981/82. This included 192 000 day visitors in a year, making up about 60% of the total. These numbers are not great—Phillip Island in Victoria sustains around two million visits annually—but are substantial in relation to the kind of experience people have looked for from Rottnest. The number of boats attempting to anchor at Rottnest is increasing steadily, and swing mooring around the island is already at capacity. On the January 1980 long weekend there were 1 000 private craft in Thomson Bay alone. A marina is under consideration.

The next five-year plan for Rottnest was released by the Premier on 23 September 1982 (p82/758); it includes an upgrading of existing accommodation at Thomson Bay, the demolition of 23 old weatherboard bungalows, the construction of 40 new villa-style units (which currently have the best occupancy rates) and the undergrounding of power lines. Reforestation and dune control will continue and additional boating facilities will be considered. A new nursing post will be built if funds are available. These modest and conservative proposals met with some criticism in the press, mainly on the grounds that the simplicity of Rottnest is being lost as it is progressively 'upgraded'. A major concern is that every new development brings more sealed roads and more vehicles on them.

T.S. Martin and Associates (1973) predict that:

> 'at the turn of the century, Rottnest will have to accommodate a normal seasonal population of up to 10 000 persons'
>
> 'peak holiday patronage will escalae to 25 000 persons on public holidays'.

An English planner who advised on the future of Rottnest a few years ago gave his opinion that peak numbers might reach about 19 000, but that people would then say 'Rottnest is too crowded' and stay away. I know I would.

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Inland waters of Rottnest Island

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Abstract

Aspects of the limnology of the inland waters of Rottnest Island are presented. Physical features and chemistry of the waters parallel values for other inland saline waters in southern Australia. The fauna is clearly salt-tolerant, many species tolerating salinities above previously recorded levels. Similarity to the fauna of inland coastal saline waters in southern Australian is noted. Twelve species are shared with south east Australia.

Introduction

The inland waters of Rottnest Island were described by Hodgkin (1959) and Edward and Watson (1959) and then comprised six permanent salt lakes, two ephemeral salt lakes, eight variably-saline ephemeral swamps and three freshwater ephemeral pools. Since 1959 a number of changes has occurred to these water bodies. In the early seventies, five ephemeral swamps (Bickley, Bulldozer, Lighthouse, Parakeet and Salmon) were excavated to provide marl for road construction. These swamps now contain permanent water. Road construction formed two ephemeral freshwater pools, one (named Gull Wash Pool) on the eastern shore of Bagdad Lake, the other (named Frog Pool) on the western shore of Herschell Lake. Landscaping on the eastern shore of Garden Lake modified Garden Pool.

There has been little research on these water bodies since 1959. Chemical and physical characteristics of some lakes and swamps were briefly presented by Playford (1977) and Riggert (1977) and salinities in Pink and Negri Lakes in relation to *Daphniopsis pusilla*, a salt-tolerant cladoceran were noted by Bayly and Edward (1969). Two studies, the population dynamics of *D. pusilla* (Edward, Bunn and Tomney) and meromixis in the salt lakes of Rottnest Island (Edward and Bunn) are in preparation.

Apart from these studies, there has been irregular sampling of the chemistry and biota of most of the water bodies as part of a long-term survey and for undergraduate field courses in the Zoology Department, University of W.A. In 1967, Bagdad, Negri and Pink Lakes and Lighthouse Swamp were sampled fortnightly for physical and chemical parameters and biota. These data, presented in this paper, provide an account of the limnology of the inland waters of Rottnest Island.

Methods

Field measurements of salinity below $40^{0}/_{00}$ were by salinity-temperature bridge (Yeo Kal Model 602). For salinities above $40^{0}/_{00}$, total dissolved solids were determined gravimetrically and converted using the equation, Salinity = T.D.S. × 0.95 (determined from analyses for five salt lakes 29-iii-1966). The W.A. Government Chemical Laboratories analysed water samples from 1966 to 1968. Phosphate analysis was by the molybdate-ascorbic acid method (Strickland and Parsons 1972).

Temperature was recorded by salinity-temperature bridge or by maximum minimum thermometer and oxygen was measured using the azide modification of the Winkler technique.

Benthic and planktonic faunal collections were made with coarse and fine hand nets (500 µM and 100 µM mesh) and preserved in 70% ethanol. Fortnightly samples in 1967 were standardised by collecting samples over 15 paces. Relative abundance of species was estimated as rare (< 50 specimens), common (<500 speciments) and abundant (> 500 specimens).

Results

The inland waters of Rottnest Island can be grouped into ephemeral freshwater pools, ephemeral and permanent variably-saline swamps and ephemeral saline lakes and permanent high saline lakes.

Ephemeral freshwater pools comprise Garden north, Corio, Gull Wash and Frog but for this study only the last three were investigated. If an upper limit for salinity of $3^{0}/_{00}$ is accepted for freshwater (Williams 1964) then these pools fall into the freshwater category. The pattern of drying shows considerable variation. Gull Wash and Frog Pools have little bottom sediment and as evaporation proceeds the salinities increase to levels above $3^{0}/_{00}$ (Table 1). Corio Pool, a small pool with a thick ooze bottom is situated in an area of freshwater seepage and as drying proceeds there is no notable salinity increase. Flora in these pools is mainly filamentous algae, with small patches of *Elodea canadensis* in Corio Pool. The fauna (Table 1), consists of a few freshwater with mainly salt-tolerant freshwater species.

The ephemeral and permanent variably-saline swamps and ephemeral saline lakes comprise the major proportion of water bodies on the Island. The waters showed Na^{+} and Cl^{-} ionic dominance, high pH (Figs. 1 and 2) and extremely low phosphate concentration (0-2.48 µg l^{-1} range for five swamps in November 1982). Originally all ephemeral waters, three swamps (Barkers, Riflerange and Aerodrome) and two lakes (Negri and Sirius) are still in a natural state, however the other swamps, after excavation for marl now contain permanent water. Lighthouse swamp, prior to excavation, was consistently fresh with only freshwater and salt-tolerant freshwater species (Table 1). There were 12 dominant species of fauna in the swamp during the 1967 survey (Fig 1).

Lighthouse Swamp is now permanent and saline and the fauna (Table 1) consists of salt-tolerant freshwater species which appear with suitable

Table 1

Fauna of the inland waters of Rottnest Island

Classification Code	Fauna	Range of field salinity at Rottnest $^0/_{00}$	Corio			Gull Wash		Frog		Lighthouse					Salmon				Bickley		
			$1\cdot1^0/_{00}$S 18-x-1958	$0\cdot7^0/_{00}$S 29-viii-1982	$1\cdot4^0/_{00}$S 20-x-1982	$2\cdot5^0/_{00}$S 26-ix-1982	$6\cdot2^0/_{00}$S 20-x-1982	$2\cdot4^0/_{00}$S 2-ix-1978	$8\cdot7^0/_{00}$S 20-x-1982	$3\cdot1^0/_{00}$S 18-x-1958	$1\cdot4^0/_{00}$S 14-vii-1967	$6\cdot7^0/_{00}$S 2-ix-1978	$10\cdot4^0/_{00}$S 26-ix-1982	$14\cdot2^0/_{00}$S 28-xi-1982	$4\cdot7^0/_{00}$S 18-x-1958	$12\cdot5^0/_{00}$S 2-ix-1978	$15\cdot0^0/_{00}$S 26-ix-1982	$38\cdot7^0/_{00}$S 28-xi-1982	$4\cdot3^0/_{00}$S 18-x-1958	$13\cdot0^0/_{00}$S 26-ix-1982	$22\cdot9^0/_{00}$S 20-x-1982
Ol	OLIGOCHAETA	1 – 2·2	*	*	*						*										
Am	*Litoria moorei*	1 – 2·4	*	*	*			*			*										
Tu	TURBELLARIA	1 – 2·5				*					*										
Cl	*Chydorus sphaericus*	1 – 2·5		*							*										
Cl	*Ceriodaphnia quadrangula*	1 – 2·5				*															
Cl	*Alona quadrangularis*	1 – 2·5				*															
Cu	*Aedes camptorynchus*	1 – 4·3						*			*										
Os	*Candonocypris novaezelandiae*	1 – 4·3	*	*	*						*										
Cl	*Simocephalus elizabethae*	1 – 4·7	*							*	*				*						
Od	*Anax papuensis*	1 – 4·7								*	*				*				*		
Hy	*Berosus* sp.	1 – 4·7								*	*				*				*		
Os	*Sarscypridopsis aculeata*	1 – 6·2		*		*	*	*			*										
Ch	*Chironomus* aff. *alternans*	1 – 8·7		*	*		*	*	*		*				*						
Cx	*Sigara* sp.	1 – 8·7	*	*	*			*	*						*						
Co	*Mesocyclops albicans*	1 – 10·7		*	*	*	*	*	*		*	*	*								
Cx	*Micronecta* sp.	1 – 12·5	*	*	*		*	*	*		*	*	*			*			*		
Cl	*Daphnia carinata*	1 – 12·6				*	*	*		*	*				*				*		
Ch	*Tanytarsus fuscithorax*	1 – 14·8							*		*		*			*			*		
Cl	*Echinisca capensis*	1 – 14·8						*	*	*	*				*	*					
Os	*Kennethia cristata*	1 – 14·8									*		*		*						
Os	*Alboa woroa*	1 – 14·8	*							*	*	*	*		*	*			*		
Os	*Mytilocypris ambiguosa*	1 – 14·8		*							*		*		*				*		
No	*Paranisops* sp.	1 – 14·8	*							*			*								
Co	*Boeckella triarticulata*	1 – 15·7				*		*	*	*	*	*	*	*	*	*	*		*	*	
No	*Anisops* sp.	1 – 22·9	*	*	*		*			*	*	*	*	*	*	*	*		*	*	*
Od	*Austrolestes annulosus*	1 – 24·1								*	*	*	*	*	*	*	*		*		
St	*Odontomyia* ? sp.	1 – 36·0	*							*	*		*		*	*	*		*	*	
Ch	*Cryptochironomus curtivalva*	1 – 38·7							*				*	*		*	*	*	*		
Os	*Diacypris spinosa*	2·4 – 44·0						*	*			*	*	*		*	*	*		*	*
Ap	*Austrochiltonia subtenuis*	1 – 45·0							*		*	*	*	*	*	*	*	*	*	*	*
Cl	*Daphniopsis pusilla*	8·7 – 59·0														*	*			*	*
Dy	*Necterosoma penicillatus* (larva)	1 – 70·0	*	*	*	*	*	*	*	*	*	*	*		*	*	*	*	*	*	*
Os	*Mytilocypris minuta*	2·4 – 70·0						*	*			*	*	*		*	*	*		*	*
Co	*Microcyclops dengizicus*	8·7 – 70·0											*			*	*	*		*	*
Mo	*Coxiella striatula*	10·4 – 70·0											*				*	*		*	*
Cu	*Aedes ashworthi*	10·4 – 70·0											*			*				*	
Os	*Diacypris* aff. *spinosa*	15·9 – 81·0																			
Co	*Heterolaophonte wellsi*	15·9 – 87·0																			
Ch	*Procladius paludicola*	1 – 98·0							*				*	*		*	*	*		*	*
Co	*Mesochra baylyi*	10·4 – 104·0											*				*				
Po	POLYCHAETA	21·6 – 106·0																			
Co	*Calamoecia clitellata*	12.5 – 113·0														*	*	*		*	*
Dy	*Necterosoma penicillatus* (adult)	1 – 145·0	*							*	*		*	*	*	*	*				
Is	*Haloniscus searlei*	8·0 – 173·0											*	*			*			*	*
Tr	*Symphitoneuria wheeleri*	10·4 – 173·0											*	*			*	*			
Ch	*Tanytarsus barbitarsis*	12·5 – 173·0														*	*				
Ep	EPHYDRIDAE (larva)	15·0 – 173·0																			
Ce	*Culicoides waringi*	17·6 – 173·0																			
Ar	*Artemia* sp.	69·0 – 173·0																			

Classification code:

Ol, Annelida: Oligochaeta; Am, Vertebrata: Amphibia;

Tu, Platyhelminthes: Turbellaria; Cl, Crustacea: Cladocera;

Cu, Insecta: Diptera: Culicidae; Os, Crustacea: Ostracoda;

Od, Insecta: Odonata; Hy, Insecta: Coleoptera: Hydrophilidae;

Ch, Insecta: Diptera: Chironomidae; Cx, Insecta: Hemiptera: Corixidae;

Co, Crustacea: Copepoda; No, Insecta: Hemiptera: Notonectidae;

St, Insecta: Diptera: Stratiomyidae; Ap, Crustacea: Amphipoda;

Dy, Insecta: Coleoptera: Dytiscidae; Mo, Mollusca: Gastropoda;

Po, Annelida: Polychaeta; Is, Crustacea: Isopoda; Tr, Insecta: Trichoptera: Ep, Insecta: Diptera: Ephydridae; Ce, Insecta: Diptera: Ceratopogonidae; Ar, Crustacea: Anostraca.

Table 1—continued

Barkers				Para-keet		Bulldozer				Rifle Range			Aerodrome			Negri			Sirius		Pink				Bagdad			Govt. House		
8·7‰S 18-x-1958	7·7‰S 2-ix-1978	11·5‰S 26-ix-1982	14·8‰S 20-x-1982	21·6‰S 26-ix-1982	34·8‰S 28-xi-1982	12·6‰S 18-x-1958	15·7‰S 2-ix-1978	25·1‰S 26-ix-1982	44·0‰S 28-xi-1982	8·7‰S 2-ix-1978	23·8‰S 26-ix-1982	70·0‰S 28-xi-1982	8·0‰S 18-x-1958	22·0‰S 28-viii-1982	68·5‰S 28-xi-1982	15·9‰S 1-vii-1967	51·3‰S 21-xi-1967	33·7‰S 20-x-1982	45·0‰S 26-ix-1982	69·7‰S 20-x-1982	29·0‰S 25-viii-1967	145·0‰S 11-iii-1968	61·8‰S 20-x-1982	104·0‰S 28-xi-1982	173·0‰S 7-iv-1967	70·0‰S 7-ix-1967	98·0‰S 28-viii-1982	167·0‰S 7-iv-1967	107·0‰S 29-vii-1967	134·0‰S 28-viii-1982
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salinities and halobiont species (salinity range 10-300+‰, Bayly 1972).

The other swamps and lakes reflect the species composition now seen in Lighthouse Swamp with fewer species as the minimum salinities increase (Table 1). In Negri Lake during the 1967 survey there were eight dominant species and their relative abundances are shown in Fig. 2. Permanent saline swamps have the species shown in Lake Negri and the halobiont species *Haloniscus searlei*, *Symphitoneuria wheeleri* and *Culicoides waringi*. In 1958, the flora of some of these waters consisted of freshwater and saline species however, in latter years only the salt-tolerant *Cladophora spp*, *Lamprothamnium papulosum*, *Lepilaena preissi* and *Ruppia tuberosa* (Brock 1981, 1982 pers comm.) were recorded.

The permanent salt lakes have waters with Na^+ and Cl^- ionic dominance, high pH, extremely low phosphate concentrations (0-3.1 $\mu g\ l^{-1}$ range for five lakes in November 1982) and high salinities. Meromixis occurs in Government House, Herschell and Serpentine lakes and details together with mean depths are presented in Edward and Bunn (in prep.) on meromixis in the salt lakes of Rottnest Island.

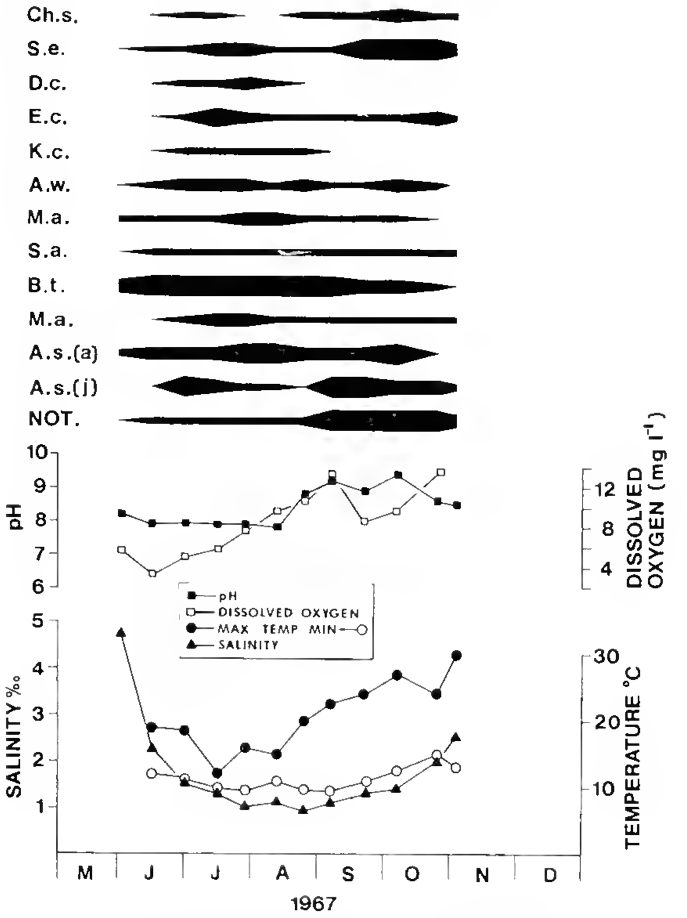

Figure 1.—Seasonal variations in the salinity, temperature, pH, dissolved oxygen and macrofauna of Lighthouse Swamp, Rottnest Island. Horizontal bars indicate presence and relative abundance of species. Abbreviation of species: Ch. s., *Chydorus sphaericus;* S.e., *Simocephalus elizabethae;* *D.c.,* *Daphnia carinata;* E.c. *Echinisca capensis;* K.c., *Kennethia cristata;* A.w., *Alboa woroou;* M.a., *Mytilocypris ambiguosa;* S.a., *Sarscypridopsis aculeata;* B.t., *Boeckella triarticulata;* M.a., *Mesocyclops albicans;* A.s., *Austrochiltonia subtenuis* (a., adults; j., juveniles) NOT., Notonectidae.

Fortnightly records of temperature, dissolved oxygen, pH and salinity are shown for Pink Lake (Fig. 3) and Bagdad Lake (Fig. 4). The usefulness of fortnightly oxygen analyses can be questioned. Samples were collected between 1200 and 1500 hours when dissolved oxygen concentrations are highest (Fig. 5). The values do indicate when oxygen levels in these high saline waters could be potentially limiting to biota.

The salt lakes have no macrophytes except Pink Lake which has *Ruppia tuberosa* throughout most of winter and spring. Apart from *Botryococcus* sp. recorded by Hodgkin (1959) and Playford (1977) the blue-green algae *Aphanothecae halophytica*, *Oscillatoria* sp., *Anacystis* sp. and *Spirulina* sp. and the diatom *Navicula* sp. form benthic microbial mats up to 10 cm thick in the deeper lakes. The green alga *Dunaliella salina* is also present (T. Moulton pers comm).

The fauna is restricted to six halobiont species, except for Pink and Bagdad lakes where other species appear with lower winter salinities (Table 1, Figs. 3 and 4).

Table 1 lists the fauna for all of the inland waters with the range of field salinities recorded at Rottnest Island for each species. The sample dates cover the widest range of salinities for each locality. Unidentified species from the initial study by Edward and Watson (1959), now identified, are

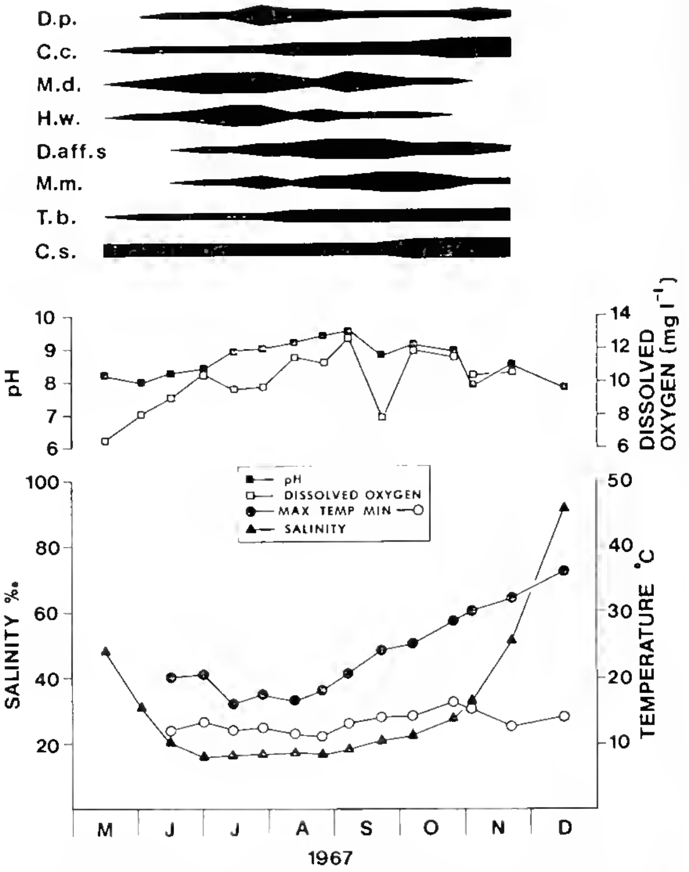

Figure 2.—Seasonal variations in the salinity, temperature, pH, dissolved oxygen and macrofauna of Negri Lake, Rottnest Island. Horizontal bars indicate presence and relative abundance of species. Abbreviation of species: D.p., *Daphniopsis pusilla;* C.c., *Calamoecia clitellata;* M.d., *Microcyclops dengizicus;* H.w., *Heterolaophonte wellsi*; D.aff.s., *Diacypris* aff. *spinosa*; M.m., *Mytilocypris minuta;* T.b., *Tanytarsus barbitarsis;* C.s., *Coxiella striatula.*

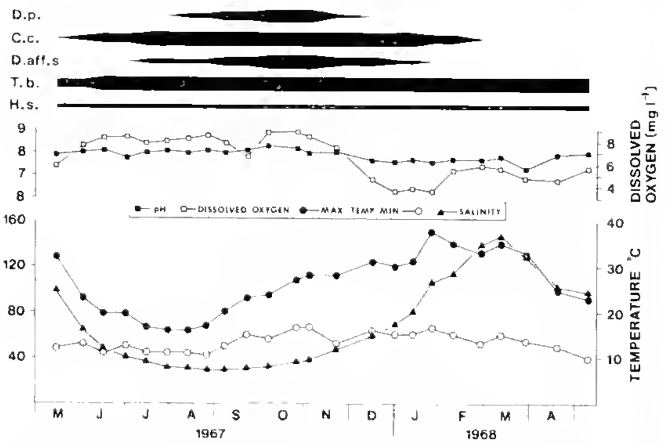

Figure 3.—Seasonal variations in the salinity, temperature, pH, dissolved oxygen and macrofauna of Pink Lake, Rottnest Island. Horizontal bars indicate presence and relative abundance of species. Abbreviation of species: D.p., *Daphniopsis pusilla*; C.c., *Calamoecia clitellata*; D.aff.s., *Diacypris* aff. *spinosa*; T.b., *Tanytarsus barbitarsis*; H.s., *Haloniscus searlei*.

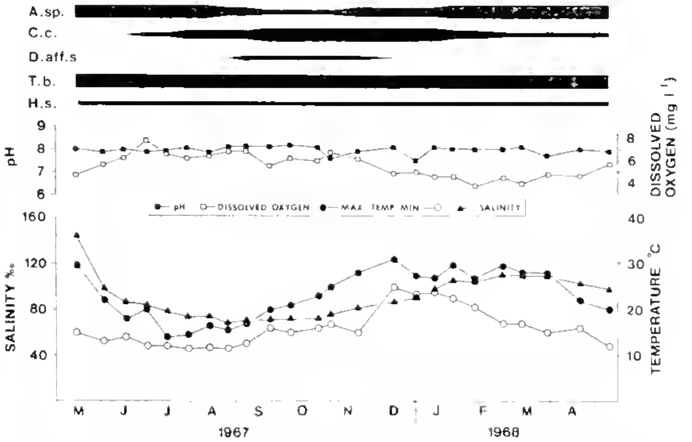

Figure 4.—Seasonal variations in the salinity, temperature, pH, dissolved oxygen and macrofauna of Bagdad Lake, Rottnest Island. Horizontal bars indicate presence and relative abundance of species. Abbreviation of species: A.sp., *Artemia* sp.; C.c., *Calamoecia clitellata*; D.aff.s., *Diacypris* aff. *spinosa*; T.b., *Tanytarsus barbitarsis*; H.s., *Haloniscus searlei*.

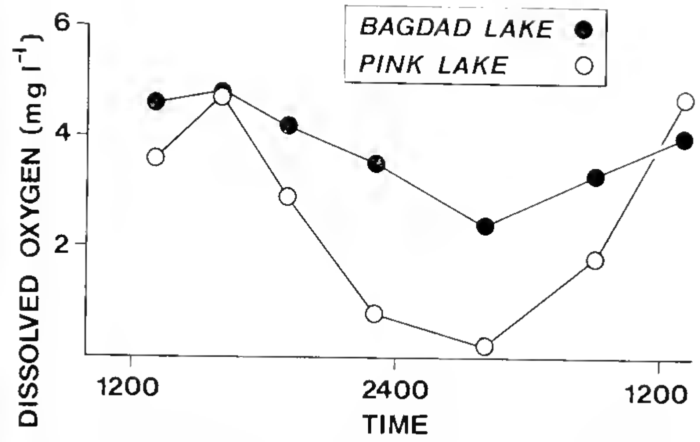

Figure 5.—Diel dissolved oxygen in Bagdad and Pink Lakes, Rottnest Island. (25.i.1968).

included. Garden, Herschell and Serpentine Lakes are not listed as they contain the same species as Government House lake. In addition there are single records for a number of species; chironomids, *Corynoneura scutellata* and *Polypedilum nubifer* (Lighthouse Swamp, 22-ix-1967, 1.3$^{0}/_{00}$S), *Dicrotendipes conjunctus* Corio pool, 10-x-1959, 1.8$^{0}/_{00}$S); cyclopoid copepods, *Halicyclops* sp. (Salmon Swamp, 3-ix-1978, 12.5$^{0}/_{00}$S) and *Neocyclops* sp. (Pink Lake, 25-i-1968, 106$^{0}/_{00}$S); cladoceran *Biapertura rigidicaudis* and rotifer *Brachionus* sp. (both shallow pool, south side of Serpentine Lake, coll. I.A.E. Bayly, 11-viii-1973); isopod *Alloniscus nicobaricus* (Serpentine Lake, 25-vii-1982, 126$^{0}/_{00}$S); conchostracans *Limnetis* sp. and *Limnadia* sp. (small shallow freshwater area, east end of airstrip, coll. I. A. E. Bayly, 11-viii-1973).

The data in Table 1 were used to explore the relationship between salinity and number of species in the inland waters of Rottnest Island. Excluding 1958 data which are incomplete and samples from freshwater pools, the number of species in each sample decreases with increasing salinity according to the relationship; number of species = 23.16 — 3.34 (ln salinity in $^{0}/_{00}$). [n = 37, p ($\beta = 0$) 0.005; $r^2 = 0.51$].

Discussion

The inland waters of Rottnest Island range in salinity from freshwater ($< 1^{0}/_{00}$) to high saline ($> 100^{0}/_{00}$), however only one small water body, Corio Pool, is consistently freshwater. Physical and chemical aspects of the saline waters require little comment: high pH and Na^+ and Cl^- ionic dominance parallels the values for other saline waters in Western Australia (Williams and Buckney 1976, Geddes *et al.* 1981, Halse 1981) and south east Australia (Williams 1981). The waters show extremely low phosphate concentrations and are characterised by changing salinities and temperatures. Fauna utilizing the waters must be tolerant of these changes and this is attested by the high number of freshwater salt-tolerant and halobiont species.

Some comment can be made about the fauna in relation to known biology and field salinities. Although Cladocera are a predominantly freshwater group some species adapt to higher salinities. For *Chydorus sphaericus*, *Ceriodaphnia quadrangula*, *Simocephalus elizabethae* and *Daphnia carinata* the salinities tolerated on Rottnest Island are the highest recorded. In eastern Australia they are only known from freshwater (Timms 1981). *Echinisca capensis* tolerated salinities up to 14.8$^{0}/_{00}$ and was occasionally found with the halobiont cladoceran *Daphniopsis pusilla*. The range of salinities recorded for *D. pusilla* is similar to that known for the species throughout southern Australia (De Deckker and Geddes 1980, Geddes *et al.* 1981, Williams 1981) with a maximum salinity of 71$^{0}/_{00}$ recorded by Halse (1981).

The Ostracoda *Kennethia cristata* and *Alboa worooa* are freshwater species (De Deckker pers comm, De Deckker 1981a) however on Rottnest Island salinities of 14.8$^{0}/_{00}$ are tolerated. *Sarscypridopsis aculeata* a cosmopolitan species is recorded from salinities up to 21.3$^{0}/_{00}$ (De Deckker 1981b). *Mytilocypris ambiguosa* a freshwater species tolerated salinities of 14.8$^{0}/_{00}$. and *M. minuta* is known from similar salinities (Geddes *et al.* 1981, Halse 1981) on mainland Western Australia. *Diacypris spinosa* is reported by De Deckker (1981c) from a similar salinity range, 4-52$^{0}/_{00}$ and *D.* aff. *spinosa*, which is close to *D. spinosa* (De Deckker pers comm) is a halobiont species.

Copepoda include the freshwater salt-tolerant *Mesocyclops albicans* and *Boeckella triarticulata*, a common and widely-distributed Australasian species occurring in salinities up to 22$^{0}/_{00}$ in highly alkaline lakes in eastern Australia (Bayly 1969, Bayly 1979). *Microcyclops dengizicus*, *Heterolaophonte wellsi*, *Mesochra baylyi* and *Calamoecia clitellata* are all halobiont species.

The amphipod, *Austrochiltonia subtenuis* is a widespread southern Australian species (Williams 1962). Halse (1981) has recorded the species from a Western Australian mainland lake at a salinity of 71$^{0}/_{00}$.

Two species of Isopoda occurred in the salt lakes. *Haloniscus searlei* is a common halobiont in southern Australia and is reported from salinities of 30-110$^{0}/_{00}$ by Williams (1981). On Rottnest Island the species occupied all permanent saline waters with a salinity range of 8-173$^{0}/_{00}$. *Alloniscus nicobaricus* was collected from Serpentine Lake at a salinity of $126^{0}/_{00}$ and is the first record for this species from high saline inland waters.

The Anostraca was represented by the cosmopolitan *Artemia*, recorded by Hodgkin (1959) as *A. salina*. Because of confusion in the taxonomy it is best referred to as *Artemia* sp. (Geddes 1981). The species was confined to the permanent salt lakes, which is contrary to the statement by Geddes (1981) that *Artemia* is not found in any natural salt lake in Australia. The explanation lies in the previous use of part of Government House Lake for salt production and eggs must have been introduced with the salt-cleaning machinery. The single species of *Artemia* on Rottnest Island contrasts with the ten species of Anostraca recorded from saline lakes on the Western Australian mainland by Geddes *et al.* (1981).

The mollusc, *Coxiella striatula* occupies shallow littoral areas over a range of salinity consistent with ranges for other species of *Coxiella* in southern Australia (Bayly and Williams 1973, De Deckker and Geddes 1980, Halse 1981).

Among the Insecta, *Necterosoma penicillatus* adults were collected from all waters, however, the larvae, were restricted to waters with salinities less than $70^{0}/_{00}$. The species is common in salt lakes in southern Australia (Watts 1978) and the salinity range at Rottnest Island is considerably wider than those recorded by Bayly and Williams (1966) and Halse (1981). All chironomid larvae, apart from *Chironomus* aff. *alternans* have been recorded by Halse (1981) from saline waters on the mainland of Western Australia. *Tanytarsus barbitarsis* is a halobiont species occurring over southern Australia (Glover 1973, Williams 1981). The range of salinity tolerated by each species on Rottnest Island is the widest recorded. Larvae of *Culicoides waringi* have been collected from coastal salt marshes in southern Australia (Dyce and Murray 1967). On Rottnest Island, larvae were common in the salt lakes and inhabited detritus in littoral and deep areas, including the benthic microbial mats.

The fauna is clearly adapted to changes in salinity with many freshwater salt-tolerant species, particularly *Daphnia carinata*, *Echinisca capensis*, *Kennethia cristata*, *Alboa worooa*, *Cryptochironomus curtivalva*, *Procladius paludicola* and *Necterosoma penicillatus*, tolerating high salinities. For halobiont species the lowest salinity tolerated is important allowing some species to colonise and persist in waters in association with freshwater salt-tolerant species.

Comparing species from Rottnest Island with those recorded from saline waters in south east Australia (De Deckker and Geddes 1980, Williams 1981) and mainland Western Australia (Geddes *et al.* 1981, Halse 1981) further confirms the view of Geddes *et al.* (1981) that similarities exist between the faunas of saline waters in south west and south east Australia. Of 43 species recorded from Rottnest Island with salinity tolerances between 4.3 and $173^{0}/_{00}$, 12 species, *Simocephalus elizabethae*, *Daphnia carinata*, *Daphniopsis pusilla*, *Boeckella triarticulata*, *Calamoecia clitellata*, *Mesochra baylyi*, *Mytilocypris ambiguosa*, *Tanytarsus barbitarsis*, *Haloniscus searlei*, *Austrochiltonia subtenuis*, *Culicoides waringi* and *Necterosoma penicillatus* are shared with south east Australia. Overall, the fauna is similar to other coastal saline water fauna in Western Australia (Halse 1981) and southern Australia (Bayly 1970, De Deckker and Geddes 1980) and lacks the richness of species in the Anostraca, Copepoda and Ostracoda recorded for saline waters in inland Western Australia (Geddes *et al.* 1981).

Previous studies on the fauna of saline waters (Bayly and Williams 1966, De Deckker and Geddes 1980, Williams 1981) noted a relationship between the number of species and salinity. For inland saline waters of Rottnest Island there is a significant negative correlation between species diversity and salinity.

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The birds of Rottnest Island

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Abstract

The literature on the birds of Rottnest Island is reviewed and presented in a Table which lists the species of bird which have been seen on, around or over the island. Each species has been classed as resident (N=28), breeding migrant (N=6), non-breeding migrant (N=21) and vagrant (N=54) and listed under the habitats in which it has been recorded. In addition 4 species which formerly occurred on the island are also listed.

The importance of Rottnest Island as a conservation reserve is pointed out and the need for a long-term management plan for the island is stressed.

Introduction and literature review

In reviewing the literature, it is convenient to regard publications relating to the birds of Rottnest Island as coming from two periods: before the Biological Field Station was opened, and after. Before this event it was difficult for biologists to spend long periods on the island and publications reflect both this and the fact that ornithology in Australia was at the stage of producing inventories. Information on the birds appeared as: annotated species lists based on one visit (Lawson 1905, Kilpatrick 1932); annotated species lists based on more than one visit and incorporating observations of people other than the author (Alexander 1921, Glauert 1929, Serventy 1938, 1948); notes adding to existing birds lists (Conigrave 1909, Storr and Dunnet 1955, McCrum and Slater 1955, Storr 1957, Ford 1957, 1958); comments on breeding (Robinson 1935, Serventy 1947, Reid 1949, 1950, Serventy 1950). None provided detailed analyses of any of the birds, although Serventy (1950) gave an account of three breeding seasons of the Fairy Tern *Sterna nereis* based on a few visits each season (2 in 1947: 4 in 1949: 1 in 1950).

The early phase of the Field Station was reviewed by Hodgkin and Sheard (1959) and included a bird list for each habitat on the island (Serventy and Storr 1959). Since then the literature has been dominated by biologists operating from the Field Station, resulting in more detailed publications (Storr 1964a, 1964b, 1965a, 1965b, 1976; Holsworth 1965; Riggert 1969, 1977; Williams 1971, 1979; Williams and Main 1976, 1977). Notes which add to distribution lists are still published (Storr and Ford 1962, McMillan 1963, Smith and Saunders 1980), as are notes about breeding (Abbott 1977, Abbott *et al.* 1978), feeding (Farmer 1961) and longevity (Robin 1966).

Of these publications, Storr's papers (1964b, 1965a, 1965b) are the most comprehensive. Based on data collected during 275 days on the island from January 1953, together with previous literature and data from his colleagues, he presented detailed information on the status and habitat preferences of each species.

Since this work appeared there have been several studies of single species. Holsworth (1965) gathered data over three years on the breeding and juvenile dispersal of the Osprey *Pandion haliaetus*. During the period 1961-1963, three pairs bred each season, producing a total of 15 young of which 10 were banded. The three band returns showed that the immature birds disperse widely from the island.

Between October 1964 and December 1974 a study of the breeding biology and population dynamics of the Mountain Duck *Tadorna tadornoides* was carried out on the island (Riggert 1969, 1977). In addition, the possible effects on this population of shooting pressure on the mainland during the annual duck-hunting season was investigated. During the study 1690 ducks were banded, and of these, 1012 were marked with "A-frame" bill tags to enable individuals to be recognized from a distance. Counts of broods and of the population on the island were made at monthly intervals while band recoveries gave estimates of dispersal and mortality. Riggert found that the Rottnest Island population forms part of the mainland population with migration to and from the island. Breeding numbers are limited by the number of brood territories, each of which must have fresh water available for the successful rearing of ducklings. Decreases in numbers during the year are related to dispersal of birds in summer caused by a reduction in the area of surface water and the number of fresh water seepages, as well as to dispersal in early winter of birds not successful in establishing brood territories. Population increases are due to recruitment in spring, as a result of breeding and to immigration in autumn of birds seeking brood territories. Riggert concluded that shooting on the mainland does not seriously affect the population of Mountain Duck on Rottnest Island.

The genus *Epthianura* (chats) consists of four Australian species which have been studied by Williams and Main (Williams 1971, 1979, Williams and Main 1976, 1977). They examined the physiological adaptations enabling chats to survive in arid conditions. The White-fronted Chat *E. albifrons* is the only species of this genus which occurs on Rottnest Island and Williams and Main (*op cit*) investigated seasonal movements, metabolism, evaporative water loss, tolerance to electrolytes in drinking water and water economy. Williams (1971, 1979) also examined the breeding biology, particularly timing of reproduction in relation to seasonal condition, nesting area and habitat with reference to availabiliy of fresh water and aspects of territoriality relevant to the maintenance of a water balance. On Rottnest Island, nesting was dependant upon winter rains with reduced nesting effort correlated with poor rainfall. Williams and Main (*op cit*) found that the conditions required for reproduction in each species are dependant upon their respective water balance physiology.

Rottnest Island and its adjacent islets, together with other islands round the south-west of Western Australia, have been used for examining theories on bird species diversity (Abbott, 1976, 1978, 1980). In addition to these studies, three general bird lists have been produced. The first, by O'Connor *et al.* (1977) is an account of the environment of Rottnest Island which includes a list of birds for each habitat. Information has been drawn mainly from the literature backed up by limited field observations made between 24 August and 16 December 1976. The second list was published by the Rottnest Island Board (Jenkins 1977) in a book on the natural features of the island but contains some inaccuracies and omissions. The most recent list was published by Saunders *et al.* (1981) which lists the birds together with information on breeding seasons, status and habitat. This was based on published information as well as personal observations of the compilers and was produced as a service to ornithologists visting the island.

The status of the birds of Rottnest Island

An account of the birds seen on, around or over Rottnest Island is given in Table 1 and is based on published literature. Each species is classed as resident, breeding migrant, non-breeding migrant or vagrant, and is listed under the habitats in which it has been seen. Literature citings are also given after each species, together with information on their abundance and breeding status, if given in the cited article. Between 19 December 1981 and 5 January 1983, a survey was conducted of the birds of the island based on visits at six-weekly intervals, during which 69 days were spent on the island. During each visit all species present on or around the salt lakes, swamps and sections of the coast were counted and the other habitats were surveyed. Those species seen during the course of the work, together with comments on their abundance are indicated in Table 1. We found evidence of breeding in 24 of the 28 resident species and 5 of the 6 breeding migrant species. In all, 71 species were seen: all of the resident species; 5 of the 6 species listed as breeding migrants; 17 of the 21 non-breeding migrants; and 21 of the 54 vagrants. Although the results of this surveys have not been analysed in detail, preliminary results make an interesting comparison with those published by Storr nearly 20 years ago. Our results indicate that at least 10 species appear to have a different occurrence from that listed by Storr (1964b, 1965a, 1965b). The Little Pied Cormorant *Phalacrocorax melanoleucos* was listed as an uncommon visitor to Thomson Bay, but is now found in small numbers around the island all year. The White-faced Heron *Ardea novaehollandiae* was an uncommon but regular visitor, but last year was a vagrant (1 seen in April). The Black Swan *Cygnus atratus* had been seen once by 1961 but more recently small numbers have been seen regularly, mainly on Garden Lake. Black Duck *Anas superciliosa* now occur in small numbers on Salmon and Lighthouse Swamps during the summer whereas Storr *(op cit)* listed them as vagrants. During the period Storr was working on the island, these swamps were ephemeral, drying up in summer. Marl was extracted from these swamps in the early 1970s for use in road building. This resulted in permanent lakes (Edward, pers. comm.) which provide more suitable habitat for Black Ducks. Red-necked Avocets *Recurvirostra novaehollandiae*, now present in small numbers most of the year, were listed as rare visitors. Grey-tailed Tattlers *Tringa brevipes* and Bar-tailed Godwits *Limosa lapponica* appear now to be non-breeding migrants occurring in small numbers whereas Storr did not list the former and regarded the latter as a rare visitor. In the past, the Sacred Kingfisher *Halcyon sancta* was uncommon and of uncertain status, whereas now it is a common breeding resident particularly round the main settlement. The Rainbow Bee-eater *Merops ornatus* was not recorded on Rottnest Island until December 1977 (Abbott *et al.* 1978) and since then it has established itself as a breeding migrant. The Tree Martin *Cecropis nigricans*, formerly an uncommon visitor with a few birds visiting the island most summers, is now a common non-breeding migrant which can be seen in large groups all over the island.

More detailed analysis of our survey results may indicate other changes and reveal some of the reasons for the changes in status.

Discussion

As Seddon (1972) points out, Rottnest Island is an outstanding refuge, nesting ground and seasonal feeding ground for a great variety of birds because it offers a multiplicity of habitats. In all, 113

Table 1

Status of the birds of Rottnest Island and the habitats in which they may be found. Numbers after the specific name refer to articles in which that species is mentioned. The numbers are shown after each reference in the reference list at the end of the text and follow alphabetic order. Letters after a number indicates that the reference makes some comment about the species: either it's numerical status, C = common, U = uncommon, **X** = extinct; or some other point of interest, B = breeding noted, E = ecological study, F = feeding record, S = sight record, T = taxonomic record. The symbol * indicates that species was seen during the survey conducted by us over 69 days between 19 December 1981 and 5 January 1983. (± 3) after specific names of vagrant species indicates that species has been recorded as seen more than three times (+3) or less than three times (–3).

A. RESIDENT SPECIES (N=28)

HEATH

Nankeen Kestrel (*Falco cenchroides*) 6, 13, 16, 17U, 18U, 24C, 32UB, 35, 36, 37, 46CB, *UB.

Peafowl (*Pavo cristatus*) 16, 17C, 24U, 32UB, 35, 36, 37U, 46UB, *UB.

Ring-necked Pheasant (*Phasianus colchicus*) 10F, 16, 17C, 24C, 32CB, 35, 36, 37, 46CB, *C.

Banded Plover (*Vanellus tricolor*) 16, 24C, 32UB, 35, 37B, 45CB, *UB.

Spotted Turtledove (*Streptopelia chinensis*) 16, 24C, 32C, 34S, 35, 36, 37, 46C, *UB.

Laughing Turtledove (*Streptopelia senegalensis*) 16, 24C, 32C 34S, 35, 36, 37, 46CB, *CB.

Welcome Swallow (*Hirundo neoxena*) 6CB, 13C, 16, 17CB, 18CB, 24CB, 32CB, 35, 36B, 37C, 46CB, *CB.

Richard's Pipit (*Anthus novaeseelandiae*) 6, 13C, 16, 18CB, 24U, 32C, 35, 37, 46CB, *U.

Singing Honeyeater (*Lichenostomus virescens*) 6C, 13C, 16, 17CB, 18C, 22T, 24C, 32C, 35, 36, 37C, 46C, *CB.

White-fronted Chat (*Epthianura albifrons*) 6, 13C, 16, 17CB, 18U, 24C, 32CB, 35, 36B, 37, 46CB, 50E, 51E, 52E, 53E, *CB.

Silvereye (*Zosterops lateralis*) 2S, 6, 13C, 16, 17CB, 18C, 24C, 32CB, 35, 36C, 37C, 46CB, *CB.

Australian Raven (*Corvus coronoides*) 6C, 13C, 16, 17C, 18U, 24C, 32C, 35, 37, 46CB, *CB.

WOODLAND

Nankeen Kestrel. See under HEATH.

Peafowl, See under HEATH.

Ring-necked Pheasant. See under HEATH.

Spotted Turtledove. See under HEATH.

Laughing Turtledove. See under HEATH.

Sacred Kingfisher (*Halcyon sancta*) 16, 17U, 24C, 32U, 35, 37, 46UB, *CB.

Welcome Swallow. See under HEATH.

Red-capped Robin (*Petroica goodenovii*) 6CB, 13CB, 16, 17CB, 18CB, 24C, 32CB, 35C, 36, 37, 46CB, *CB.

Golden Whistler (*Pachycephala pectoralis*) 6, 13, 18C, 24C, 32U, 35, 36, 37, 46C, *CB.

Spotted Scrub Wren (*Sericornis maculatus*) 6, 13, 18U, 24U, 32U, 35, 36C, 37U, 46C, *UB.

Western Warbler (*Gerygone fusca*) 24C, 32U, 37, 46C, *CB.

Singing Honeyeater. See under HEATH.

Silvereye. See under HEATH.

Australian Raven. See under HEATH.

SALT LAKES/SWAMPS

Black Swan (*Cygnus atraus*) 16, 24, 32U, 45, *U.

Mountain Duck (*Tadorna tadornoides*) 6U, 13CB, 16, 17C, 24C, 28E, 29E, 31B, 32CB, 35B, 36B, 37B, 45CB, *CB.

Pied Oystercatcher (*Haematopus ostralegus*) 13, 17U, 24U, 32UB, 36, 37, 45UB, 47UB, *UB.

Red-capped Dotterel (*Charadrius ruficapillus*) 6CB, 13CB, 17B, 18CB, 24, 32CB, 36B, 37, 45CB, *CB.

Silver Gull (*Larus novaehollandiae*) 2B, 6C, 13C, 16, 17CB, 18C, 24CB, 26B, 32CB, 36CB, 37B, 44CB, 47CB, *CB.

Caspian Tern (*Hydroprogne caspia*) 17U, 24UB, 32UB, 37B, 44UB, 47UB, *UB.

Crested Tern (*Sterna bergii*) 2B, 6CB, 13C, 16, 17C, 18CB, 24CB, 26B, 30S, 32CB, 36CB, 37B, 44CB, 47CB, *CB.

Rock Parrot (*Neophema petrophila*) 6CB, 13CB, 16, 17C, 18CB, 24U, 32UB, 35, 36CB, 37B, 46UB, *UB.

Welcome Swallow. See under HEATH.

White-fronted Chat. See under HEATH.

Australian Raven. See under HEATH.

COAST

Pied Cormorant (*Phalacrocorax varius*) 2B, 6CB, 13, 16, 18CB, 24CB, 27B, 32CB, 37B, 44CB, 47C, *CB.

Reef Heron (*Egretta sacra*) 6U, 13UB, 24UB, 32U, 36U, 37, 44UB, 47UB, *U.

Mountain Duck. See under SALT LAKES SWAMPS.

Osprey (*Pandion haliaetus*) 2B, 6UB, 13B, 15B, 16, 18UB, 24UB, 31B, 32UB, 36, 37B, 44UB, *UB.

Pied Oystercatcher. See under SALT LAKES/SWAMPS.

Red-capped Dotterel. See under SALT LAKE/SWAMPS.

Silver Gull. See under SALT LAKES/SWAMPS.

Caspian Trn. See under SALT LAKES/SWAMPS.

Crested Tern. See under SALT LAKES/SWAMPS.

Rock Parrot. See under SALT LAKES/SWAMPS.

Welcome Swallow. See under HEATH.

OCEAN

Silver Gull. See under SALT LAKES/SWAMPS.

Crested Tern. See under SALT LAKES/SWAMPS.

B. MIGRANT SPECIES WHICH BREED ON ROTTNEST (N=6).

HEATH

Rainbow Bee-eater (*Meerops ornatus* 5S, 24, 32, *UB.

WOODLAND

Fan-tailed Cuckoo (*Cuculus pyrrhophanus*) 6C, 13, 16, 24C, 32U, 35, 36, 37C, 46C, *UB.

Golden Bronze Cuckoo (*Chrysococcyx plagosus*) 13, 16, 24U, 32U, 35, 46U.

Rainbow Bee-eater. See under HEATH.

SALT LAKES/SWAMPS

Fairy Tern (*Sterna nereis*) 5B, 6CB, 13B, 17B, 18U, 24CB, 32CB, 36CB, 37B, 38B, 44CB, 47CB, *CB.

COAST

Wedge-tailed Shearwater (*Puffinus pacificus*) 2B, 6CB, 13CB, 16, 17B, 18UB, 24C, 32CB, 36B, 37B, 39B, 44CB, 47CB, *CB.

Bridled Tern (*Sterna anaethetus*) 2B, 6B, 13B, 17B, 24CB, 32UB, 36B, 37B, 44CB, 47CB, *CB.

Fairy Tern. See under SALT LAKES SWAMPS.

OCEAN

Wedge-tailed Shearwater. See under BEACH.

Bridled Tern. See under BEACH.

C. MIGRANT SPECIES WHICH DO NOT BREED ON ROTTNEST (N=21)

HEATH

Tree Martin (*Cecropis nigricans*) 13, 24U, 32U, 35, 46U, *C.

WOODLAND

Tree Martin. See under HEATH.

SALT LAKES/SWAMPS

White-faced Heron (*Ardea novaehollandiae*) 13, 24, 32U, 35, 37C, 45U, *.

Grey Teal (*Anas gibberifrons*) 16, 24, 32U, 37U, 45U, *U.

Eastern Golden Plover (*Pluvialus dominica*) 6, 13, 24, 32U, 37U, 45U, *U.

Grey Plover (*Pluvialus squatarola*) 16, 24, 32U, 37, 45C, *U.

Hooded Dotterel (*Charadrius rubricollis*) 11S, 13, 18U, 24, 32U, 36, 37U, 45U.

Large-billed Dotterel (*Charadrius leschenaultii*) 24, 32U, 37U, 45U, *.

Banded Stilt (*Cladorhynchus leucocephalus*) 6C, 13, 16, 17, 18C, 24C, 32C, 35, 36, 37, 41, 45C, *C.

Ruddy Turnstone (*Arenaria interpres*) 6U, 13, 18U, 24C, 32C, 36C, 37C, 45C, *C.

Sharp-tailed Sandpiper (*Calidris acuminata*)13, 16, 17, 18C, 24, 32U, 36C, 37U, 45U, *.

Red-necked Stint (*Calidris ruficollis*) 6C, 13, 16, 18C, 24C, 32C, 37C, 45C, *C.

Curlew Sandpiper (*Calidris ferruginea*) 6C, 13C, 16, 18U, 24C, 32C, 37C, 45C, *C.

Sanderling (*Calidris alba*) 24U, 32U, 37U, 45U, *U.

Tree Martin. See under HEATH.

COAST

Grey Plover. See under SALT LAKES-SWAMPS.

Large-billed Dotterel. See under SALT LAKES/SWAMPS.

Ruddy Turnstone. See under SALT LAKES/SWAMPS.

Whimbrel (*Numenius phaeopus*) 9S, 11S, 24U, 32U, 37, 45U, *U.

Red-necked Stint. See under SALT LAKE/SWAMPS.

Sanderling. See SALT LAKES/SWAMPS.

OCEAN

Yellow-nosed Albatross (*Diomedea chlororhynchos*) 13, 24, 32C, 44C, 47, *.

Southern Giant Petrel (*Macronectes giganteus*) 13, 24, 32, 44, 47, *.

Cape Petrel (*Daption capense*) 24, 32U, 44, 47.

Wilson's Storm Petrel (*Oceanites oceanicus*) 24, 32U, 44.

Australian Gannet (*Morus serrator*) 24, 32U, 37, 42S, 44U, 47, *.

Great Skua (*Stercorarius skua*) 24, 32U, 44U.

Arctic Skua (*Stercorarius parasiticus*) 24, 32U, 37, 44U, *.

D. VAGRANT SPECIES (N=54)

HEATH

Black-shouldered Kite (*Elanus notatus*) (–3), *.

Brown Goshawk (*Accipiter fasciatus*) (–3), 24, 35, 46.

Brown Falcon (*Falco berigora*) (+3), 13, 18U, 24, 32U, 35, 46.

Australian Magpie Lark (*Grallina cyanoleuca*) (+3), 13, 24, 32, 35, 46.

WOODLAND

Brown Falcon. See under HEATH.

White-tailed Black Cockatoo (*Calptorhynchus latirostris*) (–3), 24, 35, 46.

Galah (*Cacatua roseicapilla*) (–3), 24, 46.

Purple-crowned Lorikeet (*Glossopsitta porphyrocephala*) (–3), 32.

Twenty-eight Parrot (*Barnardius zonarius*) (–3), 24, 46.

Pallid Cuckoo (*Cuculus pallidus*) (+3), 6, 13, 16, 17U, 18U, 24, 32, 35, 46, *.

Horsefield's Bronze Cuckoo (*Chrysococcyx basalis*) (–3), 24, 32, 46.

Boobook (*Ninox novaeseelandiae*) (–3), 13, 24, 32, 35, 46.

Black-faced Cuckoo Shrike (*Coracina novaehollandiae*) (+3), 13, 24, 32, 35, 46, *.

White-winged Triller (*Lalage sueurii*) (–3), 13, 24, 32, 35, 46, *.

Grey Fantail (*Rhipidura fuliginosa*) (–3), 24, 32, 46.

Willie Wagtail (*Rhipidura leucophrys*) (+3), 17U, 24, 32, 35, 36, 46, *.

Red Wattle bird (*Anthochaera carunculata*) (–3), 24, 32, 35, 46.

Striated Pardalote (*Pardalotus striatus*) (+3), 24, 46.

Australian Magpie (*Gymnorhina tibicen*) (+3), 16, 24, 35, 46, *.

SALT LAKES/SWAMPS

Australasian Little Grebe (*Tachybaptus novaehollandiae*) (–3), 13, 24, 32, 35, 45.

Hoary-headed Grebe (*Poliocephalus poliocephalus*) (+3), 13, 24, 32, 35, 45U, *

Darter (*Anhinga melanogaster*) (–3), 24, 32, 44.

Large Egret (*Egretta Alba*) (–3), *.

Little Bittern (*Ixobrychus minutus*) (–3), 24, 32, 45.

Straw-necked Ibis (*Threskiornis spinicollis*) (–3), 13, 24, 32, 35, 36, 45.

Black Duck (*Anas superciliosa*) (+3), 13, 16, 18U, 24, 32, 35, 45, *U.

White-eyed Duck (*Aythia australis*) (–3), 24, 32, 45.

Mongolian Dotterel (*Charadrius mongolus*) (–3), *.

Pied Stilt (*Himantopus himantopus*) (+3), 24, 32, 35, 45.

Red-necked Avocet (*Recurvirostra novaehollandiae*) (+3), 6, 13, 24U, 32, 45U, *U.

Grey-Tailed Tattler (*Tringa brevipes*) (+3), 32, *U.

Greenshank (*Tringa nebularia*) (–3), 16, 24, 32, 37U, 45U.

Common Sandpiper (*Tringa hypoleucos*) (+3), 16, 24, 32, 36C, 45U, *.

Terek Sandpiper (*Tringa terek*) (–3), *.

Knot (*Calidris canutus*) (–3), 16, *.

Northern Phalarope (*Phalaropus lobatus*) (–3), 32, 40S.

COAST

Little Pied Cormorant (*Phalacrocorax melanoleucos*) (+3), 24, 32, 44, 47, *U.

Black Cormorant (*Phalacrocorax carbo*) (–3), *.

Little Black Cormorant (*Phalacrocorax sulcirostris*) (–3), 24, 32, 44, 47.

Red-tailed Tropic Bird (*Phaethon rubricauda*) (+3), 24, 32U**B**, 36, 44U**B**, 47U**B**.

White-breasted Sea Eagle (*Haliaeetus leucogaster*) (–3), 24, 32, 44.

Sooty Oystercatcher (*Haematopus fuliginosus*) (+3), 6U, 11S, 13, 18U, 19S, 32U, 45U, 47.

Common Sandpiper. See under SALT LAKES/SWAMPS.

Bar-tailed Godwit (*Limosa lapponica*) (+3), 24, 32, 36, 45, *U.

White-winged Black Tern (*Chlidonias leucoptera*) (–3), 24, 32, 44.

Roseate Tern (*Sterna dougallii*) (–3), 24, 32, 44, 49S.

OCEAN

Little Penguin (*Endyptula minor*) (+3), 24, 32, 44.

Rockhopper Penguin (*Eudyptes chrysocome*) (+3), 6, 7S, 11S, 13, 24, 32, 36, 44, 47.

Wandering Albatross (*Diomedea exulans*) (–3), 24, 32, 44.

Black-browed Albatross (*Diomedea melanophrys*) (–3), *.

Grey-headed Albatross (*Diomedea chrysostoma*) (–3), 24, 32, 44, 47, *.

White-headed Petrel (*Pterodroma lessonii*) (–3), 24, 44.

Antarctic Prion (*Pachyptila desolata*) (–3), 24, 44, 47.

Antarctic Fulmar (*Fulmarus glacialoides*) (–3), 20S, 24, 32, 44, 47.

Red-tailed Tropic Bird. See under BEACH.

Pacific Gull (*Larus pacificus*) (–3), 13, 24, 32, 44.

SKY

Fork-tailed Swift (*Apus pacificus*) (+3), 12S, 21S, 24, 32, 46, 48S, *.

E. MISCELLANEOUS SPECIES

Little Shearwater (*Puffinus assimilis*) Formerly bred, last recorded 1935. 24, 31**B**, 32, 36**B**, 44, 47.

Black-faced Cormorant (*Phalacrocorax fuscescens*) 17**B**. Mistaken identification of Pied Cormorant.

Whistling Kite (*Haliastur sphenurus*) 24, 35. Based on one doubtful record queried by 46.

Red-kneed Dotterel (*Charadrius cinctus*) 13, 24, but based on second hand report according to 45.

Domestic Pigeon (*Columba livia*) Introduced, now extinct 24X, 46X.

Brush Bronze Wing (*Phaps elegans*) Believed to have occurred. 13, 16X, 24X, 32X, 35X, 36X, 37X, 46X.

Rufous Whistler (*Pachycephala rufiventris*) Resident, now extinct. 6, 13, 18U, 24X, 32X, 35, 37X, 46X.

species of bird have been reliably recorded on, over or around the 1900 ha of Rottnest Island (Table 1). This is nearly twice as many as has been recorded from the 1100 ha of Garden Island (Abbott 1980, Davies 1980). It is not profitable to make a detailed analysis of the differences in the avifauna of the two islands because Garden Island has been poorly studied in comparison with Rottnest Island and the seemingly low species total for Garden Island may reflect lack of ornithological interest.

One conspicuous feature of Rottnest Island is the chain of salt lakes which occupy about 200 ha or 10.5% of the land area (Playford and Leech 1977). Rottnest Island is the only island in the south-west of Australia which is so endowed. Of the 55 species reguarly found on the island (resident and migrant species, Table 1), 25 (45%) may be found on this area. Of these species, 14 are migrants, the majority of which use the area as a refuge during the non-breeding season. Rottnest Island is an extremely important refuge in the south-west for several of these species. The Ruddy Turnstone *Arenaria interpres*, for example, breeds in the Northern Hemisphere and spends the non-breeding season in the Southern Hemisphere. The Royal Australasian Ornithologists Union Wader Study Group counted 487 Ruddy Turnstones in Western Australia during February 1982 (Mills 1982) and during the same period we counted 264 (54.2%) on Rottnest Island. Many of the species which feed around the salt lakes are trans-equatorial migrants which spend the Northern winter in the Southern Hemisphere. As a result, the largest numbers of birds are present on or around the lakes in the summer which concides with the largest human population. If the island is to remain a valuable conservation reserve as well as an important holiday resort, it is time to follow Seddon's (1972) advice of implementing a programme in environmental education coupled with a long-term management plan.

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The nutritional myopathy of the quokka as a model for research in muscular dystrophy

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Abstract

Muscular paralysis in the captive quokka was investigated because it seriously handicapped laboratory research. *Inter alia* the inherent ability of muscle to regenerate completely was conclusively demonstrated for the first time in this work.

Since then the regenerative capacity of muscle has been well established in many animals and in man. In all of these regeneration occurs in a well-defined sequence when the cause of myonecrosis is removed or corrected.

Principles of myopathology which govern the muscle lesions in those myopathies in which muscle fibre necrosis is the primary event have been formulated from these studies and are now widely accepted.

Field studies including vitamin E status at various times of the year and other biological observations are also described.

Introduction

The quokka *(Setonix brachyurus)* in its natural habitat is prone to a number of nutritional problems which are well-described in the literature (See Hodgkin and Sheard 1959). This deterioration is due to the long summer drought which, combined with a high reproduction rate and an absence of predators, causes the quokka population on Rottnest to be at the limit sustainable by the food supply.

One of the more dramatic effects of this poor nutritional state is the development of muscular paralysis. This myopathy is caused by vitamin E *(α-tocopherol)* deficiency. On Rottnest the myopathy is usually subclinical with the disorder becoming overt in captivity (Kakulas 1982). Quokkas maintained in cages on the mainland are subject to the effect of an "enclosure size factor" which aggravates the deficiency and which is remarkably specific (Kakulas 1963). Thus the vitamin E requirement of quokkas in small cages is much higher than that of animals housed in pens or larger enclosures. The basis of this phenomenon is at present unknown, but a similar effect has been observed in other conditions e.g. in dogs with vitamin D deficiency (Mellanby 1919).

Many of the biological aspects of the quokka myopathy are described in "Man Marsupials and Muscle" (Kakulas 1982). This work contains a scientific record of the investigation of the myopathy, an account of the pathology of the muscle disorder and its reproduction in the laboratory. The results of a field survey of the vitamin E status of quokkas on many parts of the island revealed high levels in winter and spring and very low levels toward the end of summer.

One of the most noteworthy features of these investigations was the observation of full regeneration of muscle leading to total restoration of architecture. This discovery was made in paralyzed quokkas which were treated with vitamin E (Kakulas 1961). The phenomenon of muscle regeration has relevance to many, as yet incurable human diseases, especially the progressive muscular dystrophies. The quokka studies have shown that full regeneration is a possibility, in the future, and thus serves as a powerful stimulus to further medical research.

Additionally by using the quokka myopathy as a model for the duplication and study of acute and chronic muscle disorders the principles which govern the reaction of muscle to injury have been greatly extended. These new concepts are now part of the general body of knowledge of the subject and include the standard teaching with regard to the pathogenesis of muscular dystrophy. In brief, necrosis and regeneration occur in a cyclical fashion which eventually leads to "end-stage muscle disease" through the exhaustion of regeneration and with fat and fibrous tissue replacing lost muscle fibres.

It, *inter alia*, was also shown that selenium was ineffective in preventing or treating paralysis (Kakulas 1963). This finding suggests that vitamin E is the sole anti-oxidant available to the quokka. This might explain the ease with which quokkas develop a deficiency of the vitamin. As a practical outcome of the investigation a dietary régime was developed, which maintains the animals in a healthy condition with the vitamin E requirement being between 35-70 mg per kg diet.

History of muscle paralysis in the quokka

The first reference to nutritional muscular paralysis in a macropod marsupial is that of Goss (1940) who reported the development of paralysis of the hind limbs of four Australian tree kangaroos. The animals, which were on exhibition during the World's Fair in New York had been fed large quantities of fish oil to make them sleek and presentable with the result that they developed muscular dystrophy. Three died and one recovered when fish oils were withdrawn and large doses of vitamin E were given.

The development of muscle paralysis in captive quokkas on the local scene became a problem only when for special reasons they were housed in small pens or cages. The difficulty greatly increased when large numbers of animals were kept in cages during the study of trace element metabolism by Barker (1960). The disease was observed on several occasions and affected both quokkas and tammar wallabies (*Macropus eugenii*) captive in the yards of the Zoology Department. The principle manifestations of the disease were, wasting of skeletal muscles of the hind limbs, paralysis of the hind limbs and eventual death. At about the same time the disease appeared in domesticated quokkas, held by Kaldor in the Department of Physiology for the study of iron metabolism.

Robinson (1960), while working on quantitative amino acid excretion in West Australian marsupials experienced a similar high incidence of the disease in quokkas housed in small cages and he mentions slight differences in the disease in animals kept in large yards. The disorder was abrupt in onset and was often precipitated in apparently normal animals by the stress of capture. Although administration of vitamin E to quokkas with the disease at the South Perth Zoological Gardens had failed to change the condition Robinson thought that biochemical tests might show some change. Accordingly 2 animals with the disease were fed relatively small quantities of *α-tocopherol* for a period of 2 weeks. The supplement was administered 3 times weekly and doses equivalent to 20 mg per kg body weight were given. One animal became very weak and died within 30 days while the other showed some clinical improvement. He found that with the administration of *α-tocopherol*, urinary excretion of creatine was lowered, β alanine excretion ceased and the ratio of L-methyl histidine to glycine excretion fell abruptly. Robinson suggested, from these results, that the cause of the disease was a complicated deficiency of vitamin E but was unable to prove this.

It was also at this time when paralysis in the quokka was first observed overseas. Carmichael and Reed, (1958), report that in November, 1957, 8 quokkas were received by the Smithsonian Institutional Zoological Park, Washington D.C. A week after arrival one quokka was found dead from fighting and the autopsy revealed infestation with large numbers of the nematode worm *Austrostrongylus minitus* and smaller numbers of *Dipetalonema annulipapillata*. The remaining animals were given antibiotics and anthelminhics (piperazine). A short time later a second quokka died from an intestinal intussusception and it was noticed that most of the remaining animals were exhibiting an exfoliative type of skin lesion. Scrapings from these did not reveal the cause. Necropsy findings on another animal dying at this time were negative, except for parasitism. Between February and late May 1958 the remaining five quokkas developed progressive posterior paralysis. The skin trouble had virtually disappeared and the appetites remained generally good. In addition to the vitamin and mineral supplements which these animals were receiving for several months, injectable forms of vitamin E were administered. During this time all recommended diets had been offered and eaten. Despite the treatments and nutritional changes the paralysis progressed; two of the animals were sacrificed and the remaining ones died. Necropsies were done at the National Institutes of Health, Bethesda, U.S.A., and Armed Forces Institute of Pathology (A.F.I.P.), Washington D.C. The report of one of these necropsies conducted by Dr P. Craig was kindly made available by the A.F.I.P. The main findings were, myopathy, cause unknown, multiple abscesses in skin of thigh; focal myocarditis; adenocarcinoma of lung, heart, brain and kidney.

Barker (1960) quotes a similar paralysis in quokkas in the Zoological Gardens of Alipore, Calcutta in 1959. A number of animals developed hind limb paralysis and skin lesions soon after arrival and again there was failure of all forms of treatment. In 1962 an outbreak of a similar disease in quokkas was reported from the Zoological Gardens at Healesville, Victoria, Australia.

As the problem had increased in magnitude, apparently did not respond to vitamin therapy, and had certain features suggestive of a communicable disease, paralyzed animals were submitted by Barker, to Professor N. F. Stanley at the university of Western Australia, who attempted to isolate a virus. Muscles from affected animals were examined histologically by Dr J. B. Blackwell, Pathologist at the Royal Perth Hospital, who found widespread segmental necrosis and minimal inflammatory change. Two positive results were obtained on animal inoculation. The first was with a suspension of the brain of an affected quokka which produced emaciation in a litter of suckling mice and the second was with a suspension of hind limb muscle which again produced emaciation in a litter of suckling mice. Both these litters showed histological changes in skeletal muscle similar to those found in the quokka.

These results however, were open to some doubt as the agent responsible could not be serially propagated. This impression was substantiated over the course of time as further suspensions from affected quokkas have failed to disclose a transmissable pathogenic agent. Similar material of muscle was examined by Professor R. E. J. ten Seldam, from the Pathology Dept., University of Western Australia, at this time and he concluded that the changes were consistent with vitamin E deficiency although the possibility of a muscle virus infection could not be excluded. Dr M. Sadka, Neurologist, Royal Perth Hospital, who shared this opinion, suggested that sections of muscle be sent to Dr R. D. Adams, Bullard Professor of Neuropathology, Harvard Medical School, Boston. He was also convinced that dietary deficiency of vitamin E was the most likely cause of the disease.

The significance of the quokka myopathy to muscle research

The nutritional myopathy of the quokka highlighted the regenerative potential of muscle, a discovery which is of great significance to human muscle disease. As indicated above, the current relevance of the work is due to the theoretical support it gives to a future cure being found for progressive muscular dystrophy which is at present a serious world-wide disease.

Before the discovery, in 1960, of complete and total regeneration of skeletal muscle voluntary muscle was believed to possess only limited regenerative potential. Notwithstanding this general view there were a number of excellent prior studies in the late 19th and early 20th centuries which demonstrated regeneration of muscle following local injury.

These papers were fully reviewed by Adams, Denny-Brown and Pearson (1962) in their monograph of muscle pathology. These authors also added their own studies on muscle regeneration including the concept that, for regeneration to be complete, the endomysial sheath should be preserved. In the early investigations attention was usually confined to a small selectively injured area of muscle using a variety of physical methods. However, the technique of crushing, cutting or tearing the muscle partly or completely destroyed the supporting fibrous tissue framework. In this situation when regeneration ensued the multiplying myoblasts, being undirected, became admixed with other elements so that such regeneration which did occur became "aberrant" and "disorganised".

Therefore, what was the contribution of the quokka? Principally it was the demonstration of total and overall muscle regeneration observed in paralyzed animals after treatment with vitamin E. A similar phenomenon may have been encountered previously, possibly within nutritional experiments, but if this was so it was given scant attention or not recorded. Indirectly the quokka work also demonstrated that regeneration continued to complete restoration of muscle architecture provided that the cause of the original necrosis was removed or corrected. This fact is now one of the principles of myopathology which was derived from the quokka studies. Most naturally-occurring myopathies are characterized by focal muscle fibre necrosis with preservation of the endomysium. The *polyfocal*, and *polyphasic* myonecrosis which is typical of the lesions in the nutritional myopathy of the Rottnest Island quokka is also the common histopathological denominator of most animal and human muscle diseases. Examples are the muscular dystrophies, polymyositis and the toxic, drug metabolic and endocrine myopathies. In all of these the endomysial and supporting fibrovascular framework is intact so that the situation is more or less akin to that found in the nutritional myopathy of the quokka.

Agricultural veterinarians knew for very many years that vitamin E, and other anti-oxidants, were effective in the prevention of so-called "nutritional muscular dystrophy" in farm animals (Blaxter 1957). However, these substances and selenium, were usually used for prophylaxis in herds and flocks where treatment of an individual animal would not be contemplated for practical reasons.

The principles of pathogenesis of the lesions in the quokka, which rest upon the observations of experimentally-controlled, chronic and continuing, myonecrosis, were first described at a meting of the New York Academy of Sciences in 1965 when they were used to explain the natural history and pathogenesis of muscular dystrophy.

Discussion

Although it has been well known since the last century that the muscular dystrophies are genetically-inherited disorders, the metabolic or biochemical expression of the inherited factor has not been identified. From the precedents offered by the reversible quokka myopathy and other recent work on human muscle regeneration, one may expect similar regeneration in human muscular dystrophy to occur when the biochemical defect is corrected.

The contributions to myopathology of the quokka work are threefold. Firstly, there is the principle that skeletal muscle, throughout the body and in most animal species, inherently possesses great power of regeneration. This potential does not require to be stimulated but always follows necrosis of which it is the natural consequence. Secondly, there is the fact that if the cause of myonecrosis is removed or neutralized, regeneration is full and complete, and thirdly, there is the formulation of a system to explain the pathogenesis and evolution of the histopathology of the necrobiotic myopathies. This incorporates a new nomenclature introduced to describe the microscopic lesions. Using the terms *monofocal*, *polyfocal*, *monophasic*, and *polyphasic* myonecrosis the necrobiotic myopathies can be accommodated within a simple terminology (Kakulas 1975).

An accelerating factor in the pathogenesis of muscular dystrophy is the fact that regeneration is abnormal and abortive in those conditions so that exhaustion occurs sooner. Outfall of muscle fibres follows with fat and fibrous tissue replacement being secondary and passive. To some extent the "end-stage" lesions are also due to hypertrophy, atrophy, incomplete regeneration and muscle fibre splitting, central nucleation and partial denervation: all of which have been reproduced in the quokka. These concepts are now established as the standard teaching for the pathogenesis of the lesions in the human muscular dystrophies.

However, there are still many questions to be answered in the actiology and pathogenesis of the nutritional myopathy of the quokka and in muscular dystrophy. Useful comparisons of the muscle lesions in the two conditions have been in terms of the common principles which are responsible for the histopathogenesis of the respective myopathies and it is probable that necrosis in both is due to a basic membrane defect. However, apart from this, very little has been gained from the quokka investigation which has shed light upon the aetiology of muscular dystrophy. Vitamin E as an anti-oxidant is known to prevent the peroxidation of membrane lipids and there is evidence that the human dystrophies, especially dystrophia myotonica, are also basically due to membrane disorders (Rowland 1976). This common ground between the animal and human myopathies deserves further exploration.

The quokka myopathy is primarily due to nutritional deficiency of vitamin E, while human muscular dystrophy is genetically determined. However, this does not preclude the possibility that both conditions act within the same biochemical pathway, i.e. the metabolic disorder in the animal is an "acquired" defect of the system, which is responsible for the maintenance of membrane integrity, and that the biochemical disturbance in man is a hereditary "inborn error" of membrane metabolism. The naturally-occurring myopathy of the quokka is clinically, a more acute disorder than the Duchenne and other forms of human muscular dystrophies, otherwise their pathological manifestations are remarkably similar.

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Recent endocrinological research on the Rottnest Island quokka (*Setonix brachyurus*)

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Abstract

Recent endocrinological work on the macropodid marsupial, the quokka, (*Setonix brachyurus*) is reviewed, concentrating on pituitary, adrenal and reproductive hormones. Studies of adeno- and neurohypophysial hormones are in their infancy and the significance of the suite of newly-discovered hormones in the pars nervosa needs to be established. Recent research on circulating levels of progesterone in the quokka have shown that the oestrous cycle and the pregnant cycle are not hormonally equivalent, as was previously thought. The chorio-vitelline placenta of the quokka has also been shown to be capable of progesterone synthesis *in vitro* and there is mounting evidence in this species, and in other marsupials, that the conceptus exerts a strong local effect on the uterus.

Introduction

Despite the fact that the quokka is a member of a monotypic genus restricted virtually to insular habitats in Western Australia, it has proven a particular accommodating vehicle for a wide variety of research, due primary to its ready availability and ease of maintenance in the laboratory. Such is the extent of this work since the last major review of the animal's biology in 1959, that this report will be concerned only with pituitary, adrenal and reproductive hormones. Research on the thymus gland and immunology is reviewed by Stanley (this volume) and the ecological relevance of much of these data is discussed by Main (this volume). McDonald (1977) has recently reviewed what little is known of adrenocortical function in marsupials and McDonald and Waring (1979) combined to produce a major review of hormones and their effects in marsupials and monotremes. For a broad and succint overview of the physiology of the quokka however, the reader is referred to Waring *et al.* (1966) which still remains current as one of the best reviews of the comparative physiology of marsupials.

Pituitary function

Traditionally, pituitary function is assessed following surgical hypophysectomy but this has never been reported in the quokka, only in the closely-related tammar wallaby, *Macropus eugenii* (Hearn 1975). The cytology of the quokka pituitary was described by Wingstrand (1966) and the neurohypophysial peptides tentatively identified as arginine vasopressin and oxytocin (Ferguson and Heller 1965, Acher 1974). Bakker and Bradshaw (1978) developed a sensitive bioassay for the measurement of circulating levels of antidiuretic hormone in the tammar and the quokka but recent studies from Acher's laboratory have revolutionised our knowledge of marsupial neurohypophysial hormones.

Acher and his colleagues in Paris, using separation and detection methods with greatly heightened sensitivity, have shown that the major neurohypophysial hormone in the quokka is not arginine vasopressin, but lysine vasopressin, a rare hormone thought previously to occur only in members of the pig family (Suina) and Peru strain mice (see Acher *et al.* 1981). A second novel peptide was also identified as phenypressin (Phe^2 -Arg^8- vasopressin) (see Chauvet *et al.* 1980) and, even more surprising, was their discovery that the oxytocic principle of the quokka pituitary is not oxytocin, as in other mammals, but mesocotin (Ile^8-oxytocin), previously thought to occur only in lower vertebrates (Chauvet *et al.* 1981). The structure of these novel hormones is given in Table 1 from which it may be seen that they differ only by single amino-acid substitutions in the 2, 3 and 8 positions. Acher's work has also shown that the quokka is by no means unique amongst marsupials in its possession of such a constellation of peptides in the pars nervosa and there is evidence that phenypressin occurs as well in *Didelphis*, the North-American opossum.

The significance of these findings is difficult to assess at this stage as nothing is known of the physiology of these hormones. As Bakker and Waring (1976) were able to induce diabetes insipidus in the tammar by the placement of electrolytic lesions in the base of the hypothalamus, clearly one of these peptides must function as an antidiuretic hormone, and one would opt for lysine vasopressin which is slightly less active than arginine vasopressin in eutherian mammals. Similarly, mesotocin presumaly functions as the galactogenic hormone in marsupials but the rôle of phenypressin is obscure. More research in this area is imperative, especially as early work by Acher *et al.* (1973) established that the prototherian echidna (*Tachyglossus aculeatus*) has arginine vasopressin and oxytocin in its pituitary and thus does not differ from the conventional eutherian pattern.

Very little is known of the nature and structure of the adenohypophysial hormones of the quokka, or of any other marsupial for that matter. Farmer and Papkoff (1974) reported the presence, in whole pituitary glands from the red kangaroo, of separate fractions with chemical properties similar to eutherian luteinizing hormone (LH), follicle-stimulating hormone (FSH), prolactin and growth hormone. Bona Gallo *et al.* (1978) reported further fractionation of pituitary gonadotrophins from tammar pituitaries and further studies on marsupial adenohypophysial hormones were reported recently by Farmer *et al.* (1981).

Adrenal hormones

Ilett (1969) first reported the presence of cortisol and corticosterone in adrenal venous and heart blood of the quokka, and he noted that they were in roughly equal concentrations. Oddie *et al.* (1976) subsequently reported a cortisol: corticosterone ratio in the peripheral blood of the quokka of 2.03 which probably indicates that sample collection was attended by some stress. McDonald and Bradshaw (1977) again found roughly equal concentrations of cortisol and corticosterone in the plasma of unstressed quokkas but, with stress, cortisol levels rose disproportionately to reach a ratio of 2.59.

McDonald and Bradshaw (1977) used indwelling jugular catheters to obtain blood samples from un-

Table 1

Amino-acid sequences of arginine, lysine vasopressin and phenypressin, oxytocin and mesotocin

Peptide	Amino-acid sequence	Distribution
Phenypressin	1 2 3 4 5 6 7 8 9 CYS - *PHE* - PHE - GLN - ASN - CYS - PRO - ARG -GLY - (NH_2)	Red kangaroo, tammar plus (?) quokka, grey kangaroo, euro and *Didelphis*
Arginine Vasopressin	2 CYS - TYR - PHE - GLN - ASN - CYS - PRO - ARG -GLY - (NH_2)	Eutherian mammals plus echidna
Lysine Vasopressin	8 CYS - TYR - PHE - GLN - ASN - CYS - PRO - *LYS* - GLY - (NH_2)	Pig, warthog, peccary, hippopotamus, Peru strain of mice, red kangaroo, grey kangaroo, euro and (?) quokka and tammar
Oxytocin	3 8 CYS - TYR - ILE - GLN - ASN - CYS - PRO - *LEU* - GLY - (NH_2)	Eutherian mammals plus echidna
Mesotocin	8 CYS - TYR - ILE - GLN - ASN - CYS - PRO - *ILE* - GLY - (NH_2)	Quokka, red kangaroo, euro, tammar and possum

restrained animals and repeated sampling at three-hourly intervals over a period of two days failed to disclose any evidence of a diurnal cycle in corticosteroid levels. Irregular fluctuations occurred over the range of 0.4-5.0 μg/dl but there was no evidence of a regular periodicity. Similarly, short-term sampling at five-minute intervals, gave no evidence of episodic secretion by the adrenals. Constant-rate intravenous infusion of either porcine adrenocorticoptrophic hormone (ACTH) or synthetic β^{1-24} ACTH caused a significant increase in the concentration of total corticosteroids in the plasma, being detectable at a dosage of 0.05 i.u./kg/hr and rising to approximately 15 times the control value at a dosage of 2.0 i.u./kg/hr. This increase in the rate of adrenal corticosteroidogenesis was log-dose related and both porcine and synthetic ACTH were found to be equipotent. This increase in circulating steroid levels was due almost exclusively to increased secretion of cortisol and levels of corticosterone and the minor component, 11-deoxycortisol, remain virtually unchanged.

Herrick (1961) was the first to attempt some assessment of adrenal function in quokkas on Rottnest Island and relate this to seasonal changes in condition of field animals. The techniques available at this time however did not permit measurement of circulating corticosteroid concentrations and adrenal ascorbic acid levels were used as an index of secretory activity. He found that dehydration was associated with depletion of adrenal ascorbic acid levels but, contrary to expectations, quokkas collected from "dry" areas of Rottnest in the summer 1958 did not have significantly lower ascorbic acid levels than those maintained on adequate supplies of food and water in the yards.

The development by Bakker and Main (1980) of a Condition Index based upon the regression of the length of the tibia on the cube root of the body weight has considerably simplified the assessment of seasonal changes in physiological condition. Miller and Bradshaw (1979) employed the Condition Index to follow seasonal changes in a discrete population of quokkas on Rottnest Island, localised just West of Green Island. Whereas previous reports have emphasized the dramatic loss of condition of the quokka over the summer season (e.g. Barker 1974; Barker *et al.* 1974, Main 1970), Miller and Bradshaw (1979) found that animals were in significantly better condition during the hot-dry period (November-March) than in the cool-wet season (April-October) (Condition Index of 6.3 ± 0.19[*] versus 5.3 ± 0.15, $p < 0.001$). Plasma corticosteroid levels were also significantly higher in the cool-wet season, indicative of greater environmental stress, and the total body water content was increased, indicating poorer condition. These changes are plotted seasonally in Figure 1 from which it is clear that the quokka experiences a progressive decline in body condition from a peak in about November; and mid-winter, rather than mid-summer, is the most difficult period physiologically. Plasma corticosteroid concentrations were negatively correlated with the Condition Index ($r = -0.85$, $p < 0.01$) indicating the incidence of adrenal-mediated stress in a natural population of marsupials.

Aldosterone concentrations in the peripheral circulation of the quokka of 6.6 ± 3.4 ng/dl were reported by Oddie *et al.* (1976) and Miller and Bradshaw (1979) recorded on overall mean of 7.78 ± 0.40 ng/dl from their field study. They also found that aldosterone concentrations did not differ on Rottnest between the hot-dry and cool-wet seasons, but that there was a marked fall to levels of about 4 ng/dl in mid-winter. Laboratory experiments by these authors with quokkas maintained on high and low-salt diets showed that plasma aldosterone levels are very sensitive to changes in sodium status, falling from a mean of 16.95 ng/dl on the low salt diet to a mean of 2.33 ± 0.57 ng/dl on the salt-replete régime. These figures suggest that quokkas on Rottnest experience an adequate sodium intake for the majority of the year but may experience a surfeit in mid-winter.

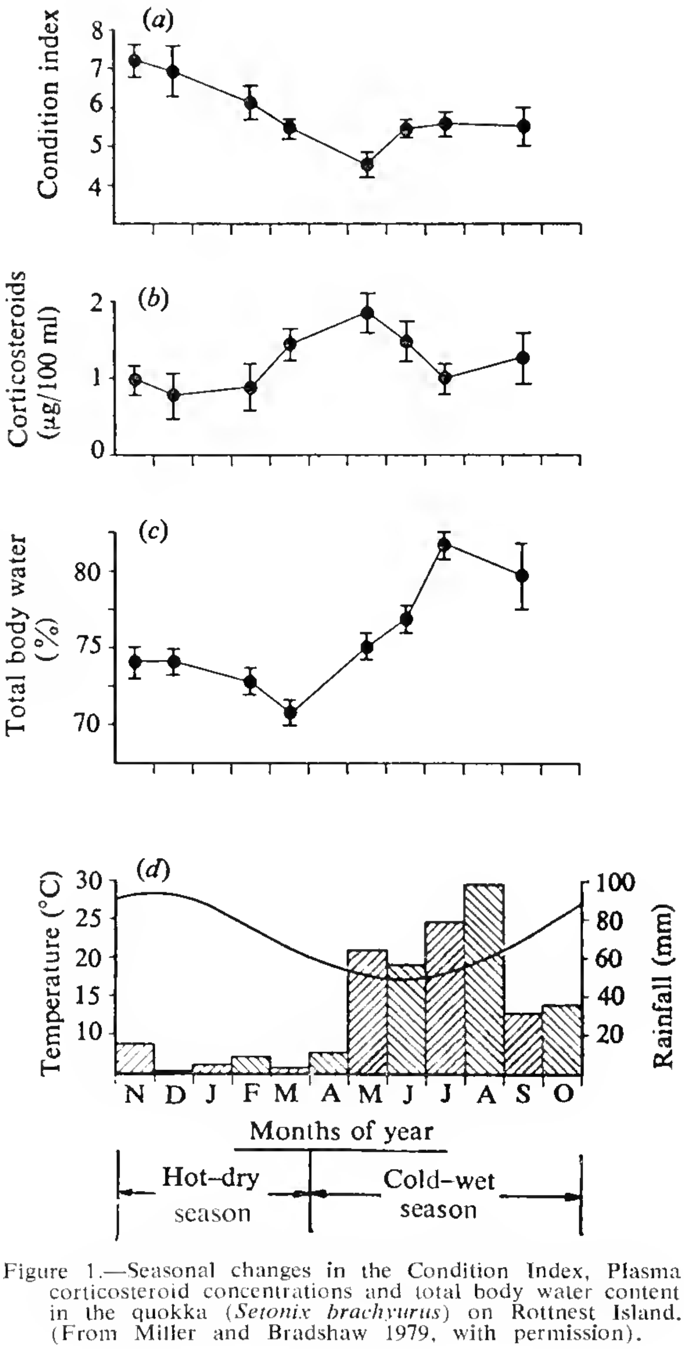

Figure 1.—Seasonal changes in the Condition Index, Plasma corticosteroid concentrations and total body water content in the quokka (*Setonix brachyurus*) on Rottnest Island. (From Miller and Bradshaw 1979, with permission).

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[*] All values in text presented Mean ± S.E.

Dramatic confirmation of this comes from the study of Miller and Bradshaw (1979) who measured circulating levels of aldosterone in "coastal" and "inland" quokkas and found a highly significant difference, with the level of aldosterone in the plasma of "coastal" animals being almost half that of "inland" individuals and the urine was significantly more concentrated in sodium. Subsequent unpublished work has confirmed, with the use of salt traps that winter storms deposit large quantities of salt on the vegetation on Rottnest (see Ambrose *et al.* 1980) which is then ingested and subsequently excreted by the quokkas.

One striking aspect of adrenal function which deserves mention is the apparent lack of a diabetogenic action of steroids such as cortisol in the quokka and some other marsupials. McDonald and Bradshaw (1981) found that injections of cortisol at dosages of from 1 to 5 mg/kg per day were without appreciable effect on urea nitrogen excretion and did not elevate blood glucose levels. One of the major actions of glucocorticoids in eutherian mammals is to enhance catabolism of muscle and hence urea excretion (thus "diabetogenic" action). This refractoriness to the nitrogen-mobilizing action of cortisol does not appear to be a marsupial characteristic however, since Than & McDonald (1974) found the brush-tailed possum to be quite conventional in this respect.

These data force one to reconsider the metabolic role of glucocorticoids in such marsupials as the nitrogen-mobilizing effect is thought to be fundamental to the metabolic action of glucocorticoids in mammals (see Munck 1971). Bradshaw and McDonald (unpublished) have recently examined renal function in adrenalectomised quokkas in an effort to identify the rôle of adrenal corticosteroids such as cortisol and aldosterone. Glomerular filtration rate (GFR) and renal plasma flow were measured simultaneously in conscious unrestrained animals by clearance of ^{14}C-inulin and ^{3}H-PAH as detailed by Bakker and Bradshaw (1983) working with the hare wallaby, *Lagorchestes conspicillatus*.

Adrenalectomised animals were maintained post-operatively on a daily régime of 0.2 mg/kg cortisol plus 10 μg/kg aldosterone injected intra-muscularly This régime seemed adequate to maintain the animals in good health indefinitely, but interesting differences were noted in renal function when compared with intact individuals. The clearance of PAH for example was reduced in the operated animals on maintenance therapy (from 15.1 to 10.3 ml (kg.hr)$^{-1}$) and the filtration fraction increased from 27% to 38%. It is apparent therefore that, despite a fall in renal blood flow consequent upon surgery, glomerular filtration was still maintained, apparently by autoregulation. Withdrawal of the maintenance régime for a period of from 48-72 hours resulted in

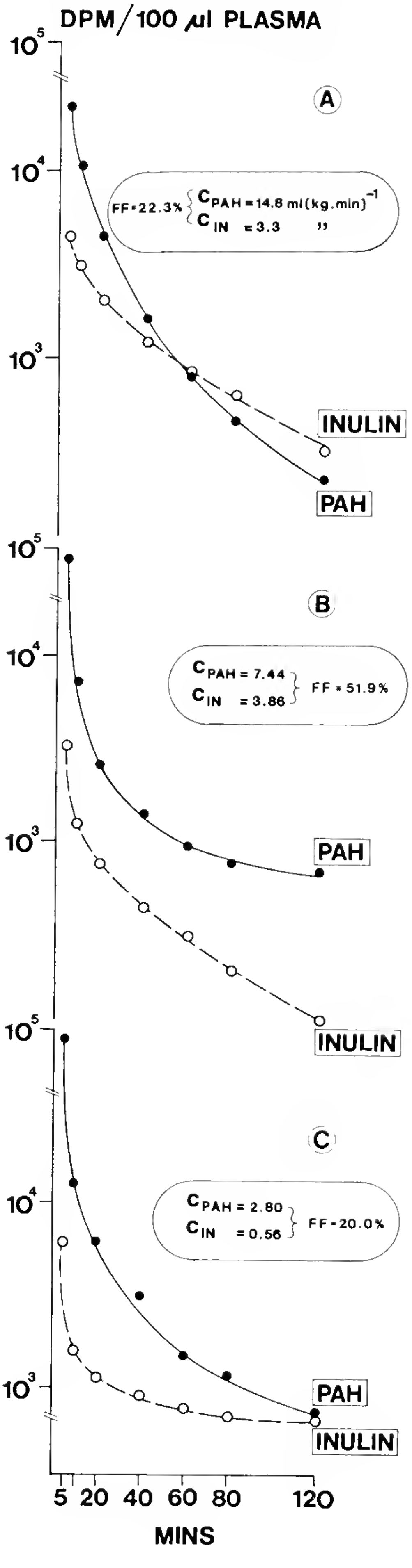

Figure 2.—Disappearance curves for 14C-inulin and 3H-para-amino-hippuric acid (PAH) following a single intravenous injection in the quokka (*Setonix brachyurus*). The injection was given at time zero and samples taken subsequently at times 5, 10, 20 etc., mins. A = intact individuals; B = bilaterally-adrenalectomised animals on maintenance régime of 0.2 mg/kg cortisol plus 10μ g/kg aldosterone per day; C = bilaterally-adrenalectomised animals 48-72 hours after withdrawal of maintenance régime. (From Bradshaw and McDonald, unpublished).

Table 2

Clearance of inulin (C_{IN}), para-amino hippuric acid (C_{PAH}), rate of urine production (V) and the filtration fraction (FF) in intact and adrenalectomised quokkas and the effect of steroid maintenance therapy. (Data as means ± S.E.). From Bradshaw & McDonald (unpublished).

Treatment (N = 6)	V	C_{IN} ml (kg.min)$^{-1}$	C_{PAH}	FF %
Intact	0·021 ±0·003	3·71 ±0·38	15·07 ±2·35	26·9 ±4·7
Adrenalectomised +Maintenance Régime*	0·073 ±0·022	3·50 ±0·20 p0·05	10·30 ±2·24	38·1 ±4·2
Adrenalectomised	0·026 ±0·008	<1·47 ±0·59	5·02 ±1·93	23·0 ±5·8
Adrenalectomised +Aldosterone ...	0·048 ±0·002	3·11 ±0·10	7·98 ±1·23	40·4 ±4·7

* 0·2 mg(kg.day)$^{-1}$ cortisol + 10 μg(kg.day)$^{-1}$ aldosterone.
p<0·05 compared with intact animals.

a rapid decline in the condition of the animals and both the GFR and the PAH clearance fell markedly under these circumstances. Representative clearance curves for both PAH and inulin from intact and adrenalectomised quokkas with and without maintenance therapy are shown in Figure 2 and the virtual complete renal failure in the absence of steroid injections is quite evident. In those animals which did die, the classical symptoms of anorexia, muscular weakness and listleness were evident and death resulted from circulatory collapse. Renal parameters from intact and adrenalectomised animals are summarised in Table II.

Reproductive hormones

The control of reproduction in macropodid marsupials was reviewed by Tyndale-Biscoe *et al.* in 1974 but is it important to note that only the most preliminary of hormonal data were available at the time. Influential reviews of reproductive physiology of marsupials such as that of Sharman (1970) have thus not benefited from an extensive literature on circulating hormone levels as is the case with eutherian mammals and, as more of this information becomes available, it is forcing a revision of earlier standpoints. Primary amongst these is the assertion that the pregnant and non-pregnant states are endocrinologically equivalent in marsupials. In the eutherian mammal of course pregnancy is "recognised" by the mother on implantation of the blastocyst by the failure of the corpus lutem to degenerate. Hormonal differences are also evident from an early stage, emanating both from the conceptus and the altered maternal physiology. In the latter stages of pregnancy in eutherians, the placenta as a potent progesterone-secreting endocrine organ, dominates gestation.

The marsupial situation is of course very different from this. Pregnancy *per se* does not inhibit ovulation and gestation is contained within the length of a single oestrous cycle. Birth can occur at any stage throughout the cycle and the uteri from pregnant and non-pregnant animals appear identical histologically. Blastocysts have also been transferred successfully and developed to term in the uteri of virgin recipients and it is not perhaps surprising that the idea of hormonal equivalence gained sway. Recent studies with the quokka and other species however have forced a reappraisal of this position.

Poole (1975) noted, in hybridization experiments between eastern and western grey kangaroos, that the length of the gestation period is determined by the genotype of the foetus rather than that of the mother. Renfree (1972) found that there is a significant local effect of the conceptus in the pregnant horn in the tammar which possesses a hypertrophic endometrium when compared with the contralateral horn. More significantly, the pregnant horn secretes a specific β-globulin not present in the non-pregnant horn, thus establishing a local effect of the conceptus. Heller (1973) was sceptical of the claims that the placenta is not an endocrine organ in the marsupial and studied the pharmacological effects of oxytocin and vasopressin on the contractility of the quokka uterus during pregnancy and the oestrous cycle. He found the response of the pregnant uterus to be always greater to oxytocin than to vasopressin whereas the reverse was true in non-pregnant animals. Differences were also observed in the reactivity of the endometrium during the follicular and luteal phases of the oestrous cycle which were indicative of an effect of progesterone. Following on from this study, Bradshaw, *et al.* (1975) reported that the chorio-vitelline placenta of the quokka was capable of transforming the steroid precursor pregnenalone into progesterone *in vitro*, thus establishing its steroidogenic capability. Heap, *et al.* (1980) subsequently confirmed that the placenta of the tammar is also capable of progesterone synthesis.

The first clear evidence of an hormonal difference between pregnant and non-pregnant marsupials comes, however, from a recent study of plasma progesterone levels in the quokka. Cake *et al.* (1980) developed a highly specific and sensitive radio-immunoassay for the measurement of peripheral progesterone concentrations and employed the technique of indwelling chronic jugular catheterisation to obtain daily blood samples from unrestrained and unstressed animals. Daily mean plasma progesterone concentrations in three pregnant and three non-pregnant quokkas are shown in Figure 3 and the spike on day 3 in the pregnant cycle is quite obvious. Both pregnant and non-pregnant cycles were initiated in these quokkas by the removal of a pouch young, a stimulus sufficient to initiate the development of a dormant blastocyst if the quokka is pregnant as the result of a successful post-partum mating. A similar spike of progesterone has since been confirmed in the pregnant tammar by Hinds and Tyndale-Biscoe (1981) although a spike of lesser proportions is also evident in the non-pregnant cycle.

Circulating levels of progesterone in the maternal circulation are of course one of the crudest indices of the reproductive state of an animal and it is important to assess tissue reactivities to such hormones. Owen, *et al.* (1982) have recently characterized a high-affinity progesterone-binding receptor in the uterus of the quokka and monitored changes in this receptor throughout the oestrous cycle and pregnancy. Receptor

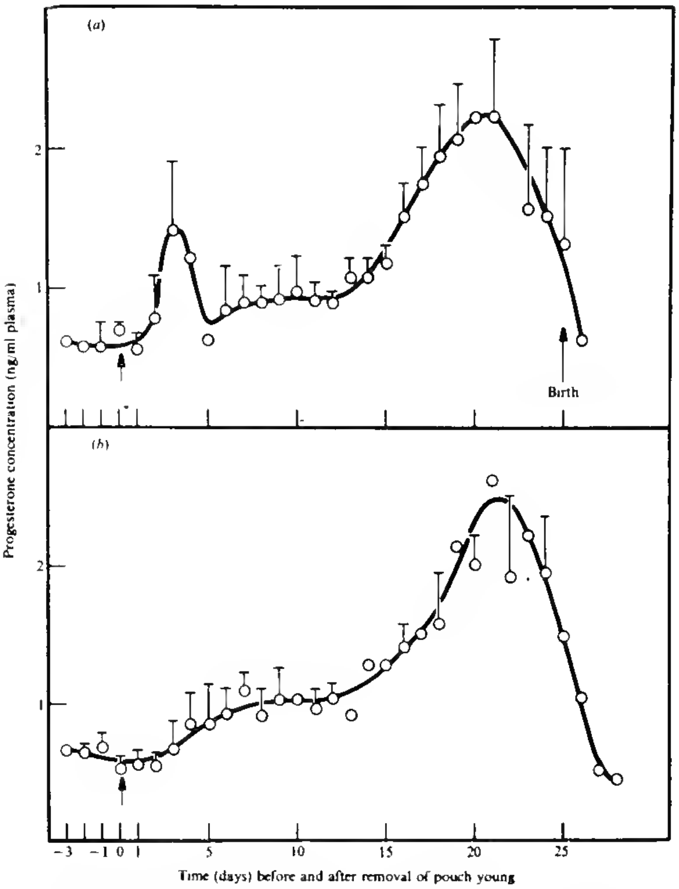

Figure 3.—Plasma progesterone concentrations in quokkas (*Setonix brachyurus*) following removal of a pouch young at time zero. A = pregnant cycle; B = non-pregnant (i.e. oestrous) cycle. The data are presented as Means ± S.E. of three individuals in each instance. (From Cake *et al.* 1980, with permission).

concentrations are always higher in the ipsilateral horn following ovluation than in the contralateral horn and this argues for a local circulation by which progesterone from the corpus luteum can differentially affect the adjacent uterus (see Lea and O'Shea 1977). There appears to be an effect of the blastocyst as receptor concentrations remain elevated in the pregnant horn on day 3 when compared with the non-pregnant horn (20.1 ± 5.9 pmoles/g wet weight versus 9.5 ± 2.1 pmoles/g wet weight, $p < 0.05$), whereas they are not different on day 3 in the oestrous cycle (Owen unpublished).

Conclusion

It is impressive to attest to the extent to which the quokka *(Setonix brachyurus)* has served as a vehicle for much of the research that has been carried out on the endocrinology of marsupials. Much of the early work on marsupial reproduction was done with the quokka and it has returned to prominence as a result of the recent progesterone studies. There is little doubt now that earlier conclusions as to the endocrine equivalence of the pregnant and oestrous cycles in marsupials were in error and recent studies have found differences, albeit subtle ones. Work on anterior pituitary hormones in marsupials is still in an early stage and sensitive homologous radio-immunoassays for the measurment of circulating levels of FSH and LH have yet to be developed. The significance of Acher's discovery that the neurohypophysial hormones of marsupials (but not monotremes) are unique will only be clarified by further study. Similarly the metabolic effects of corticosteroids such as cortisol are obscure in species such as the quokka and future research on this interesting animal should prove highly rewarding.

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Meteorites in the desert: a review of meteoritics in Western Australia

Presidential Address 1981

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Abstract

The history of meteorites in Western Australia since the first meteorites were discovered near Quairading on 4 January 1884, is reviewed. Several individuals have made a significant contribution to the Collection during that period of time, so that it now comprises approximately 190 local and 120 other Australian and overseas meteorites. The science of meteorites has played and will continue to play an essential role in our understanding of the formation and evolution of the solar system. Because of the unique characteristics of a number of Western Australian meteorites, many of them have been the subject of detailed petrological and isotopic studies. The meteorites which have been recovered from the desert regions of this State represent a rich store of extra-terrestrial material which now comprises part of our heritage and will continue to contribute to our expanding knowledge of planetary science.

Out of the Sky

A meteorite is a solid body which has arrived on the earth from outer space. The name is derived from the Greek word *meteora*, which means "things in the air". Material from interplanetary space is colliding with the earth in amounts estimated at between a few thousand and a few million tonnes per year. Most of this solar system debris is too small to penetrate the atmosphere and is vaporised by frictional heating to form a "shooting star" or meteor. A few objects however, are sufficiently large to reach the earth's surface as meteorites.

Although the science of meteorites is very young man's experience with meteorites probably dates from the very dawn of the human mind. Philosophers of ancient Greece and writers of the Han Dynasty in China described meteorite falls. The sacred stone of Kaaba in Mecca to which Moslems pay homage, is apparently a meteorite. We also know that the American Indians revered meteorites, and that yearly pilgrimages were made by the Cree and Blackfeet tribes to the top of a hill in Southern Alberta on which lay the Iron Creek meteorite. The Winona meteorite was found in a stone cyst such as was used for child burials among ruins near Winona, Arizona. Some iron meteorites have been made into weapons reputed to confer supernatural powers on the bearer.

The fall of a meteorite can often be a spectacular event. On September 2nd 1967, a stone meteorite fell near Wiluna in Western Australia (McCall and Jeffery 1970). According to witnesses the sky was lit by a flash "like a welding arc—white and blue." One man saw "an object about 20 feet long throwing out balls of fire." There were reports of "a terrific rumbling noise" and "bangs up to six or seven in number." The violent explosive reports are caused by atmospheric shock waves which accompany the fragmentation of a meteorite during its passage through the atmosphere.

Most evidence suggests that the majority of meteorites are from the asteroid belt, although it is believed that some of the smaller debris encountering the Earth's atmosphere may in fact be derived from comets. Asteroids are small, solid bodies, enormous numbers of which orbit between Mars and Jupiter. The largest, Ceres, is 770 km in diameter. It has been estimated that there may be 10^4 asteroids larger than 10 km and perhaps 10^{14} larger than 1 m in diameter. The atmospheric entry trajectories and velocities of three meteorites have been determined from multiple-station meteor cameras to permit calculations of their pre-terrestrial orbits in space. These orbits resemble the orbits of known asteroids that cross the Earth's orbit.

The column of air a meteoroid must displace as it falls to earth varies as its cross-sectional area, whilst the mass of the meteoroid varies as the cube of its dimension. Thus meteoroids of several metres in diameter which weigh in excess of 100 tonnes are more massive than the column of air they displace—so the atmosphere cannot slow them down significantly. Pressure of air against the face of incoming large stone meteorites tends to break them up and a shower of small stones results. Large iron meteorites on the other hand, are much more durable and may reach the ground at velocities of tens of kilometres per second.

Figure 1.—The Wolf Creek Meteorite Crater which is located some 106 km south of Halls Creek, Western Australia. The diameter of the crater is approximately 800 m and it is 40-55 m deep.

If a 100 tonne iron meteorite fell, its kinetic energy at impact would be enormous (perhaps 2 x 10^{1} J g^{-1}), and it would explode as violently as a nuclear bomb. The only explosive encounter in recent times occurred near the Tunguska River in Siberia in 1908. Some degree of mystery surrounds the devastation which occurred in this region, as no scientific expedition was mounted until 1927. A bright fireball accompanied the explosion which was heard up to 1 000 km away. Some have argued that the explosion was caused by a small comet, or by an anti-matter object, or even by a black hole.

Some 35 structures in the Earth have been identified with varying degrees of certainty as ancient meteorite explosion craters—the largest being the Arizona Meteor Crater which is 1.2 km in diameter and 140 m deep. Specimens of an iron meteorite have been recovered from the site. Twisted and deformed, these irons are called "Canyon Diablo", after a canyon which winds its way across the surrounding terrain.

The Wolf Creek crater near Halls Creek in Western Australia is an impressive structure some 800 m in diameter. It was only discovered in 1947 when it was recognised from the air. The crater is partly filled with wind-blown sand and gypsum. Shale balls, up to 136 kg in weight were recovered from the crater (Cassidy 1954), but little meteoritic material has been found. A photograph of the Wolf Creek crater is shown in Figure 1. The only other crater in Western Australia where meteoritic material has been found is at Dalgaranga, north of Yalgoo. This crater is approximately 25 m in diameter and 3 m in depth. Discovered in 1923 by Mr. G. E. P. Wellard, it has stony iron (mesosiderite) and metallic fragments associated with it, and is undoubtedly of meteoritic origin.

The Veevers Crater (Yeates *et al.* 1976) between the Great Sandy and Gibson Deserts and, more doubtfully, certain structures in the Kimberley region (Roberts *et al.* 1965), may also prove eventually to be of meteoritic origin. Small pieces of stony meteorite were found within a probable impact crater (as distinct from an explosion crater) on the Nullarbor Plain (McCall and Cleverly 1968).

History of meteoritics in Western Australia

The first recorded meteorites in Western Australia were a number of irons discovered by a policeman named Alfred Eaton, towards the end of the 19th century, when agriculture was being established to the east of the early settlement at York. These became known as the "Youndegin" meteorites after a police outpost, although they were actually collected near Pikaring Rock in the Quairading district.

While most of these meteorites were identified in the period 1884-1893, a number of other irons of similar structure were found in the same vicinity—the last in 1929. The four meteorites discovered by Alfred Eaton on January 5th 1884, were subsequently shipped to England, where they were sold to a scrap-metal dealer. Fortunately they were recognised in time and acquired by museums around the world. Youndegin I (of mass 11.7 kg), is now in the British Museum (Natural History); Youndegin II (10.9 kg), at the National Museum, Melbourne; Youndegin III (7.9 kg) at the Western Australian Museum, whilst Youndegin IV (2.7 kg), is also in the British Museum (Natural History). Other samples of the Youndegin meteorites are located in museums in Chicago, New York and Vienna, whilst a piece of Youndegin VIII was made into a horseshoe and hung for many years in a blacksmith's shop in York. In 1954 Mr E. C. Johnston presented a large 2 626 kg iron meteorite to the Western Australian Museum. Originally found in 1903 on a gravel ridge approximately 34 km south-east of Quairading, it was rediscovered by Mr Johnston whilst scrub-rolling with a World War II General Grant tank. This meteorite, which was called "Quairading", is now on display in the Museum. A detailed examination of the geographical location, microstructure and chemical composition of the Mt. Stirling, Mooranoppin, Quairading and the Youngdegin meteorites by de Laeter (1973, a), has shown that they are all members of the one meteorite shower.

Western Australia is in an extremely fortunate position with respect to meteorites. Approximately 190 have been found in this State and on an areal basis this represents a recovery rate treble that of the world average. Despite the sparse population and the relatively recent time of settlement by European man in Western Australia, there are a number of factors which have led to our excellent record in meteorite recovery:—

(i) The large regions of arid country enable meteorites to be preserved for long periods of time after falling to the earth's surface, and to be recovered more easily than in heavily vegetated terrain. Ploughed farmland also increases the possibility of finding meteorites.

(ii) As far as can be ascertained, the Aboriginal people of Australia were not interested in meteorites, either as objects of reverence or for their use as metals, whereas in many other countries with ancient civilisations, meteorites have been collected and used for a variety of purposes over the centuries.

(iii) The people of Western Australia who have presented their discoveries to the Museum for identification and display without thought of personal gain, but in the recognition that these objects are of tremendous value to science and represent part of our common heritage.

These factors have enabled Western Australia to develop an excellent meteorite collection. Not only do we have a fine collection of local meteorites, some of which are unique, but we have been able to exchange our meteorites with other Museums, so that we now have in excess of 100 meteorites from other parts of the world in our collection. The collection is administered by a Meteorite Advisory Committee, which has the responsibility of assessing proposals from scientists around the world who wish to analyse Western Australian meteorites. Under the Western Australian Museum Act of 1969, legal ownership of meteorites found in the State rests with the Crown.

The doyen of Western Australian meteorite collectors is undoubtedly Mr A. J. Carlisle. Approximately 80 meteorite specimens have been found by members of the Carlisle family. It is doubtful if anyone else in the world has been responsible for finding as many meteorites as Mr Carlisle. The Nullarbor Plain has been a happy hunting ground for meteorite collectors, and the collaboration between Mr Carlisle and Messrs W. H. Cleverly and M. K. Quartermaine, former staff members of the W.A. School of Mines, has been instrumental in enabling these meteorites to be recovered, identified and displayed. The most amazing discovery made by Mr Carlisle was in recovering a small, rare carbonaceous chondrite called "Lookout Hill". The specimen only measured a few centimetres in diameter and was covered in red soil, yet was recognised by Mr Carlisle as a meteorite, and later confirmed to be of extreme rarity.

The person who was instrumental in laying the foundation for the State's meteorite collection in the first 40 years of this century was Dr. E. S. Simpson, who from 1922 to 1939 was Government Mineralogist and Analyst. Although mostly remembered for his pioneering work on Western Australian minerals, he was also a keen meteoriticist who assiduously collected and analysed a variety of meteorites, and ensured that they were placed in museum collections (Simpson 1938). Dr. Simpson was an active member of the Royal Society and was President in 1939. It is generally conceded that the meteorite collections in Western Australia would be incalculably poorer but for the pioneering work of Dr. Simpson.

The years from 1940-1960 were barren ones in meteoritics in Western Australia. Few meteorites were recovered, and with the death of Simpson, the meteorite collections fell into disuse. In 1963 Dr G. J. H. McCall (from the Geology Department at the University of Western Australia), became interested in meteoritics, and the meteorites in the State were classified, resulting in the first Catalogue of Western Australian Meteorite Collections (McCall and de Laeter 1965). This catalogue overcame the lack of information on the various meteorite collections in the State, at a time when there was an increasing awareness of the scientific importance of meteoritic material in deciphering the early history of the solar system, and in the formation of planets. In fact shortly thereafter some of the State's meteorites were used in a study of the nuclear processes which had synthesised the element tin in stars (de Laeter and Jeffery 1965); this being the first of many scientific investigations in many laboratories around the world in which Western Australian meteorites played an important role.

At that time there were only 50 meteorites in the collection, but many of them—like the Youndegin meteorites—were specimens of the one meteorite shower. It was also of interest to note that 29 of the 50 meteorites were irons, in contrast to the world-wide figure in which only about 6% of the number of meteorite specimens are irons. This situation reflected the fact that irons are more easily recognisable than stony meteorites, require less sophisticated scientific techniques for proper identification, and are preserved for greater periods of time on the Earth's surface than the more readily weatherable stone meteorites. There were only three meteorites which had been recovered after they had been observed to fall. The remainder were all "finds". The small proportion of "falls" to "finds" is probably due to the sparse population of the State.

Dr McCall remained the driving force behind meteoritics in this State for approximately 10 years, in which time the collection was properly organised and many meteorites were recovered. When the Second Supplement to the Catalogue was published (McCall 1972), 93 meteorites were recorded, most of the additional meteorites being stones, many of which had been identified and classified by Dr McCall.

It was fortuitous that Dr McCall's replacement on the Geology Department staff at the University of Western Australia was Dr R. Binns. A distinguished meteoriticist, Dr Binns assumed the Chairmanship of the Meteorite Advisory Committee, and his international contacts proved invaluable in arranging for meteorite exchanges and in amending the names of some Western Australian meteorites to conform with the International Meteorite Nomenclature Committee. Meteorites are named after the nearest geographical feature to where they are found, but the Western Australian deserts are not well endowed with such features, and thus there are meteorites from the Nullarbor Plain which carry such titles as "Laundry Rock Hole", "Mulga West", "Pannikin" and "Billy Goat Donga".

Messengers from space

Nobel Prize winner, Harold Urey, once said that meteorites are the only samples of extra-terrestrial matter delivered to our doorsteps free of charge. While the genesis of meteorites is by no means fully understood, there is no doubt that they are the most primitive material we have in our possession. They have remained virtually unchanged since the time the solar system formed, and are more representative of the composition of the solar system than the highly differentiated crust of the Earth. In consequence, element and isotope abundances measured in meteorites provide some of the basic facts to be explained by astrophysical theories of the synthesis of the elements. The amount of information contained in a few grams of meteoritic material is quite remarkable.

Meteorites may be classified into three major groups—stones, irons and stony-irons; the former being by far the most abundant in number in spite of the fact that irons are often the most publicised and well-known to the layman. Mineralogically meteorites consist of varying amounts of nickel-iron alloys, silicates, sulphides and other minor phases. Stony meteorites most closely resemble terrestrial rocks and have the greatest variety in composition, colour and structure. These meteorites consist of olivine, pyroxene and plagioclase feldspars together with metallic nickel-iron and the iron sulphide troilite. One particular structural feature called chondrules divides the stony meteorites into two major sub-groups—*chondrites* and *achondrites*.

Chondrules are small, nearly spherical silicate inclusions which have been formed under melting or reheating conditions. The ordinary chondrites consist entirely of high temperature minerals and are remarkably uniform in composition. They approximate the equilibrium mineral assemblage that would be expected to develop in a rock of chondritic composition if held at moderately high temperatures (500-1 000° C) in a closed system.

The chondrules are embedded in a matrix of a similar mineralogy, and the boundaries between the chondrules and the matrix are often indistinct—the result of thermal metamorphism. Van Schmus and Wood (1967) have used a binary classification in which each chondrite is assigned a chemical group and a petrologic group on the basis of the degree of chondrule—matrix intergrowth.

A very important subset of the chondrites are the *carbonaceous chondrites*, which are grey to black in colour and consist of high temperature, anhydrous minerals embedded in a fine grained, blackish earthy matrix. The carbonaceous chondrites take their name from the fact that the matrices are impregnated with a tarry mixture of organic compounds up to 5% by weight. The presence of this low temperature material implies that they are very primitive meteorites and closely approximate the unaltered primordial material of the solar system. Although the carbon compounds do not necessarily indicate biological matter, they do closely resemble the organic molecules upon which life is based. In fact the chemical composition of the C1 carbonaceous chondrites closely match the composition of the Sun and have been used as the basis of the Standard Distribution of the elements (Anders and Ebihara 1982). This distribution is the basis for all theories of element formation in stars, (Burbidge *et al.* 1957), and without it our present knowledge of the evolution of the Universe would be greatly reduced.

The *achondrites*, as the name implies, do not possess chondrules, and are similar to terrestrial igneous rocks. They are of interest because they are broadly similar to many lunar samples, implying that they came from a part of the solar system where geological processes once operated much as they did on the moon.

Iron meteorites consist largely of nickel-iron, generally with a nickel content of 5-10% and a cobalt content of approximately 0.5%, but often contain troilite, which is an iron sulphide. In fact the high nickel content is an effective method of identifying iron meteorites. Irons consist of two metallic alloys arranged in a characteristic geometry-kamacite (6-7% nickel) and taenite (30-50% nickel). Depending upon the proportion of nickel to iron, iron meteorites are subdivided into three groups—hexahedrites, octahedrites and ataxites. Hexahedrites have 4-6% nickel occurring as kamacite, whereas at the other end of the scale, ataxites have a nickel content in excess of 12%, and consist mainly of taenite with an intergrowth mineral of kamacite and taenite called plessite.

The most abundant type of iron meteorites are the octahedrites which contain both kamacite and taenite, forming an interlocking crystal structure called the Widmanstatten pattern. If the surface of an octahedrite is polished and etched, this beautiful metallurgical pattern is revealed. An example of the Widmanstatten pattern of the Youndegin meteorite is shown in Figure 2. This structure developed during the slow cooling of meteorites from high temperatures—the kamacite plates nucleated from taenite crystals, then grew in thickness with the nickel contents of both the kamacite and taenite alloys changing as they adapted to new equilibrium conditions at lower temperatures. Solid state diffusion of nickel and iron atoms across the crystal faces was the mechanism which enabled the separation of the alloys to occur. Laboratory studies carried out on the diffusion rates in nickel-iron alloys have enabled deductions to be made of the declining temperatures that the octahedrites must have experienced to establish the present compositional gradients. It has been found that the octahedrites cooled through the temperature range 600 to 400° C at rates of a few degrees every million years (Goldstein and Short 1967).

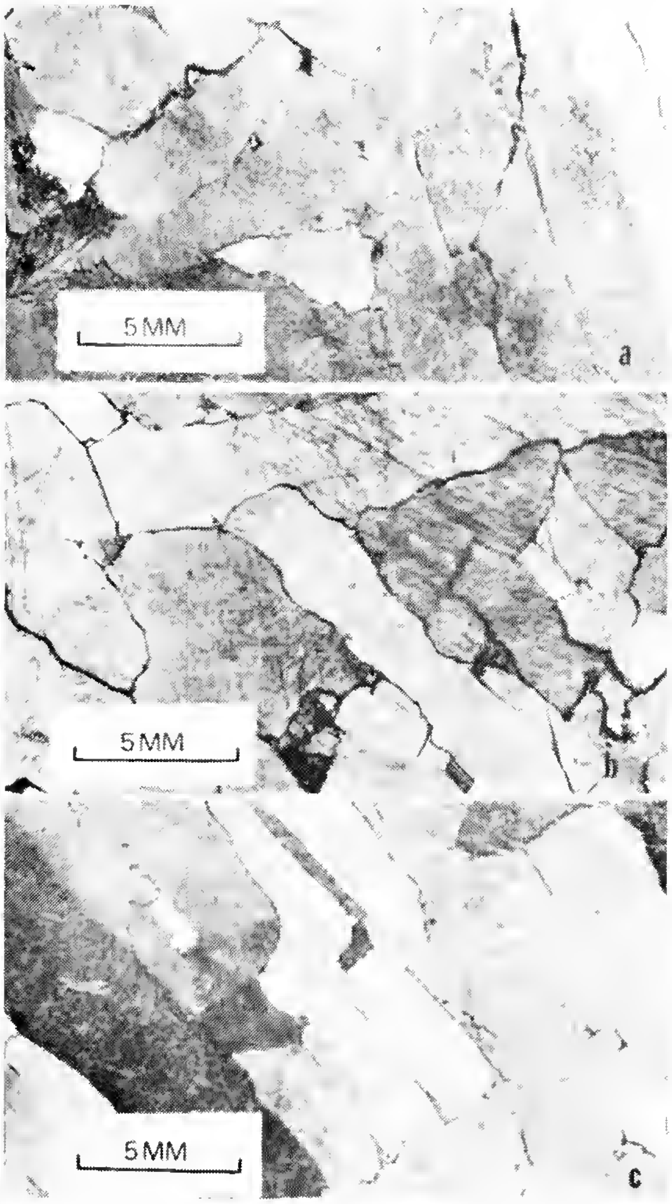

Figure 2.—Polished and etched section of the Youndegin II iron meteorite, showing the coarse Widmanstatten pattern typical of octahedrites.

The question of the number of parent meteorite bodies involved has been tackled by John Wasson and his colleagues at the University of California at Los Angeles (Scott and Wasson 1975). By analysing a number of trace elements in iron meteorites—principally gallium, germanium and iridium together with their correlation with nickel—it has been shown that meteorites cluster in chemical groups which can be interpreted as characterising a geochemical regime corresponding to a number of parent bodies. Other trace elements also show similar correlations and enable other fractionation mechanisms to be identified (e.g. Mermelengas *et al.* 1979).

The final group of meteorites are the relatively rare *stony-irons* or *mesosiderites*, which consist of silicate minerals and nickel-iron in approximately equal proportions.

Ages of meteorites and the birth of the solar system

Radioactive decay is the systematic transformation of a parent radioactive nuclide into a daughter nuclide, which more often than not is stable. If the half-life of the radioactive transmutation is known and we can measure the amounts of parent and daughter nuclides present today, we should, in principle, be able to determine the age of the material in which the radioactive nuclide occurs. The most commonly used geochronological decay scheme is based on the decay of the radioactive isotope ^{87}Rb to the stable isotope ^{87}Sr. Thus if a rock containing some rubidium was formed early in the solar system and has remained a closed system ever since, we should be able to calculate its age by measuring the isotopic composition of strontium in a mass spectrometer—an instrument which measures the abundance of the isotopes of a given element.

The age of the solar system can be measured by analysing meteorites, for these objects have been relatively undisturbed since the beginning of the solar system. Accurate measurements have been carried out on chondritic meteorites to give a consistent age of 4 600 million years, which we now accept to be the age when the cold and dark of space was transformed by crushing gravitational forces into a fiery thermonuclear inferno—which heralded the birth of a brand new star which we call the Sun.

But what was the mechanism that triggered off the birth of our solar system? Perhaps the answer lies in the meteorites.

In 1960 a physicist named John Reynolds at the University of California in Berkeley, was measuring the isotopic composition of the rare gas xenon which he had extracted from the Richardton chondrite. To his surprise he found that the proportion of one of the isotopes of xenon—^{129}Xe—was approximately 50% greater than that of ^{129}Xe from the earth's atmosphere (Reynolds 1960). He realised that the excess ^{129}Xe had come from the decay of the radioactive parent ^{129}I which no longer exists on earth because its half life is only 17 m.y. Thus if ^{129}I is synthesised in stars it would disappear after about 170 m.y. (or 10 half lives). Reynolds concluded that if the decay product of ^{129}I was present in meteorites as ^{129}Xe, then the meteorites must have formed into solid objects less than 170 m.y. after ^{129}I had been synthesised in stars. In other words, the birth process itself was relatively short—certainly less than 170 m.y.

Subsequent work with another short-lived radionuclide ^{26}Al (half life 0.72 m.y.) has shown that condensation of nebular gas took no longer than 10 m.y.. We also believe it was these short-lived radioactive nuclides that provided the heat necessary to melt the meteorite parent bodies and allow gravitational separation to occur. (Lee *et al.* 1977).

In the last few years some exciting discoveries have been made by examining the isotopic composition of elements from the high temperature inclusions in the carbonaceous chondrite Allende, which fell in Mexico in 1969. It has been found that many elements extracted from the Allende inclusions have an anomalous isotopic composition in comparison to other meteoritic or terrestrial material, and this has stimulated astrophysicists to consider new models for the formation of the solar system (Begemann 1980). The evidence now points to the fact that a supernova explosion may have "triggered off" the birth of the solar system. In fact some scientists believe that the Sun was born amidst a fireworks of supernova explosions, presumably connected with the passage of one of the spiral arms of our Galaxy through the region of space from which the Sun originated. The various isotopes of the elements synthesised by a variety of nuclear processes in supernova explosions have been well mixed into a homogeneous pool of isotopic composition throughout most of the solar system, but in the primitive high temperature inclusions in Allende, we can start to unravel the very nuclear processes which gave us birth.

Western Australian meteorites

In 1892 a rare iron meteorite was recovered near Ballinoo on a tributary of the Murchison River. Subsequently a similar meteorite was found in 1916 near Mount Magnet. This latter specimen has a unique horseshoe-shaped form. At the time of their discovery both Ballinoo and Mount Magnet were unusual in that they contained a high concentration of nickel (9.86% and 14.71% respectively). Subsequently the Warburton Range meteorite was discovered and found to contain 18.14% nickel (de Laeter 1973b).

The discovery of the Bencubbin stony-iron meteorite (which was recovered from a field during ploughing in 1930 and was followed by a second find in 1959), gave Western Australia a meteorite of extreme rarity and scientific importance. It contains chondritic material as enclaves in a host that consists of clinoenstatite and olivine enclosed in a metal reticulation which reveals a strong directed fabric suggestive of crystallisation under directed pressure (McCall 1968).

Another unusual mesosiderite is Mount Padbury which was found by W. C. Martin in 1964. Mount Padbury is a polymict breccia containing large olivine crystals together with achondritic enclaves (McCall 1966). This is the second greatest mass of mesosiderite material ever recovered, some 272 kg having been found.

The Mount Egerton meteorite is also an unusual meteorite in that it could be regarded as an achondrite with metallic inclusions, but some of the material is metal with silicate inclusions. When a section of the metallic phase is polished and etched, it gives a curious "ruled" etch pattern which is thought to be due to the presence of a nickel iron silicide (McCall 1965).

Another unusual iron meteorite is Redfields, which is a brecciated phosphide-rich meteorite (de Laeter *et al.* 1973). The high phosphide content has apparently inhibited Widmanstätten pattern development so that although the nickel content is 6.65% no taenite is present. Furthermore the meteorite has graphite inclusions, about 1 mm across, distributed throughout the metal giving it a "raisin-bread" appearance. The unusual structure of this meteorite is thought to be due to such factors as high carbon and phosphorus content and relatively rapid cooling.

One of the most impressive meteorites which has been recovered in Western Australia in recent years is the Mt. Manning iron. Weighing 701 kg it was discovered in 1979 at a site some 3 km east of the Mt. Manning Range. The meteorite has a fan-like or delta-wing shape as illustrated in Figure 3. One side of the specimen is smooth, slightly concave with a characteristic fusion crust, whereas the other surface is convex-shaped, pitted with regmaglypts and extremely rough. It has been postulated (de Laeter 1980), that the meteorite performed a delta-wing like flight at a high angle of attack through much of the Earth's atmosphere in a stable aerodynamic configuration. In this descent path the underside of the meteorite was smoothed by atmospheric ablation, whereas the upper surface did not experience extensive melting. The thin trailing edge of the meteorite has been affected by heat as evidenced by its jagged appearance perforated in some places by holes.

Figure 3.—The Mount Manning iron meteorite displaying the rough, convex-shaped surface which contains numerous well-defined regmaglypts. The jagged, ablated trailing edge of the meteorite is distinguished by the fact that a sample has been cut from this portion of the meteorite (Scale = 30 cm).

An X-ray fluorescence spectrometric examination of the chemical composition of the Mt. Manning meteorite revealed that it belonged to the rare IC class of iron meteorites (Thomas and de Laeter 1972). However in the Western Australian Museum collection there were two other meteorites, named Gosnells and Mt. Dooling, both belonging to the Group IC classification. De Laeter *et al.* (1972) had previously shown that the 1.6 kg mass found at Gosnells was part of the Mt. Dooling meteorite, which had been found in 1909. Further examination showed that Gosnells and Mt. Dooling were both members of the Mt. Manning meteorite fall. It is believed that the original meteorite was travelling in a south-westerly direction and fragmented near the Mt. Manning Range. Presumably the Gosnells fragment was transported by human agency. It is possible that other specimens will be found in the vicinity of the Mt. Manning Range.

No discussion of Western Australian meteorites, no matter how brief, would be complete without some mention of the Mundrabilla meteorite shower, which contains the largest meteorites ever found in Australia, and one of the largest found anywhere in the world. Two large masses, weighing 11 000 kg and 5 000 kg were discovered some 182 m apart approximately 16 km north of Mundrabilla Siding on the Nullarbor Plain in 1966 by R. G. Wilson and A. M. Cooney.

Mundrabilla No. 2 was originally transported to the finder in Adelaide, but was later sent to the Max-Planck Institut für Kernphysik at Heidelburg where several slices were cut under the supervision of Professor P. Ramdohr. These slices were made available for display in various institutions around the world and one such slice is on display at the W.A. Museum. A small cut piece and the remains of the main mass are held by the South Australian Museum. The main mass of Mundrabilla No. 1 (11 000 kg), is on display in the W.A. Museum.

More recently Mr A. J. Carlisle found another two large specimens of Mundrabilla at a location some 20 km east of the site where Mundrabilla No. 1 and 2 were found. Figure 4 shows Mr Carlisle standing alongside the 840 kg specimen of Mundrabilla No. 3 in its original location in the Nullarbor Plain. Both Mundrabilla No. 3 and 4 are now on display at the Museum. De Laeter and Cleverly (1983) have recently analysed the Mundrabilla specimens and described their discovery. The meteorites were coated with a crust of iron oxides and surrounded by innumerable small, knuckle-shaped fragments which had been shed in flight due to ablation of the main masses. This is due to the fact that the Mundrabilla meteorites contain a significant amount of troilite, much of which was burnt out in the meteorite's passage through the atmosphere. Thus the characteristic feature of the Mundrabilla meteorites is the deep cavities which can readily be observed in the surface.

One of the most remarkable meteorite discoveries occurred in the early 1960's when two extremely rare achondrites, called ureilites, were found within a small area on the Nullarbor Plain. This increased the total number of ureilites from three to five. The two meteorites, named North Haig and Dingo Pup Donga were shown to be different meteorites even though they were found within 30 km of each other (Mason 1974).

Figure 4.—The 840 kg mass of Mundrabilla No. 3 iron meteorite. The finder, Mr A. J. Carlisle, is in the photograph which depicts the featureless nature of the Nullarbor Plain.

Another unusual chondrite named Coorara was also found close to Dingo Pup Donga in 1966. At the time this was only the second meteorite of its type known. This meteorite contains in veins formed either in the parent body or by shock in orbital collision of meteoroids or by shock on atmospheric entry, the high pressure minerals ringwoodite and majorite (McCall and Cleverly 1968). These high temperature minerals are of importance to our understanding of planetary bodies.

Conclusion

Meteorites have played, and will continue to play, a crucial role in our understanding of the formation and evolution of the solar system. The most important reason for this is that they stand alone among objects accessible for study as relics of the earliest stages of the solar system. The carbonaceous chondrites in particular, are thought to represent pristine material which has survived, essentially unaltered, during the past 4.6 billion years of solar system history. Samples of these meteorities have provided information on the chemical composition of the elements, and inclusions from some of them have given evidence of nucleosynthetic processes which indicate the possibility of a supernova trigger to the birth of the solar system. Even the more evolved iron, stony-iron and achondritic meteorites formed early in the solar system's history, probably before the oldest known terrestrial and lunar rocks.

Although the six Apollo missions to the lunar surface provided scientists with a precious store of extra-terrestrial materials in the early 1970's, meteorite research is extremely vigorous today, in part because of the fact that lunar studies revealed the importance of meteorities to planetary science. The facilities and techniques which were established during the "Apollo era" have however, contributed to the research effort on meteoritics which has occurred over the past decade.

In recent years an enormous number of meteorites have been found in Antarctica (Cassidy and Rancitelli 1982). The initial discovery was made in 1969 by a Japanese team of glaciologists measuring ice movement at the Yamato Mountains in Enderby Land, whilst a second recovery has been made at Allan Hills in Victoria Land by a combined U.S.-Japanese team. Approximately 4 000 specimens have so far been recovered from Yamato Mountains and about 850 in south Victoria Land. These specimens may perhaps represent 500 or so distinct meteorites and thus increase the world's stock of these precious materials by about 25%, and the search is continuing. The Antarctic environment is so cold, dry and uncontaminated that this great cache of meteoritic material will undoubtedly extend our present knowledge of meteoritics.*

Another exciting discovery in recent years has been the possibility that the extinction of dinosaurs and numerous other species some 65 million years ago at the Cretaceous-Tertiary boundary may have been caused by a gigantic meteorite impact (Smith 1982). It has been shown that the concentrations of a number of elements (such as iridium, osmium, gold and palladium), are greatly enhanced in a layer of clay at the Cretaceous-Tertiary boundary in a number of locations in different parts of the world. These elements are extremely rare in the Earth's crust, but comparatively rich in meteoritic material, and it will be of interest to see if the meteorite impact hypothesis survives the numerous tests that will undoubtedly be carried out in the near future.

The meteorites which have been recovered from the deserts and farmlands of Western Australia represent a rich store of extraterrestrial material which have been used extensively by scientists both within Australia and overseas, to study various aspects of the formation and evolution of the solar system. Meteorites are survivors from the Asteroid belt which have landed on the Earth's surface, and been discovered by observant men and women, in most cases many years after their fiery descent through the Earth's atmosphere. The Western Australian Meteorite Collection is a tribute to those people who, realising that these objects are of special significance and part of our common heritage, have unselfishly reported their occurrence and assisted in their recovery.

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* There is now evidence that some of the Antarctic meteorites are actually fragments from the surface of Mars.

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The Quaternary stratigraphy and geological history of the Australind-Leschenault Inlet area

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Abstract

The Australind-Leschenault area contains 5 Quaternary formations, 3 of which are Pleistocene, and 2 Holocene. The oldest two are: the Australind Formation (a Pleistocene unit of nodular muds and calcareous sands) overlain by the Tamala Limestone. The Eaton Sand, a yellow/orange quartz sand, also is Pleistocene and overlies the Tamala Limestone mostly as a patchy veneer. The Eaton Sand was locally reworked at a later stage in the late Pleistocene into a shoreline ridge that forms the eastern shore of Leschanult Inlet.

The Leschenault Formation and the Safety Bay Sand, are Holocene; the Leschenault Formation is an estuarine unit of sand and mud and the Safety Bay Sand is composed of aeolian and beach sands. The Leschenault Formation was deposited behind a barrier of Safety Bay Sand, and by eastward migration of dunes, the Safety Bay Sand prograded over the Leschenault Formation. Detailed stratigraphic studies show that accumulation of these Holocene units took place in 3 stages: 1) when sealevel stood 2-3 m below present level, 2) when sealevel stood 3-4 m above present level, and 3) at present sealevel. These depositional/historical stages are preserved in the stratigraphy of the Safety Bay Sand as 3 distinct lithologic and/or diagenetically altered units: the Burragenup (oldest), Rosamel and Vittoria Members. In addition modern cementation in marine and subaerial environments is generating 2 other distinct units, the Koombana Beach Rock and Binningup Calcrete.

Introduction

This paper reports the results of research on the stratigraphy of the coastal area of Australind-Leschenault Inlet-Koombana Bay (near Bunbury W.A.) The data, obtained mainly from Quaternary units, provide new information about the Quaternary history of this part of the Swan Coastal Plain and particularly about the development of the barrier dune system during the Holocene.

The study area is situated toward the southern part of the Swan Coastal Plain (Fig. 1) and forms a contemporary coastal deposition area of the Perth Basin (Playford *et al.* 1976). Several major geomorphic units have been described in this area McArthur and Bettenay 1960; Semeniuk and Meagher, 1981b; Table 1). The most eastward in this study area are Bassendean, Spearwood and Blythewood units. Leschenault Inlet forms a narrow lagoon parallel to the coast; within this lagoon are marginal flats, shoals and platforms of sand, and an interior basin of mud. Leschenault Peninsula (Quindalup Dunes), a narrow dune barrier with beach/beach ridge sediments on its ocean side, separates the lagoon from the Indian Ocean. The most westerly occurring geomorphic unit is the submarine shelf. This is underlain mainly by Tamala Limestone, ridges of Holocene beachrock and vast sheets (veneer) of unconsolidated sand/gravel; locally there is basalt and outcrops of estuarine mud.

Stratigraphic sections were examined on natural cliff exposures, in excavations (55 in total), in large costeans (8 in total) and in cores (70 in total). Cores were obtained by percussion drill in unconsolidated sediment sections and by diamond drill (9 cores) through the indurated stratigraphic intervals. Core sites are mentioned throughout the text by a number, e.g. core site 1. Locations of excavations, costeans and cores are shown in Fig. 2. Offshore stratigraphy was studied by diving and samples of indurated stratigraphic units were collected by blasting.

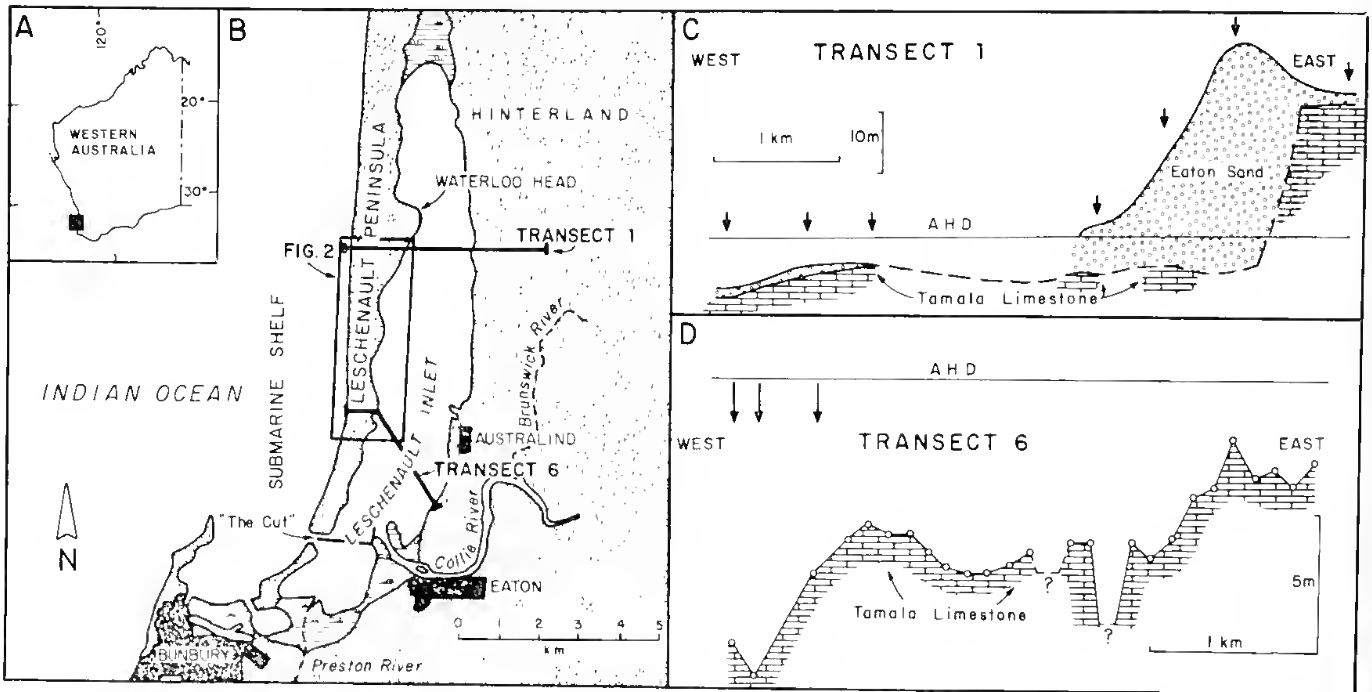

Figure 1.—A and B. Maps showing study area, location of transects and location of more detailed maps. Fig. 2. shows location of additional transects.
C. Cross section showing distribution and stratigraphic relationships of Tamala Limestone and Eaton Sand. Arrows indicate core or auger locations.
D. Cross section showing irregular surface of Tamala Limestone beneath Leschenault Inlet and Leschenault Peninsula as determining by jet-probing and coring. Dot indicates sample position; arrows indicate position of cores.

Table 1

Summary table of terminology of geomorphic units/stratigraphic units within study area

Geomorphic Units (McArthur and Bettenay 1960, Seddon 1972)	Formations (Seddon 1972, Playford *et al.* 1976)	Soil Units (McArthur and Bettenay 1960, Bettenay *et al.* 1960, Seddon 1972)	This paper
Bassendean Dune System	Bassendean Sand	Bassendean Soil Association	Adjoins east margin of study area
Spearwood Dune System	Tamala Limestone	Cottesloe Soil Association Karrakatta Soil Association	Tamala Limestone; stratigraphic equivalents of Cottesloe Soil and Karrakatta Soil are termed Eaton Sand
Quindalup Dune System	Part of Safety Bay Sand	Quindalup Soil Association	Burragenup, Rosamel, Vittoria and Binningup members of Safety Bay Sand
Beach and nearshore sediments	Part of Safety Bay Sand	Not applicable	Vittoria and Koombana members, of Safety Bay Sand
Inlets, lagoon and lakes	Not named	Vasse soil Association	Leschenault Formation

Stratigraphy

Five Quaternary formations, (3 of them new) have been encountered by mapping and coring in this area. In sequence down the profile these are:

5. Safey Bay Sand
4. Leschenault Formation
3. Eaton Sand
2. Tamala Limestone
1. Australind Formation

—Quaternary —Kwinana Group

They rest on sediments assigned to the Warnbro Group of Early Cretaceous age (J. Backhouse 1982 pers. comm.).

The main grain types and other compositionally distinct components of sediments, that were used to distinguish either sedimentary suites or end-member sediment types, are as follows: 1) quartz grains, 2) skeletal (Ca CO_3) grains (oceanic assemblages are distinguished from estuarine assemblages), 3) rutile and other heavy mineral grains, 4) calcareous mud, 5) clay-mineral mud, 6) organic matter and humus, 7) sediment-staining agents (grey due

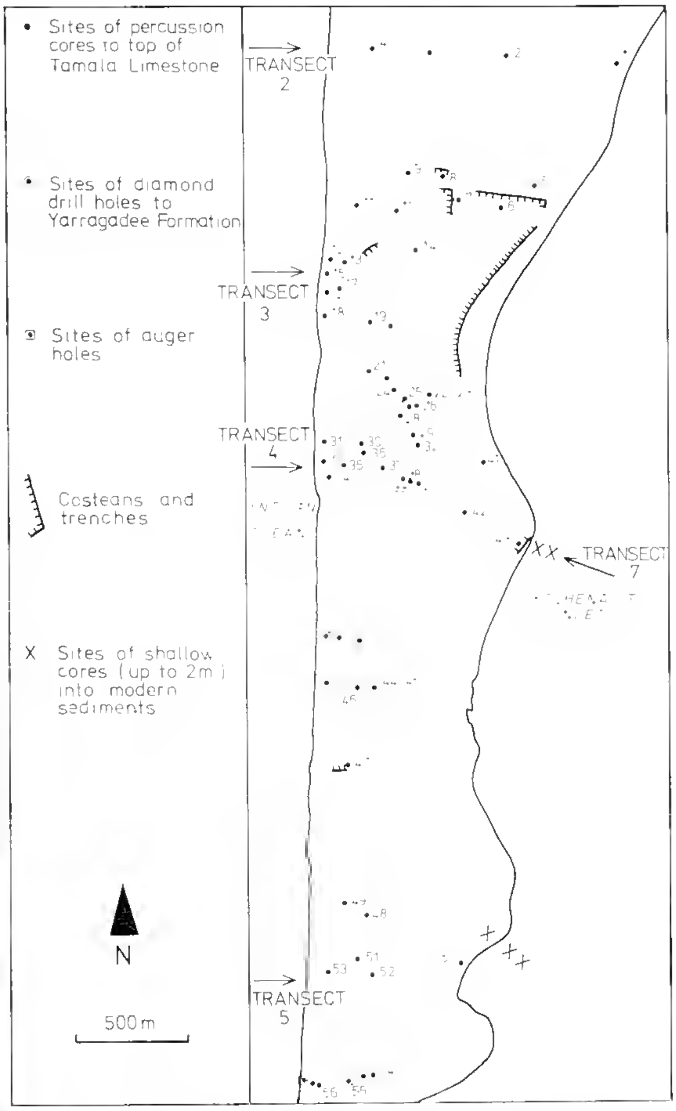

Figure 2.—Map showing location of various stratigraphic sampling sites and core sites, as well as location of transects shown in Figs. 3, 4, 5 and 7.

to humus or pyrite; orange and brown due to geothite), 8) sediment-cementing agents (cryptocrystalline $CaCO_3$ = calcrete; fine to medium crystalline $CaCO_3$ = sparry calcite; geothite, pyrite).

Australind Formation

Definition and characteristics: The Australind Formation is the name proposed for the sequence of colour variegated nodular-cemented calcareous mud, sand and shelly mud that occurs between Warnbro Group and Tamala Limestone.

Derivation of name: After Australind, grid reference 371888, Collie 1:250 000 sheet.

Type section: Core site 36 is designated as the type section.

Distribution: The unit has been intersected in core sites 1, 5, 35, 36, 46 (Fig. 2). It also is known to occur under the east shore of Leschenault Inlet.

Geometry and thickness: The formation is 3 m thick in southern parts of the Leschenault Peninsula but is missing or thin (< 50 cm) in the areas around core sites 7 and 5. Its thickness is variable (Fig. 3), probably as a result of erosion.

Lithology: There are 4 sediment types in the formation and these occur interlayered or mottled with each other. Colour mottles of brown, orange and cream are common. The sediments are:

(1) brown/orange or grey calcareous mud
(2) brown or grey shelly calcareous mud
(3) brown to cream calcareous sands
(4) lithoclast (carbonate rock fragment) gravel.

The calcareous sand commonly is cemented by $CaCO_3$ so that there are cemented sand layers and nodules dispersed through mud layers. The calcareous mud also is cemented in patches into nodules. Cementation in all lithologies results in cream-coloured nodules.

The arrangement of sediments in the formation is described best by the type sequence (Site 36):

AHD
–11.12m

Top: brown calcareous clay with limestone pebbles (= soil)	10cm
Lithified calcareous sand	45cm
Interlayered muddy calcareous packstone/wackestone light grey and dark grey in colour with horizons of cemented granule-sized nodules	75cm
lost interval	48cm
brown calcareous packstone with cream granule-sized cemented nodules	27cm
variegated brown/orange calcareous clay	75cm
variegated brown/orange calcareous clay with granule-sized shelly nodules	15cm

Bottom: ferruginous rock of the Warnbro Group.

Stratigraphic relationships: The unit rests disconformably on either ferruginous rock or weathered sediments of the Warnbro Group. The top of the unit, marked by rubble, soil and lithoclasts, is disconformably overlain by Tamala Limestone.

Age: G. W. Kendrick (1979, pers. comm.) has identified the following molluscs: *Alba monile* (A. Adams), *Cantharidus (Phasainotrochus)* sp., *Diala lauta* (A. Adams), *Hydrococcus graniformis* Thiele, *Mitrella (Dentimitrella) lincolnensis* (Reeve), *Nassarius* fragment, [probably *N. pyrrhus* (Menke)] and *Tellina (Pinguitellina)* sp.

The fauna is Quaternary and is suggestive of the mid Pleistocene (Kendrick, pers. comm.). On basis of fauna and unconformable relationship to the underlying formation, the Australind Formation is tentatively assigned a Pleistocene age.

Discussion: The lithology and molluscan fossils suggest that the Australind Formation accumulated in coastal lagoons not unlike Leschenault Inlet today. However there is overprint of $CaCO_3$ cementation and colour mottling on the sediments; the latter probably is due to pedogenesis associated with the unconformity at the top of the unit.

Tamala Limestone

The Tamala Limestone (Playford *et al.* 1976; "Coastal Limestone") crops out in the Leschenault area on the submarine shelf, on the hinterland near Australind and locally along the beach face of the peninsula. On the peninsula the limestone top was the target horizon for the shallow coring programme. Additionally, the top of the formation was investigated for the Public Works Department in 1962 by probing across Lescenault Inlet (Fig. 1D).

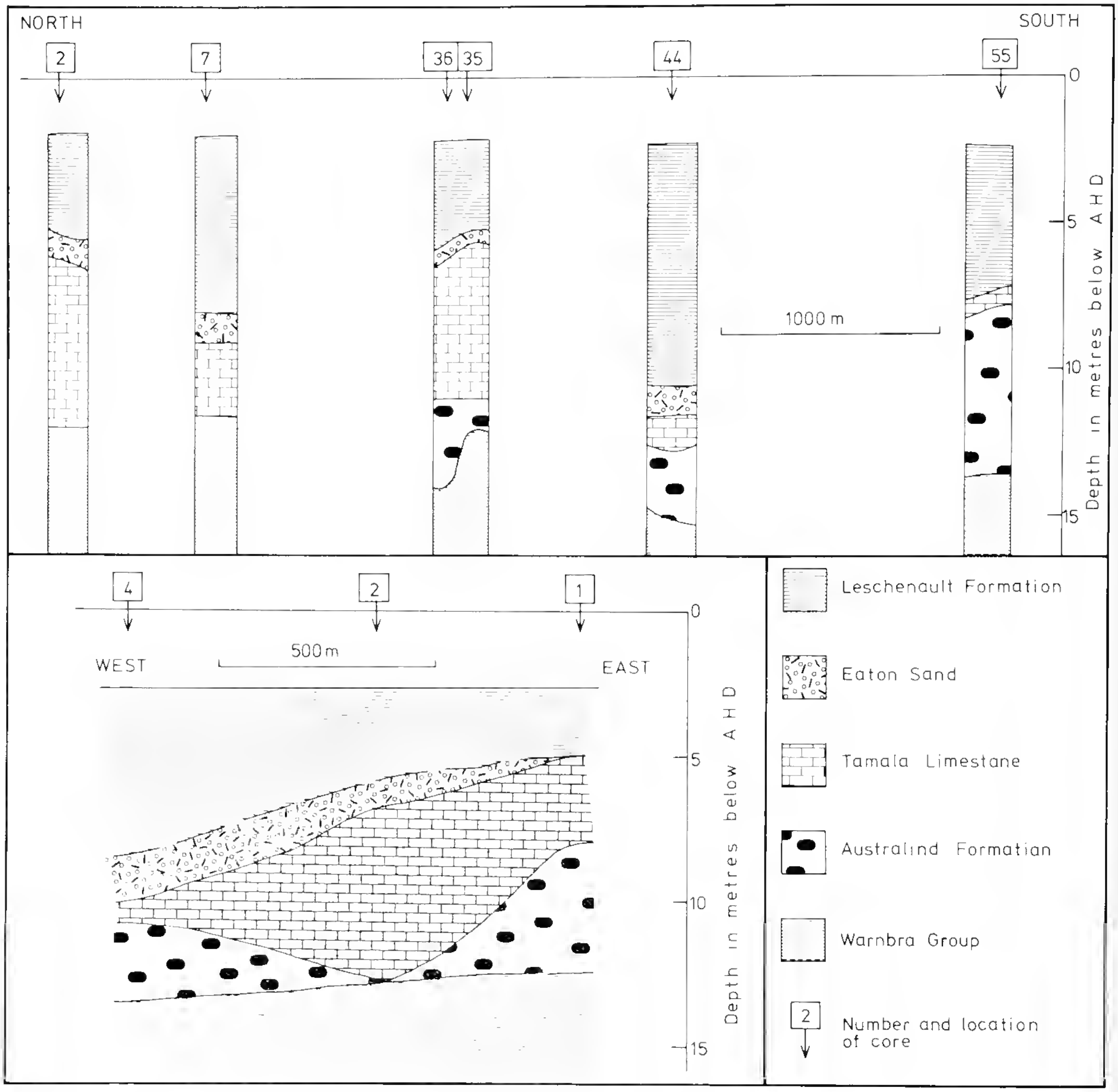

Figure 3.—Distribution and relationship of 5 stratigraphic units under Leschenault Peninsula.

Distribution: The Tamala Limestone was intersected in nearly every core; it has been traced under Leschenault Inlet in two transects; it forms much of the submarine shelf offshore and occurs in the subsurface on the hinterland (Fig. 1C). Apart from small local areas where it has been eroded or not deposited (e.g. around residual knolls of Bunbury Basalt) it may be inferred to be a relatively continuous unit underlying the entire study area.

Geometry and thickness: The depths and overall geometry of the top of the formation is shown for a transect that runs from the hinterland, under both Leschenault Inlet and Leschenault Peninsula, through to the submarine shelf (Fig. 1D). The top is undulating to irregular and has a broad westerly regional slope with a hollow developed under Leschenault Inlet. Diamond drill cores indicate that the formation is approximately 3-6 m thick under the peninsula; cores at site 55 and 56 indicate that the formation thins to south (Figs. 3 and 4). Only surface outcrops were examined in hinterland and offshore localities and thus total thicknesses here are unknown.

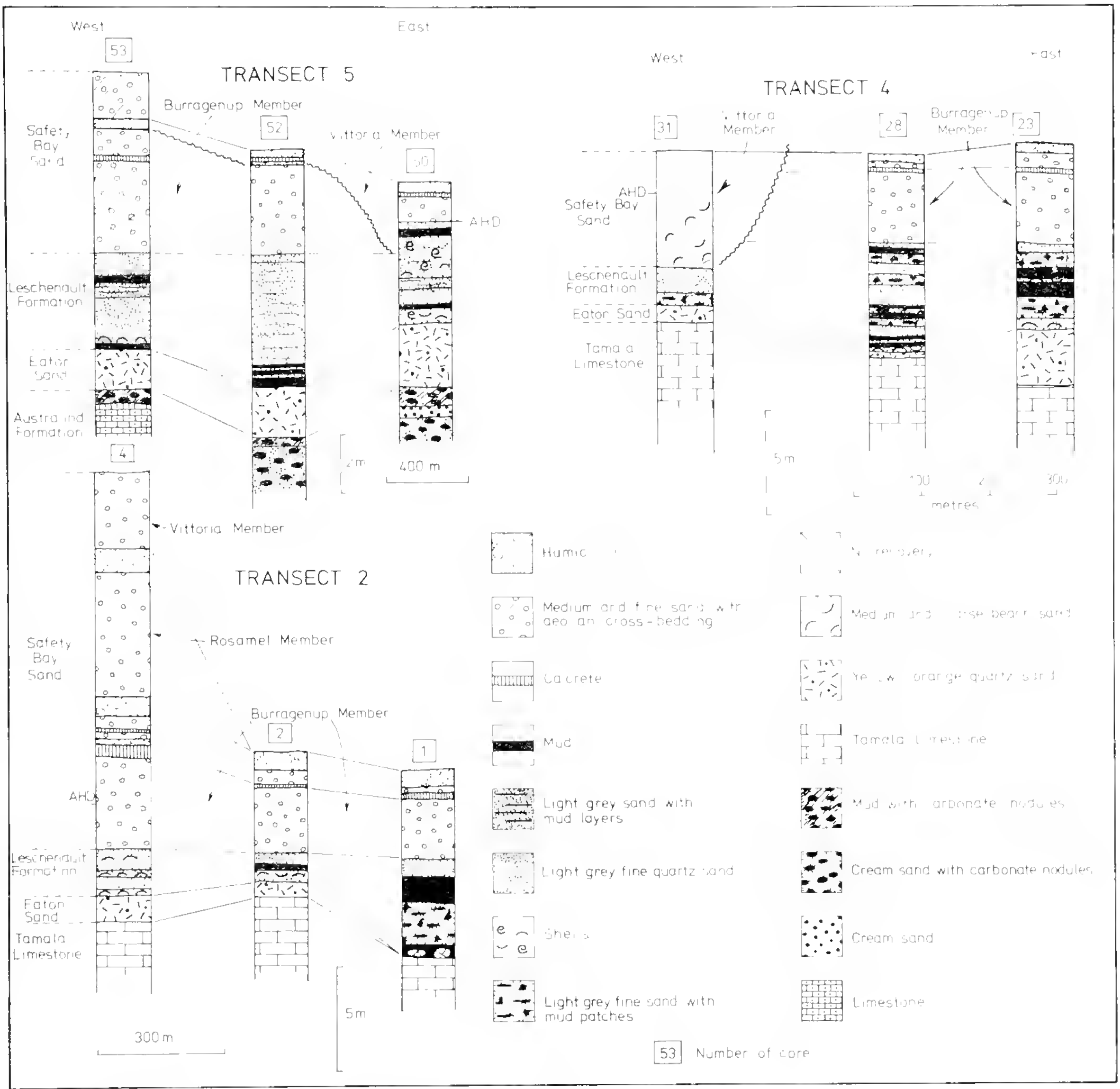

Figure 4.—Stratigraphic columns illustrating lithologic sequences within, and stratigraphic relationships between Australind, Tamala, Eaton, Leschenault and Safety Bay formations.

Lithology: Lithologically, the Tamala Limestone is varied. There are 4 main sediment or limestone types in the formation; these are:

1. quartz skeletal grainstone, composed of medium sand grains
2. shelly, lithoclastic, quartz skeletal grainstone composed of medium to coarse sand grains and gravel-sized lithoclasts and shell
3. skeletal packstone composed of sand grains with interstitial calcareous mud
4. lithoclastic skeletal packstone similar to (3) above but with lithoclast gravel.

Fauna that comprises the skeletal grains in the limestone include a variety of foraminifers, molluscs, calcareous algae debris and fragmented echinoids.

The formation mostly is comprised of quartz skeletal grainstone. However, there are thick layers of shelly, lithoclastic quartz skeletal grainstone. The other sediments (packstones) are confined largely to filling cavities or vugs in indurated grainstones. Locally, however, skeletal packstone occurs as a metre-thick sheet interlayered with quartz skeletal grainstone. The sediments are in various stages of induration, ranging from fully indurated by sparry calcite and calcrete (40%), to weakly indurated (40%), to totally uncemented (20%). Sheets of mottled, massive and laminar calcrete are relatively more indurated and are developed on top of and within the formation. Other subaerial and pedogenic features (such as colluvial breccia and soil), calcreted root-structures and karst surfaces also are commonly developed at unconformity surfaces both on top of and within the unit. Cemented colluvial breccia is plastered on the surface of the Tamala Limestone on hinterland outcrops. The limestone intersected in core commonly exhibits micro—(millimetre-sized) and macro—(centimetre-sized) vugs, with some openings up to metre-sized. These cavities are mostly filled with deposits of unconsolidated packstone (lithologies 3 and 4 above) indicating infiltration of marine sediment into a subaerially altered limestone.

Stratigraphic relationships: The formation rests unconformably on the Australind Formation, approximately 11-12 m below AHD; the contact is marked by soils. Under Leschenault Peninsula the formation is unconformably overlain by Eaton Sand; the contact is irregular with local relief in the order of 3-4 m. The Eaton Sand locally is absent on protruding knolls or pinnacles of limestone and the Leschenault Formation sediments rest directly on the limestone. In all cases, sediments overlying the Tamala contain reworked pebbles of limestone at the contact. On the hinterland the Eaton Sand unconformably overlies and buries a large cliff cut into the Tamala Limestone (Fig. 1C).

The lithology of the top of the limestone is dependent on the degree that erosion has removed the calcrete capping; the lithology may be 1) laminar calcrete, or 2) massive calcrete, or 3) calcrete cemented calcareous sand, or 4) sparry calcite-cemented calcareous sand. The lithology and geometry of the top of the formation indicates that it is a karstified calcreted surface, and it represents a major Quaternary unconformity.

Age: The age of the Tamala Limestone is considered as Pleistocene in the Perth area (Fairbridge 1950, Teichert 1967, Seddon 1972.)

Eaton Sand

This name is proposed for the yellow to orange quartz sand that overlies the Tamala Limestone.

Derivation of name: After Eaton townsite grid reference 370882 Collie, 1:250 000 sheet.

Type Section: The type section is designated in a deep road cut (grid reference 372895 Collie, 1:250 000 sheet).

Distribution; Geometry and thickness: The Eaton Sand generally is the surface material of the hinterland and forms a ridge-like body over 10 m thick along the eastern shore of Leschenault Inlet due to marine reworking along a former shoreline (Fig. 1C). The sand has been traced a short distance 100 m offshore to below sealevel under the inlet, and bores on the eastern margin of the inlet show that it extends for at least 6 m below AHD. However for the most part its distribution under the inlet is unknown. Cores on the Leschenault Peninsula show that the Eaton Sand is a generally ubiquitous sheet of irregular thickness overlying Tamala Limestone; its variable thickness (1-3 m) is dependent upon local irregularities of the underlying limestone (Figs 3, 4 and 5).

Lithology: The formation is composed largely of a crudely laminated to bedded yellow to orange quartz sand typically with medium and coarse sand-sized grains (Fig. 6); interstitial fine sand and minor clay also occur. The unit contains scattered charcoal, trace fossils (burrows and root casts) and vegetative debris, but mostly it is unfossiliferous. In thicker sections on the hinterland, the unit is composed mainly of fine and medium sand and at depth its colour becomes progressively light yellow, cream and white. Near the water table the sand may be cemented by iron oxides. Small-scale shore erosion along the eastern shore of Leschenault Inlet has locally exhumed these cemented layers.

In some locations, as exposed in excavations along the lowlands adjoining the eastern shore of Leschenault Inlet, the Eaton Sand contains a thin shelly band (*ca* 2 m thick) lightly indurated by calcite cement. Shells collected from this band include *Donax*, *Glycymeris* and *Bulla*. Radiocarbon dating of *Donax* from the band (at locality grid reference 370897 Collie, 1:250,000 sheet) gave an age of > 35,000 BP indicating a Pleistocene age.

Stratigraphic relationships: The formation disconformably overlies the Tamala Limestone. The Eaton Sand commonly exhibits one of three contact relationships with the underlying Tamala Limestone: (1) sharp contact with yellow to orange sand directly overlying limestone, or (2) gradational contact with yellow to orange sand infiltrating the vugular and interstitial network of the limestone to shallow depth (<50 cm), or (3) yellow to orange sand deeply penetrating down solution pipes. The top of the Eaton Sand passes gradationally into the overlying Leschenault Formation.

Age: The Eaton Sand, based on stratigraphic relationships and a radiocarbon date, is Pleistocene.

Discussion: The Eaton Sand under Leschenault Peninsula is blanketing a karst surface cut into Tamala Limestone and is similar to the unit termed Cottesloe Soil and Karrakatta Soil by McArthur and Bettenay (1960) and Bettenay *et al.* (1960). For most of the study area it essentially covers the Tamala Limestone but it has been reworked by coastal processes into a shoestring-shaped body along a former shoreline developed during the Late Pleistocene.

Leschenault Formation

The Leschenault Formation is the name proposed for the estuarine/lagoonal sequence of grey sand, muddy sand and mud that are shelly in layers.

Derivation of name: After Leschenault Inlet.

Type Section: The type section is designated as core site 28 (Fig. 2).

Distribution: The formation forms the modern depositional surface of Leschenault Inlet and also occurs between 2-6 m below AHD under Leschenault Peninsula (Figs. 3, 4 and 5) and Inlet. Locally, the formation occurs as sheet outcrops or as small inliers amongst Tamala Limestone outcrops on the submarine shelf; after severe storms mud clasts frequently are found along the beach indicating erosion of these offshore outcrops. The formation also is found in isolated occurrences as residuals 2-3 m above MSL on the peninsula under the woodland plains (Semeniuk and Meagher 1981 b).

Geometry and thickness: The formation presently is ribbon shaped; 15 km long, at least 2-3 km wide and up to 6 m thick. At its seaward edge it is undergoing marine erosion so that its past geometry is unknown.

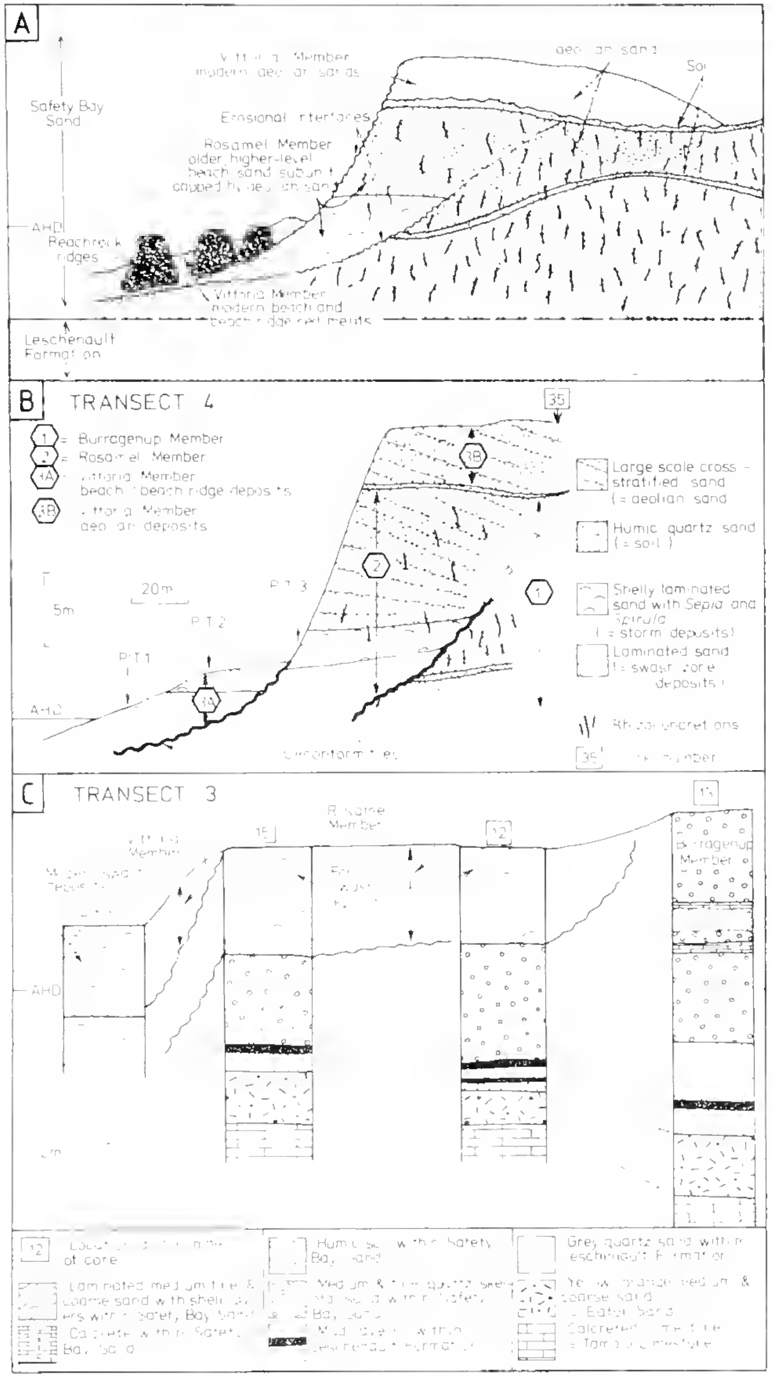

Figure 5.—A. Summary of stratigraphic relationships between members of the Safety Bay Sand.

B. Stratigraphic profile illustrating lithologic sequence within, and stratigraphic relationship between members of the Safety Bay Sand.

C. Stratigraphic profiles illustrating lithologic sequence within, and stratigraphic relationships between Tamala Limestone, Eaton Sand, Leschenault Formation and members of the Safety Bay Sand.

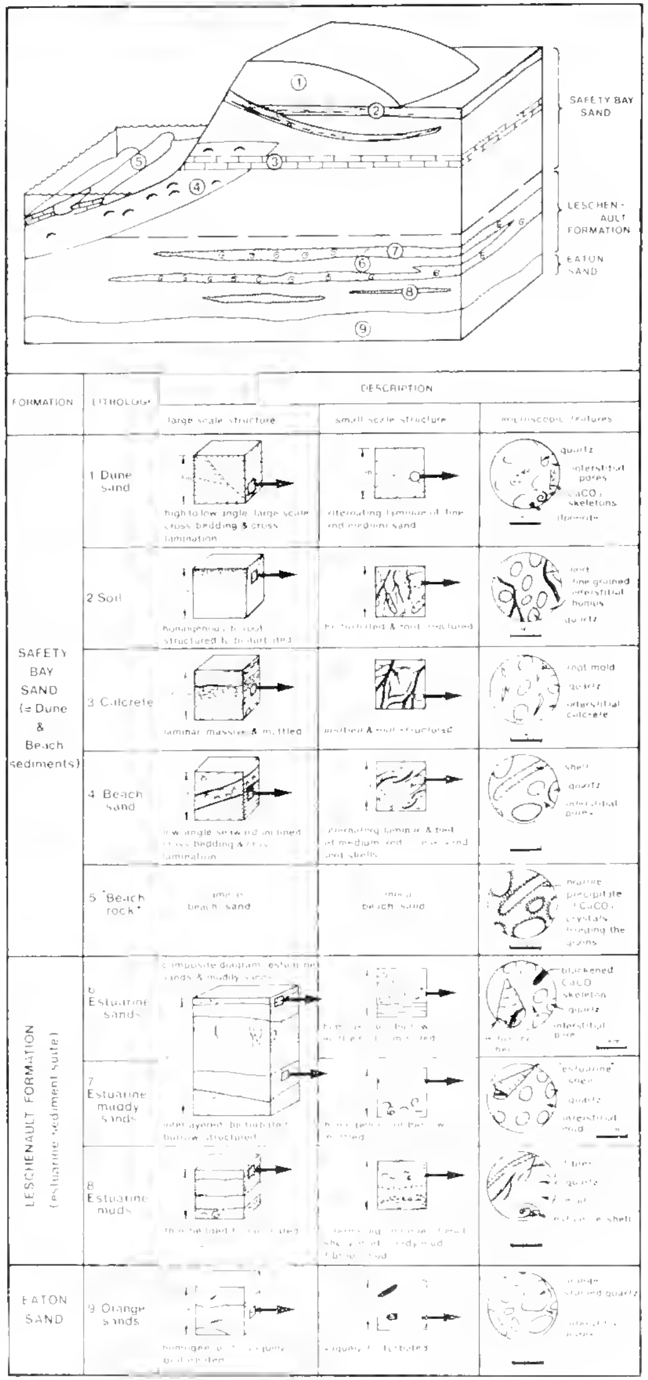

Figure 6.—Summary diagram illustrating characteristics, in terms of structure, fabric, texture and composition, of sediment types in the youngest 3 Quaternary units of the Leschenault area.

Lithology: The Leschenault Formation is composed of grey to dark grey sand (quartz skeletal and quartz), muddy sand and mud, which all may contain shells in layers; sedimentary structures include interlayering lamination and mottling (Fig. 6). The mollusc fauna (bivalve and gastropod) indicates estuarine, lagoonal or inlet environments. Several additional criteria serve to characterise sediments of this formation: 1) plant remains, specifically root fibres, 2) bioturbation structures, varying from well preserved burrows to burrow-mottle structures, and 3) iron sulphide disseminated in the sediments.

The abundance of sediments in the formation is as follows: sand > muddy sand > shelly sand > shelly mud and mud.

From east to west under Leschenault Peninsula there are facies changes in the formation. Mud and muddy sand are less common in the west where sandy sediment predominates (Figs 4 and 5). The end-member components of this lithologic suite are sand, mud and shell. Muddy sand is merely a mixture of 2 end-member components. Sand is medium and, less commonly, fine and very fine sized. The sand-sized skeletal component varies from 1% to 30%; sand composition varies therefore from quartzose to quartz skeletal. Shelly sand is similar to the sand but contains granule-sized whole estuarine gastropods, coarser sized estuarine bivalves and fragments of these shells; shells are scattered randomly through the sediment. In addition to gastropods and bivalves there is an abundance of sand-sized skeletons, floral remains and microflora in this formation. Much of the sand-sized skeletons (fragments and foraminifers) are reworked from calcareous dunes on the west margin of the depositional inlet. Most species of flora and fauna in cores or outcrops are extant.

Mud is dark grey to brown and composed of clay-sized and silt-sized particles. Frequently it is laminated, contains root fibre layers and estuarine shell layers. Mud particles are of two types: the most common is clay mineral; the other is silt-sized skeletal material. However, mud that is a homogenous and mottled mixture of these two types also is encountered. Thus, within the mud sediment suite, the mud-sized fraction may be—

- non calcareous (composed of clay minerals)
- slightly calcareous
- calcareous (composed of silt-sized $CaCO_3$)

Where bioturbation is present sediments are either mottled mixtures of the above sediments or thoroughly bioturbated and homogenous. When burrowing has not been intense, layering and lamination are present. *In situ* rootlets and accumulation of fibrous root hairs locally are abundant, especially in the muds. Sediment layers are lenticular and individual layers are not traceable for large distances. Numerous sand-filled burrows (1-3 cm diameter) may extend down several centimetres through a number of layers.

The stratigraphic distribution of sediment types in this formation is best described by the core sequence at site 28:

AHD
–2.3 m

Top: Light grey medium quartz skeletal sand; Horizontal lamination	25cm
Dark grey mud (clay)	25cm
Interlayered and mottled skeletal quartz sand and muddy sand; shelly in layers	30cm
Unrecovered interval	50cm
Interlayered and mottled skeletal quartz sand and muddy sand; shelly in layers	50cm
Light grey medium quartz skeletal sand	90cm
Interlayered and mottled grey, fine and medium sand and muddy sand; fibrous mud laminae	40cm
Grey mud (clay)	20cm
Grey muddy quartz skeletal fine sand	20cm
Grey quartz skeletal fine sand	20cm
Grey mud (clay)	15cm
Grey medium quartz skeletal sand	45cm
Grey mud (clay) and muddy sand filled burrows	20cm
Interlayered fine and medium quartz skeletal sand	20cm
Grey mud (clay) and muddy sand punctured by sand filled burrows	20cm
Grey, shelly quartz skeletal sand	20cm

Bottom: medium and coarse quartzose sand of the Eaton Sand.

Stratigraphic relationships: The base of the formation usually lies on the Eaton Sand and less commonly on the Tamala Limestone; rarely, in southern areas it rests on the Australind Formation (where both Eaton Sand and Tamala Limestone are absent, presumably due to erosion). The contact with Eaton Sand under Leschenault Peninsula is gradational due to biogenic mixing by burrowing organisms; orange sand grades up into grey (pyritic) sand and this in turn grades into grey sand mottled with muddy sand. On the east margins of Leschenault Inlet the formation is a contemporary deposit and interfingers with sand reworked off the ridge of Eaton Sand. The contact of the Leschenault Formation with the Tamala Limestone is sharp with pebbles of limestone incorporated into the base of the Leschenault Formation; locally sediment of the Leschenault Formation infiltrates cracks and fissures in the top 50 cm of Tamala Limestone.

The Leschenault Formation under Leschenault Peninsula has a sharp contact with the overlying Safety Bay Sand; this contact is mostly at 2-3 m below AHD. On the eastern margin of Leschenault Peninsula the formation interfingers with modern dunes of the Safety Bay Sand as they encroach into Leschenault Inlet; this contact is 0.3 m above AHD. At some localities on the woodland plain the contact is 2 m above MSL.

Age: The following molluscs have been identified from the formation (G. W. Kendrick 1979, pers. comm.): *Acteocina* sp. A, *Acteocina* sp. B, *Alaba monile* (A. Adams), *Alaba* sp., *Bittium icarus* (Boyle), *Bittium granarium* (Kiener), *Diala lauta* (A. Adams), *Elachorbis tatei* (Angus), *Hydrococcus graniformis* Theile, *Katelysia scalarina* (Lamarck), *Nassarius pyrrhus* (Menke), *Potamopyrgus* sp., *Sanguinolaria* (*Psammotellina*) *biradiata* (Wood), ? *Tawera* sp. (fragment) and *Thalotia conica* (Gray). This fauna is Quaternary (G. W. Kendrick pers. comm.).

The top of the formation in Leschenault Inlet is currently depositional and is Holocene. However there are sheets and outliers of Leschenault Formation 2-3 m below and 2 m above present depositional sites. These deposits on basis of their relationship to the Safety Bay Sand are inferred to be mid to late Holocene.

Discussion: Cores from Leschenault Inlet in an area of active sand and mud deposition (see Fig. 5 of Semeniuk and Meagher, 1981b) illustrate that the sedimentary sequence under Leschenault Peninsula has modern analogues. Individual facies are indicative of water depth (Table 2). Along the modern inlet margin decimetre-thick sand layers alternate with mud layers; the sand has accumulated in tongues and sheets and has been derived from the adjacent shoreline. The interior deeper water basin is accumulating mud. In areas transitional between sand shoals and the interior mud basin, are muddy sands. As active sand deposition alternates with mud deposition, a sequence typical of the Leschenault Formation accumulates replete with shells and burrow imprints of the resident benthos.

Cores under Leschenault Peninsula also indicate a facies change from east to west within the Leschenault Formation when sealevel stood 2-3 m lower than present. Muddy areas occurred predominantly to the east with sandy areas to the west. The facies change indicates that there was a sand peninsula further offshore that barred the wider ancient Leschenault Inlet from the ocean. The barrier shed sand into the inlet so that the Leschenault Formation adjoining the barrier was sandy (environmentally equivalent to the modern subaqueous platforms and shoals). Thus, the eastern margin of the ancient dune barrier is inferred to have been at least 0.5-1 km further offshore, and the crest of the barrier may have been 1-2 km offshore. Further evidence for this barrier and the corollary, a wider Lescehnault Inlet, is to be found in the Leschenault Formation muddy sediments (indicative of interior mud basin environments) and faunal remnants now occurring up to 0.5 km offshore on the submarine shelf.

Safety Bay Sand

The Safety Bay Sand is a unit of aeolian, beach and shallow marine sand and shelly sand. The formation, first defined near Rockingham by Passmore (1970), was extended by Playford and Low (1972) to include all similar deposits in the Perth Basin.

Distribution: The Safety Bay Sand is distributed over more than 30 km^2 on the peninsula and within 0.5 km of the submarine shelf, and it extends well out of the area of study.

Geometry and thickness: The top of the formation is hummocky to planar corresponding to modern depositional and hiatus surfaces. The base of the formation is subplanar (Fig. 4). Its geometry on Leschenault Peninsula and nearshore submarine shelf is ribbon-shaped with dimensions 10 km long, 400-1 000 m wide and 30-40 m thick.

Lithology: Sedimentary material typical of the Safety Bay Sand are (Fig. 6):

1. quartz skeletal sand
2. humic quartz sand
3. calcreted sand
4. medium and coarse sand and shelly sand
5. beach rock.

Quartz skeletal sand (dune sand) comprises most of the formation. The sand is cross-bedded and cross-laminated on a dune scale and has an overprint of root structures. Individual cross-laminated units are wedge-to shoestring-to lens-shaped, varying 10 cm to several metres in thickness, and are separated by erosional discontinuities and soils. The sediment is light yellow to cream, and composed of medium sand with lesser fine sand. Locally laminae contain platy granule-sized shells. Quartz is dominant (approximately 80% to over 99%). A light coating of iron oxide on quartz and $CaCO_3$ grains imparts a light yellow colouration to the sediment.

Humic quartz sand (soil) occurs as sheets (0.3-2.0 m thick) throughout the Safety Bay Sand. They are dark grey to brown, bioturbated and composed of medium and fine sand-sized quartz. There is interstitial humus and root hairs. Calcreted sand occurs as a widespread sheet within the formation near the top of the water table (1.5 m above AHD). The sheet invariably has mottled, massive, laminar and brecciod structures (Semeniuk and Meagher 1981a). Calcrete in mottled and rhizoconcretionary (= rhizotubular) structure also occurs well above the water table (2.0-30 m above AHD).

Table 2

Key stratigraphic contacts and environmentally significant sequences that are related to specific levels relative to AHD*

Type of sequence	Environmental significance	Deposition site relative to A.H.D.
Dune sand overlying thick soil with *in situ* tree trunks	Indicating dune encroachment on a vegetated plain; subaerial	2-5 m above AHD
Cream-light yellow dune sand overlying grey Leschenault Formation sand	Indicating dune encroachment into inlet; shoreline	Contact is approximately 0·3 m above AHD
Sand of Leschenault Formation overlying thick mud	Indicating shoal encroachment into interior basin; subtidal	Contact 1·5-2 m below AHD
Shoaling sequence† of trough bedded sand and gravelly sand overlain by laminated sand and shelly sand, overlain by gravelly sand with *Spirula* and *Sepia*, overlain by dune sand	Indicating beach shoaling from subtidal through the swash zone up to storm level and subaerial aeolian	Subtidal, tidal, storm tide level, and supra-tidal
Yellow/orange sand overlying limestone	Indicating subaerially exposed limestone with shallow sand cover	

* These sequences aid in the palaeo-environmental interpretations of the stratigraphy. Specific stratigraphic contacts where found in cores or cliff exposures indicate palaeo-environments or indicate position of former sealevels.

† This sequence is described in more detail in Semeniuk and Johnson (1982)

Medium and coarse sand and shelly sand (beach sediments) are light yellow to orange, laminated, cross-laminated and cross-bedded units. They are bedded on a decimetre scale, with layering inclined seaward. The sediments are composed of quartz, skeletal fragments and whole shells. Beach rock is similar to beach sediments described above, but has been indurated by marine carbonate (Semeniuk and Meagher 1981b).

Molluscs and sand-sized skeletons occur mainly in the beach and shallow marine sediments. Sand-sized skeletons reworked from the beach face are present in the dune sands. Fossil stumps of tuarts (*Eucalyptus gomphocephala*) and peppermints (*Agonis flexuosa*) occur *in situ* on buried soils in the stratigraphic profile (see Figs. 8A and 9 in Semeniuk and Meagher 1981b).

Stratigraphic relationships: The Safety Bay Sand conformably rests on, and locally interfingers with, the Leschenault Formation (Figs. 4 and 5). The base of the formation lies mostly at 2-3 m below AHD; the modern base lies at about MHW. The top of the Safety Bay Sand is the modern surface.

Detailed study has shown that there are 5 distinct and mappable lithological and or diagenetically altered units within the formation. Each of these units are related to a discrete historical phase when sea-level stood 2-3 m below, 3-4 m above, and at the present level. It is proposed here to subdivide the Safety Bay Sand into 5 members; these are: Burragenup Member, Rosamel Member, Vittoria Member, Kcombana Beach Rock, Binningup Calcrete.

Burragenup Member (named after Burragenup district, grid reference 371895 Collie 1:250 000 sheet).

The Burragenup Member, up to 40 m thick, is the oldest member in the Safety Bay Sand. It is a unit of aeolian sand and soil sheets and underlies most of the peninsula. Its distinguishing characteristics are:

(1) it is partly indurated along laminae such that up to 30% of the profile may be lithified; abundant rhizoconcretions;

(2) its contact with Leschenault Formation is at *2-3 m below AHD* showing that it was deposited with sealevel at 2-3 m below present; its top is variably eroded but it may extend to 35-40 m above AHD.

The Burragenup Member has a conformable prograding contact with older portions of the Leschenault Formation (Figs. 5 and 6); on the east margin of the peninsula the contemporary Leschenault Formation overlies it (Fig. 7). It has an erosional discordant contact with Rosamel Member and a sharp contact (marked by soil) with Vittoria Member.

Rosamel Member (named after "Rosamel" property, grid reference 371897, Collie 1:250 000 sheet).

The Rosamel Member, up to 15 m thick, is littoral sand/beach-ridge/dune unit and it occurs as a wedge cropping out on the western face of the peninsula. Its characteristics are:

(1) uncemented sand and shelly sand with patchy development of rhizoconcretions; shells include *Donax*, *Donacilla* and *Glycymeris*;

(2) within the member there is a shoaling sequence of sediments (Semeniuk and Johnson 1982); dune sand overlies beach ridge and storm gravelly sand (with *Spirula* and *Sepia*) which overlies swash zone shelly sand laminite and subtidal trough bedded gravelly sand;

(3) the individual facies of this member occur *3-4 m above their modern counterparts*, thus the member was deposited with sea-level 3-4 m higher than present.

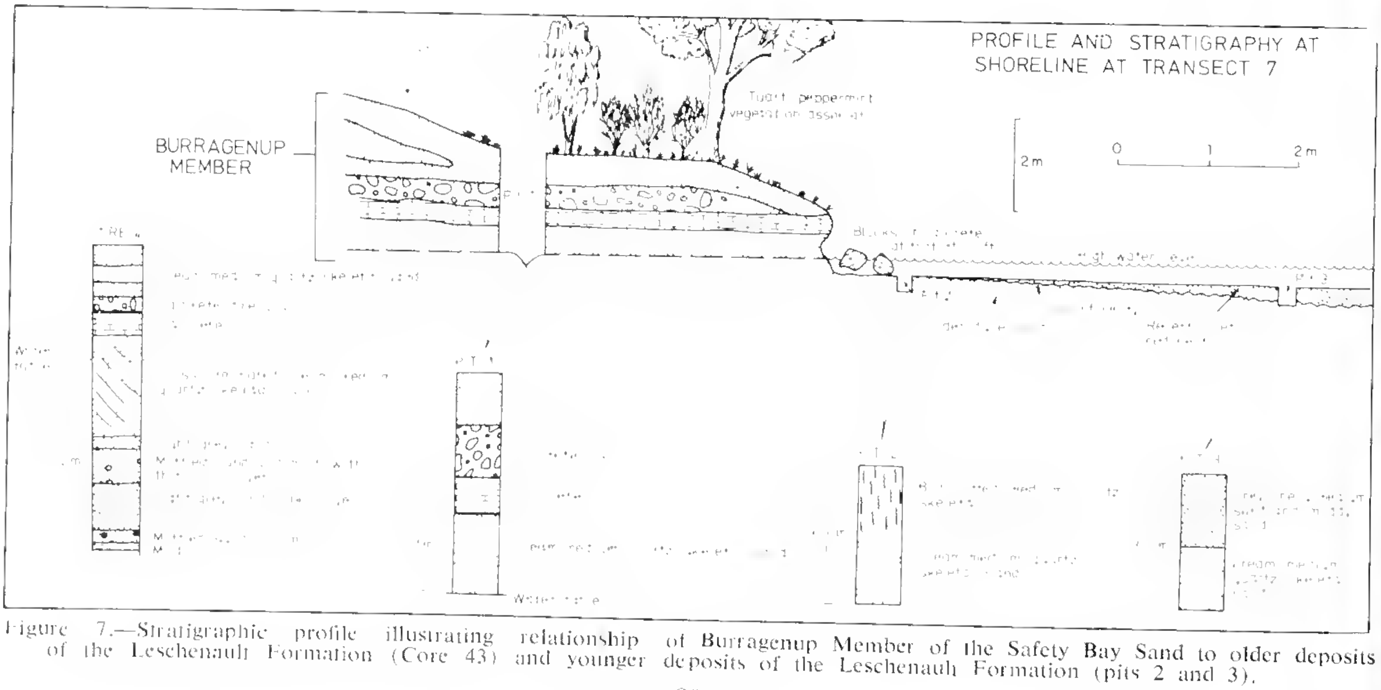

Figure 7.—Stratigraphic profile illustrating relationship of Burragenup Member of the Safety Bay Sand to older deposits of the Leschenault Formation (Core 43) and younger deposits of the Leschenault Formation (pits 2 and 3).

The Rosamel Member has an erosional contact with underlying Burragenup Member (Figs. 4 and 5) and an erosional contact with overlying Vittoria Member (Fig. 5). The outcrop of Rosamel Member widens northward and the unit also pinches out to the east. The unit was deposited along a shoreline oriented NNE. Toward the south the unit occurs only as inliers in interdune depressions of the Burragenup Member, showing that the palaeo-shoreline nearly is totally eroded away in these localities.

Vittoria Member (named after Vittoria Bay, grid reference 366883, Collie 1:250 000 sheet).

This is the modern beachridge and dune sequence of the Peninsula. Its characteristics are:

(1) aeolian and beachridge sands and related soil sheets, totally uncemented and lacking rhizoconcretions;

(2) forming with sealevel standing as at present.

This member overlies Burragenup and Rosamel Members with a sharp contact.

Typically partly indurated, root-casted and calcreted sediment of the older members are truncated by a humic soil over which the Vittoria Member rests (Figs. 4 and 5).

Koombana Beach Rock (named after Koombana Bay, grid reference 365885, Collie 1:250 000 sheet).

This is the modern sequence of beach rock developing along the shoreface of the peninsula and forming the shallow rocky reefs in the nearshore environment (see Fig. 10, in Semeniuk and Meagher 1981b). The sediment of the member is sand and gravelly sand cemented by magnesian calcite. The sand and gravelly sand are in a shoaling sequence showing shallow subtidal sand laminites underlain by trough-bedded gravelly sand and sand. The Koombana Beach Rock unconformably overlies the Tamala Limestone and remnants of Leschenault Formation.

Binningup Calcrete (named after Binningup Beach, grid reference 368902, Collie 1:250 000 sheet).

This is the widespread sheet of calcrete (0.3-0.5 m thick) that occurs just above the modern water table (Semeniuk and Meagher 1981a) and is related to a historical phase associated with the modern sea-level. Since it is parallel to the water table it transects stratigraphic boundaries and unconformities. The Binningup calcrete is exposed by cliff erosion on the ocean side of the peninsula, and locally also occurs cliffed on the inlet side.

Discussion: The disposition of members shows that the barrier dune system of Leschenault Peninsula was developed in 3 stages. All sediments in the formation have modern analogues most of which are forming in specific environments relative to AHD (Table 2). Thus it is possible to infer the relative position of former sea-level and/or water table when each of the members was deposited.

Radiocarbon dating of shells in the Rosamel Member gave the following ages:

3 845 ± 195 yrs BP on shells from site 31 (Fig. 2)

3 610 ± 190 yrs BP on *Donacilla* shells from site 15 (Fig. 2)

4 025 ± 195 yrs BP on *Glycymeris* shells from site 15

4 770 ± 210 yrs BP on *Glycymeris* shells from near site 4 (Fig. 2).

These indicate a late Holocene age. Since this member rests on an erosional interface cut into the underlying unit, the radiocarbon ages indicate deposition of Burragenup Member some time earlier in the Holocene. Unfortunately at this stage no material for dating has been obtained from the Burragenup Member. The Vittoria and Koombana Members are clearly contemporary. Charcoal and wood from three localities in the Vittoria Member gave the following ages:

< 100 yrs BP from soil 3 illustrated in Fig. 9B of Semeniuk and Meagher (1981b)

< 100 yrs BP from near "The Cut", Fig. 1

295 yrs BP from near "The Cut", Fig. 1.

The development of the Binningup Calcrete is related to the modern sea-level and it has formed under the present climatic oceanographic regime. Presumably the climate was sufficiently different (possibly more like Perth) earlier in the Holocene to preclude calcrete development.

Quaternary history

The Quaternary history of sedimentation for this area begins at the buried surface of the Mesozoic Warnbro Group. Weathering and erosion modified the top of the Warnbro Group to form an undulating surface with local relief in the order of 5 m over several kilometres. The calcareous sands and muds of the Australind Formation were deposited in the mid Pleistocene over the weathered plain; the sediments are thickest where they filled depressions in the plain. Sediments of the Australind Formation have their modern analogy in near-coastal lakes or lagoons suggesting that the Australind Formation developed as calcareous fill in a chain of saline lagoons not unlike the modern Leschenault Inlet. The shelly (fossiliferous) phases represent normal marine or estuarine conditions. Subsequent subaerial weathering/erosion of the Australind Formation formed colluvial soils, with nodules reworked from the calcareous parent sediments, and developed an undulating topography with local relief in the order of 5 m.

The Pleistocene Tamala Limestone, was the next unit to accumulate. It extended from at least several kilometres east of the present Leschenault Inlet to several kilometres offshore. The formation pinches out to the south, an area where it may be expected to be juxtaposed against a ridge of Bunbury Basalt. The history of the formation is a complex one of alternating marine sedimentation, aeolian sedimentation, soil development, alteration in a fluctuating fresh water system, induration by cementing agents, marine and aeolian erosion and colonization by coastal vegetation. These events are imprinted in the sediments as shell and aeolian sand deposits, open and filled cavity systems, calcrete products, sparry calcite cements, wind deflation deposits, calcreted root structures and so on.

During periods of subaerial exposure, the Tamala Limestone was indurated by calcrete and sparry calcite. The induration was localised as a sheet in upper parts of the profile and tended to grade downwards into unconsolidated host sediments. Subaerial exposure and solution of indurated limestone developed cave and vug systems which were filled later by infiltrating marine and vadose-water transported calcareous sediment. At the top of the formation is a major unconformity, marked by extensive calcrete, erosional surfaces, solution features, colluvial gravel and large scale karst.

The Eaton Sand was deposited, probably by aeolian action, as a sheet over the Tamala Limestone (Fig. 8A). The topography at this stage was similar to "The Pinnacles" (near Cervantes) or the "Little Desert" at Mullaloo; limestone pinnacles and knolls poke up through a sheet of yellow quartz sand, and pavements of limestone are exposed locally. A similar topography of pinnacles is exposed underwater some 300 metres offshore.

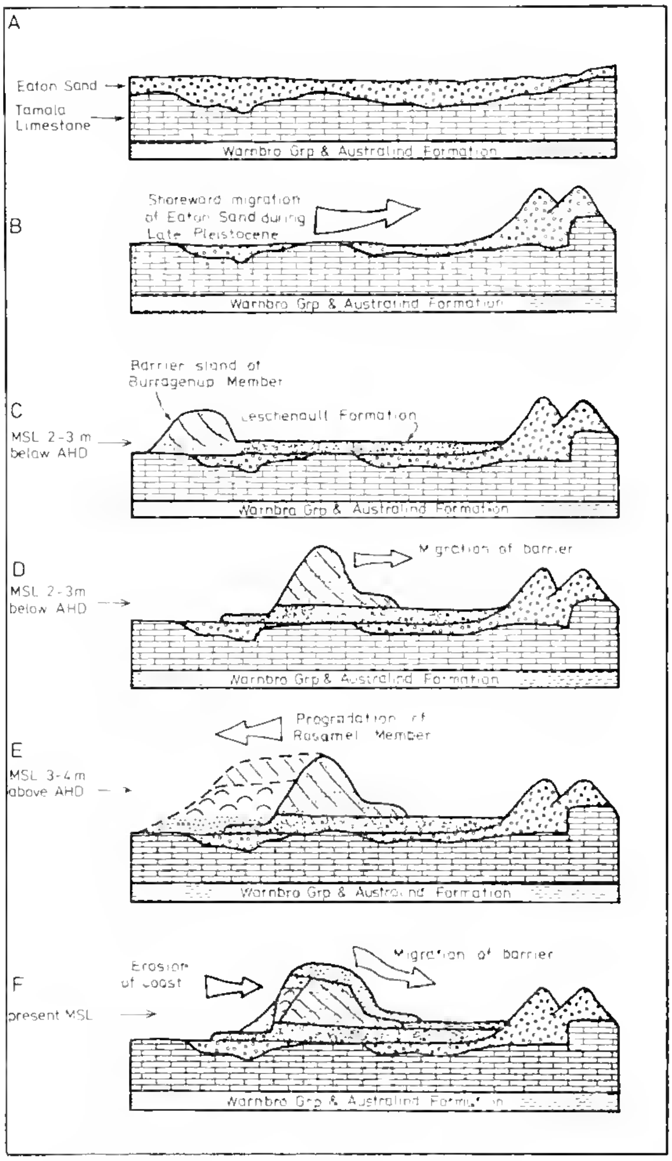

Figure 8.—Summary of Quaternary sedimentation in the Leschenault Inlet area in post-Tamala Limestone time.

The Eaton Sand was reworked as a shoreline deposit forming a coastal ridge system during a marine transgression in the Late Pleistocene (Fig. 8B). Prior to the emplacement of Eaton Sand, a large coastal cliff was cut into Tamala Limestone probably during the initial stages of this trangression. The buildup of Eaton Sand suggests open ocean wave-dominated conditions with sustained aeolian activity onto the shoreface, a palaeogeographic setting which would *preclude* an offshore barrier. It implies there was a marine stillstand after deposition of Tamala Limestone but prior to the development of coastal barrier dune systems that formed the Safety Bay and Leschenault Formations.

The last phases of deposition involved the Safety Bay Sand and Leschenault formations. The deposition and historical development of the Leschenault and Safety Bay formations are linked in that: the Leschenault Formation must accumulate behind a barrier of Safety Bay Sand and, the Safety Bay Sand by eastward migration ultimately progrades over Leschenault Formation. The stratigraphic relationships of the two formations (relative to AHD) and the ages determined by radiocarbon dating of the younger members indicate that the barrier dune system and sediments of the lagoonal/estuarine system were developed in three stages. The first stage, earlier in the Holocene, involved deposition of lagoonal/estuarine sediments behind a barrier dune system when sealevel stood 2-3 m lower than present (Fig. 8C). Initially, as indicated by facies in the Leschenault Formation, the coastal barrier stood some 2-3 km further offshore but with *still-sand conditions* the dunes of the Safety Bay Sand (Burragenup Member) migrated eastward until their eastern edge reached approximately the position the eastern margin of the peninsula occupies today (Fig. 8D).

The next phase of deposition took place with sealevel 3-4 m above present. The marine incursion initially resulted in erosion and trimming back of the dune terrain. The dune terrain however was not totally removed, so that an inlet or lagoon remained intact behind a much reduced (narrow) barrier. In the longterm however there appeared to be a net coastal progradation on the west side of the barrier, with accumulation of shoaling sequence (Rosamel Member) of subtidal sand, beach sand, beach ridge and finally, a capping of aeolian sand (Fig. 8E). This marine/aeolian deposition took place along a coastline of Burragenup Member oriented NNE; probably the coastline was linked to Casuarina Point. The details of sedimentation along the palaeo-shoreline at the onset of the marine incursion are preserved locally. Littoral sand of the Rosamel Member was deposited within corridors (interdune depressions) between east-west oriented dunes; these deposits essentially accumulated in small embayments. Soil sheets of the Burragenup were truncated by erosion during the marine incursion but in some areas soils were merely reworked and locally incorporated into the overlying strandline marine deposits.

During accumulation of Rosamel Member there was concurrent deposition of Leschenault Formation sediments. These are preserved onshore as stranded shelly sand (with estuarine shells) and minor mud deposits located now up to 2 m above AHD. Most of these deposits however are reworked, or overprinted by pedogenetic processes, or buried by later dunes.

The final depositional stage for this area is the current marine incursion (Fig. 8F). This involves accumulation of lagoonal/estuarine sediment of the Leschenault Formation, eastward dune progradation and development of beachrock and calcrete. Erosion and net northward sediment mobilization however are the major processes along the seaward edge of the barrier dune system today. As the barrier retreats eastward, sediments of the Leschenault Formation are being exposed and cliffed, and exhumed ridges of beach rock are left as outliers on the submarine shelf. Under the modern climatic and hydrologic regime a calcrete sheet is forming just above the water table on the peninsula. This calcrete is essentially a water table phenomenon related to the present sealevel and it transects the various member units of the Safety Bay Sand and the erosional interfaces between them.

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A preliminary survey of the ant fauna of the Darling Plateau and Swan Coastal Plain near Perth, Western Australia

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Abstract

Sixty-eight ant species in 22 genera were collected by pitfall traps and hand sampling made along 2 transects, one north and one south of Perth, running across the Coastal Plain and on to the Darling Plateau. Six vegetation associations were represented along each transect. There were no trends in species richness, diversity or evenness across the transects although overall species composition differed between certain vegetation associations. These differences are discussed in terms of soil type and vegetation association and the results are compared with those from a similar study in the Queensland sub-tropics.

Introduction

There are well over 1 500 species of ants in Australia (Brown and Taylor 1970), and many of them are of significant ecological or economic importance. In the southwest of Western Australia, for instance, species of *Pheidole* and *Rhytidoponera* prey on larvae of the economically significant jarrah leaf miner, *Perthida glyphopa* during spring when larvae fall to the ground and burrow (Z. Mazanec 1975 pers. comm.) In addition, *Rhytidoponera inornata* and *Melophorus* sp. 1 (ANIC) are significant agents assisting the germination of *Acacia* spp. seeds (Shea *et. al.* 1979. This is of particular importance in view of the interest in promoting a leguminous understorey in the Western Australian jarrah (*Eucalyptus marginata*) forest to suppress dieback disease caused by the pathogenic fungus *Phytophthora cinnamomi* (Anon. 1978).

The work described in this paper is a preliminary survey of the ant fauna found in areas of differing soil and vegetation association close to Perth, Western Australia. One aim of the study is to relate ant species distribution and overall community composition to soil and vegetation type. The information gained should be of value in forest management and also, since the survey is in an area of continuing high human impact, should contribute base-line data from which environmental change can be detected (O'Brian 1975).

Areas studied

The area immediately adjacent to Perth consists of a flat Coastal Plain bounded to the east by the Darling Scarp (Fig. 1) beyond which lies the Darling Plateau. The vegetation of this region was first mapped by Speck (1952) (summarised in Seddon 1972) although a more refined vegetation classification and map has recently been produced by Heddle *et al.* (1980). The soil types and major landforms have been mapped in Anon (1980). Speck's (1952) map was originally used for selecting our study plots although the vegetation associations described here are those of Heddle *et al.* (1980).

The sandy Coastal Plain may be broadly divided into a number of landform units which run more or less parallel to the coastline. These are the Quindalup Dune System which occurs adjacent to the coast, and the Cottesloe, Karrakatta, Bassendean and Southern River Dune Systems. The Darling Scarp soils are shallow red and yellow earths with considerable rock outcrop and the Darling Plateau has lateritic soils.

The area has a mediterranean climate. The 800 mm isohyet runs close to, and parallel with, the coast near Perth while the 1 000 mm isohyet corresponds closely with the top of the scarp in this region.

Two east-west transects were established respectively north and south of Perth city for surveying the ant fauna. The north transect ran from Mullaloo Beach to Old Toodyay Road on the Darling Plateau and the south transect extended from Cape Peron to Armadale (Fig. 1). Six survey plots were established along each transect at sites representing six representative vegetation associations (Fig. 1). Since much of the Coastal Plain has been cleared care was taken to select areas representative of the original vegetation.

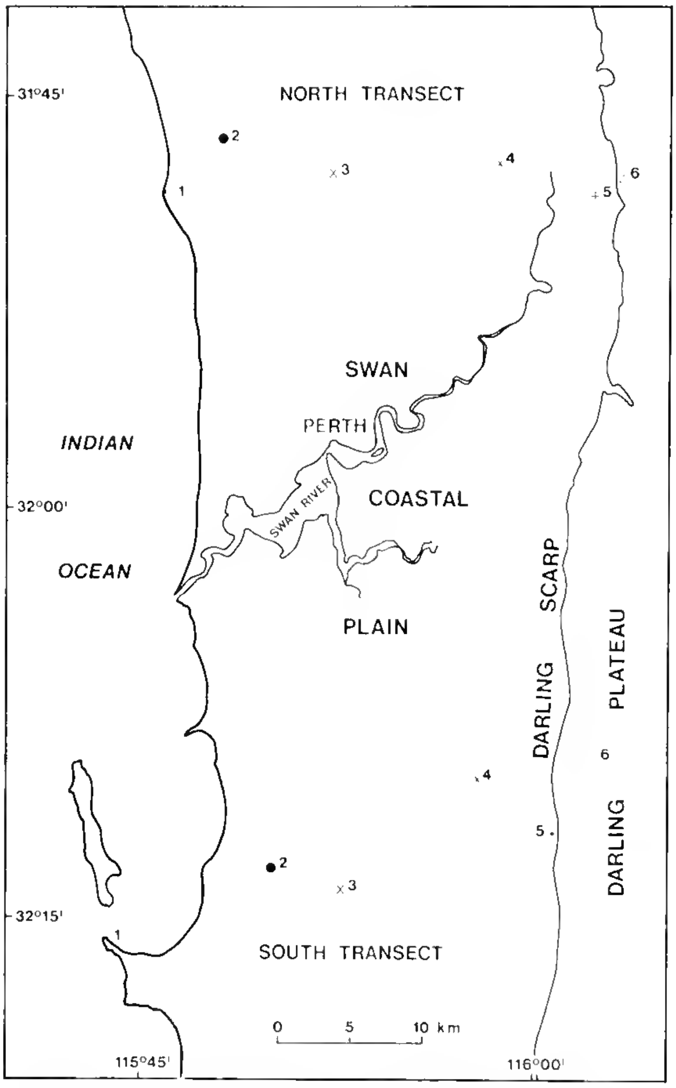

Figure 1.—Distribution of the ant survey study plots. ○, coastal closed-scrub; ●, tuart-jarrah-marri open-forest; ⊗, jarrah-banksia tall-woodland; x, banksia-sheoak-prickly bark tall-woodland; +, wandoo-marri tall-woodland; △, jarrah-marri open-forest.

The plot numbers and their respective vegetation associations are given in the caption to Table 1. Plots 1N and 1S were both situated in closed-scrub of the Quindalup Dune System. Plots 2N and 2S occurred on the Cottesloe Dune System and were covered by an open-forest of tuart *(Eucalyptus gomphocephala)*, marri *(Eucalyptus calophylla)* and jarrah. Plots 3N and 3S respectively overlapped the Karrakatta and Bassendean Dune Systems; in both cases the vegetation was a tall-woodland of jarrah and *Banksia* spp. Plots 4N and 4S occurred on the Bassendean Dune System and were situated in tall-woodland of *Banksia* spp., sheoak *(Casuarina fraserana)* and prickly bark *(Eucalyptus todtiana)*. The Darling Scarp plots (5N and 5S) were situated in tall-woodland of wandoo *(Eucalyptus wandoo)* and marri while the Plateau plots (6N and 6S) were representative of jarrah-marri open-forest.

Methods

The ant survey

Plots of approximately 2.5 ha were selected in late February, 1979. Forty pitfall traps were then established in each plot in order to sample the range of principal ground habitats within the area. Traps consisted of 18 mm internal diameter Pyrex test tubes containing 10 ml of alcohol/glycerol (70/30 mix by volume) preservative. Traps were left in the ground for 7 days in early March to give a total of 280 trap-nights per plot. Hand collections were also undertaken during March for 1 man-hour in each plot during the daytime.

The hand collections and trap samples were sorted to species level. Where ants could not be assigned specific names they were coded with Australian National Insect Collection (ANIC) or Western Australian Institute of Technology (J.D.M.) code numbers. The taxonomy of many Australian ant genera is not well known. Some of the species names given in this paper apply only in a very broad sense and therefore identify what are often species complexes. Voucher specimens are retained at the Western Australian Institute of Technology.

Data analysis

The data were subjected to several analyses. Ant species richness in plots was derived by summing the total number of species obtained by both sampling methods. The diversity of ants was further investigated using Shannon's (Shannon and Weaver 1949) H' index. This was calculated by the following formula:

$$H' = \frac{N \log N - \sum_{i} n_i \log n_i}{N}$$

where N is the total number of individuals and n the number of individuals of each species to the ith species. This index is of only limited value for describing the diversity of ant faunas since it combines two factors: species richness and species evenness. However it is a useful method for calculating the latter, which is the degree of apportionment of the individuals amongst the species present in an area. Evenness was calculated by the following formula:

$$J' = \frac{H'}{\log S}$$

where S is the total species present.

Only pitfall trap data were used for calculating these two indices since hand collections did not contribute quantitative data.

The composition of the ant fauna in each plot was compared using principal components ordination analysis. The ordination technique first compares the species content of the samples using Orloci's (1966), Weighted Similarity Coefficient (W.S.C.).

$$W.S.C = \sum_{i=1}^{n} (x_{ij} - \bar{x}_i)(x_{ih} - \bar{x}_i)$$

where x_{ij}, x_{ih} are the species scores for samples j and h, $\bar{x}_i$ is the species score for the average stand and n is the number of samples. The samples are then arranged along axes, termed components, so that the samples with the least similar species content occur farthest apart. The first component represents the combination of variables with maximum variance, subsequent components represent

Table 1

Systematic list of ants obtained by hand collection (*) or by pitfall trapping at the twelve study sites in February-March, 1979. Numbers represent total individuals caught in forty pitfall traps.

	Vegetation											
Transect and plot number	Coastal closed-scrub		Tuart-jarrah-marri open-forest		Jarrah-banksia tall-woodland		Banksia-sheoak -prickly bark tall-woodland		Wandoo-marri tall-woodland		Jarrah-marri open-forest	
	N1	S1	N2	S2	N3	S3	N4	S4	N5	S5	N6	S6
MYRMECIINAE												
Myrmecia chasei	*							1*				
PONERINAE												
Brachyponera lutea			6	6	1*	1				1	1*	1*
Cerapachys sp. J.D.M. 203						1						
Rhytidoponera inornata	32		15	1	4	5	2	4		140*	3	26*
R. violacea	369	89	338*	127		333*	36	176*	142	137*	126*	172*
R. sp. J.D.M. 121	1			4								
MYRMICINAE												
Aphaenogaster sp. J.D.M. 224	1											
Cardiocondyla nuda	2	*		1				1				
Chelaner sp.						*				1*	2	
C. sp. J.D.M. 502									35*			
C. sp. J.D.M. 503						41						
Monomorium sp. 1 (ANIC)	1			15								
M. sp. 2 (ANIC)							32					
M. sp. 3 (ANIC)	8	14	14	25	15	24	6	14	14	7	17	6
M. sp. J.D.M. 100								5			2	
M. sp. J.D.M. 225			15	134*	9		1		4	1	20	1
Pheidole latigena	4		7	2		8		16*	19	*	1	6
Podomyrma sp. J.D.M. 365										*		
Tetramorium bicarinatum											2	
T. impressun				2						2		
T. sp. J.D.M. 347	4		1	5							2	
T. sp. J.D.M. 492	2											
T. sp. J.D.M. 493												1
Crematogaster sp. J.D.M. 33	5	18			80*	78	6			1		
C. sp. J.D.M. 42			2				1					
C. sp. J.D.M. 350	3	14*	*	18	16*	*					2	
Meranoplus sp. 12 (ANIC)			7		1	20	3			4		1
M. sp. J.D.M. 74	1		2	1		8	1	13	1		8	7
M. sp. J.D.M. 157	9	2	5	1	4							
M. sp. J.D.M. 422	15		3	6		1	4		39		11	7*
M. sp. J.D.M. 491							10					12
DOLICHODERINAE												
Diceratoclinea sp. J.D.M. 211			1*			*					*	
Tapinoma sp. J.D.M. 134				2		1						
Iridomyrmex agilis gp.sp. 21 (ANIC)	15*	42*	5*	31	*	2	44*	88*	1*	2	*	23*
I. confer gp.sp. J.D.M. 72						*		29*		39	18*	
I. glaber gp.sp. J.D.M. 83	1		*		*						1	
I. purpureus gp.sp. J.D.M. 47									121*	19		
I. sp. 19 (ANIC)					*						1*	1
I. sp. J.D.M. 9	58*	20*	9*	5*	3	5*	3*	205	21*	85*	3	68*
I. sp. J.D.M. 84				*				3				
I. sp. J.D.M. 217				17*							4*	
I. sp. J.D.M. 449			2				1					
I. sp. J.D.M. 507			20									
I. sp. J.D.M. 508				1			*		4	2		
I. sp. J.D.M. 509	1	1				1	1	16				
FORMICINAE												
Camponotus calcius gp.sp.J.D.M. 27			1		*		*	*				
C. sp. J.D.M. 25				1				3		2		
C. sp. J.D.M. 106					*							
C. sp. J.D.M. 199	17		45	63*		3	75	194*	79*	1	12	84*
C. sp. J.D.M. 213										1		
C. sp. J.D.M. 233							3	1			*	
C. sp. J.D.M. 229							12	2	1			
C. sp. J.D.M. 287									*			
C. sp. J.D.M. 490						1				*		
Polyrhachis sp. J.D.M. 118		1										
Melophorus sp. 1 (ANIC)	4	*		27	*	5*	4*	8*	4	19		14
M. sp. 3 (ANIC)	2			15	1	*	3	17	*		1	
M. sp. J.D.M. 77							1				1	
M. sp. J.D.M. 221		1*		2	1		14		1			
M. sp. J.D.M. 230		*				*	12	2	1			
M. sp. J.D.M. 500				2		2						
M. sp. J.D.M. 501	2											
Notoncus gilberti	4		10				3			13		
N. sp. J.D.M. 487				1								
Plagiolepidini(gen.indet.)sp.J.D.M. 489											1	
Stigmacros sp. J.D.M. 80										2		
S. sp. J.D.M. 188				1						1		
S. sp. J.D.M. 488		1										

combinations with decreasing variance. The components may then be identified with environmental factors since these contribute to the variation in species composition. The resulting ordination is therefore a useful tool for investigating the relative influence of different environmental factors on fauna composition. Computations were performed using species presence/abence data for each plot. Austin & Greig-Smith (1968) found this provided as much information as numerical data.

Results

The ant species collected by hand and pitfall trap are listed in Table 1. Presence/absence data are indicated for the hand collections although numbers per 280 trap-days are shown for the species taken by the pitfall traps. Species richness, diversity and evenness indices for each plot are given in Table 2. The total species richness for both transects of each vegetation association is also given.

The survey yielded 68 species from 22 genera. The numbers of species collected in each plot varied from 14 to 29 (Table 2). The total species richness for each vegetation association varied from 29 to 37. There were no trends in species richness values across either transect. This was also the case with the species diversity and evenness indices which respectively ranged between 0.619-1.038 and 0.459-0.752.

It should be noted that this was a preliminary survey so the species census was incomplete. For instance, more detailed surveys in tuart-jarrah-marri open-forest at Jandakot (32° 10′ S, 115° 50′ E) and at Reabold Hill, Perth (31° 57′ S, 115° 47′ E) have yielded 43 and 57 species respectively. Thus the present census may have underestimated the true species richness values by a factor of two.

Inspection of the data shown in Table 1 indicates a surprising degree of ubiquity amongst most species found during this survey. A number of species were infrequently collected so it is not possible to confidently describe their distribution pattern. However, of the remainder, a few showed clearly definable patterns. For instance, a number of otherwise common species were absent from the coastal closed-scrub (e.g. *Brachyponera lutea*, *Monomorium* sp. J.D.M. 225 and *Meranoplus* sp. 12 (ANIC). Certain other species were widespread but absent from the open-forest of the Darling Plateau (e.g. *Melophorus* sp. J.D.M. 230). Several other species appeared to be confined to particular belts of the Coastal Plain (e.g. *Camponotus* sp. J.D.M. 229) while in this study the small purple form (Halliday 1979) of the meat ant, *Iridomyrmex purpureus*, was confined to the exposed gravelly soils of the Darling Scarp.

The ordination graph of axes 1 vs 2, which respectively represented 15.6 and 14.1 per cent of the total variance, is shown in Fig. 2. It was not possible to interpret axis 3 so it is not shown here. The most obvious trend in the plot spacings was that from the open-forest of the Plaeau to the left of axis 2 to the coastal closed-scrub fauna on the right of this axis. The other open-forest and woodland plots were grouped together near the middle of axis 2 although the tuart-jarrah-marri open-forest plots were separated on the upper part of axis 1.

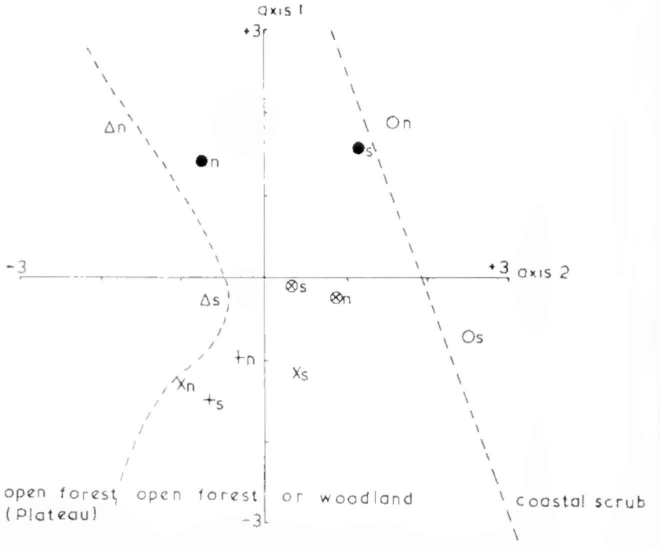

Figure 2.—Position of study plots in terms of ant species composition along axes 1 vs 2 of the principal components ordination diagram. Symbols as in Figure 1. n & s indicate north and south transect respectively.

Table 2

Ant species richness, diversity and evenness of the ant fauna sampled at the twelve study sites in February-March, 1979. The cumulative ant species richness for each vegetation association is also shown.

	Vegetation											
Transect and plot number	Coastal closed-scrub		Tuart-jarrah-marri open-forest		Jarrah-banksia tall-woodland		Banksia-sheoak -prickly bark tall-woodland		Wandoo-marri tall-woodland		Jarrah-marri open-forest	
	N1	S1	N2	S2	N3	S3	N4	S4	N5	S5	N6	S6
Species richness (S)	25	14	22	29	17	25	26	21	18	24	25	16
Cumulative species richness	29		37		32		33		32		29	
Species diversity (H^1)	0·634	0·716	0·635	0·996	0·619	0·621	1·038	0·855	0·842	0·819	0·813	0·799
Species evenness (J^1)	0·459	0·688	0·488	0·688	0·595	0·485	0·752	0·657	0·699	0·620	0·606	0·663

Discussion

The current study resembles that of Greenslade & Thompson (1981) which examined the ant faunas in different locations on sandy soils of the Cooloola sandmass and the sandstones of the Noosa River catchment on the Queensland coast. They found the ant fauna to differ within certain landforms, soil types and vegetation associations in terms of species composition, richness and community structure. These differences were explained by variation in soils, vegetation structure (e.g. its pattern, height, ground and canopy cover) and associated microclimates.

Our findings differ from those of Greenslade & Thompson (1981) in that, although species composition varied, there were no trends in ant species richness, diversity or evenness across either of the transects. On the Cooloola sandmass the areas of greater primary production, canopy height and cover were associated with a large increase in the richness of cryptic ant species which nest and forage within decaying logs, soil or litter. This trend in richness accounted for much of the ant community variation in the different study areas. In other habitats, such as vine forests, the trend of increased species richness under shade was reversed.

The microclimate is relatively harsh under the coastal closed-scrub, woodland and open-forest alike during the summer when this study was performed. Thus the opportunities for summer active cryptic species to abound under the more dense vegetation would, relatively speaking, be less in comparison with the Queensland study sites. This may not be the case for species which are more active during moister, more humid periods (Majer and Koch 1982) but the distribution of these species was not investigated. The absence of certain species under dense vegetation was attributed by Greenslade & Thompson (1981) to the relatively low temperatures experienced under such conditions. This effect is also unlikely to be as marked in the Western Australian sites studied since high ground temperatures were experienced under all densities of vegetation.

Greenslade & Thompson (in 1981) found three basic ant distribution patterns related to soil. These were:

1. only present on Cooloola sands,
2. widely distributed with respect to soils, and
3. only present on soils derived from Noosa River sandstones.

Our findings indicate a similar differentiation of distribution. Patterns we observed were:

1. absent from the Quindalup Dune System,
2. absent from the Darling Plateau,
3. confined to particular belts of the Coastal Plain or Darling Scarp, and
4. widely distributed with respect to soil.

The cumulative effect of these distribution patterns has produced the overall differentiation of ant communities on the ordination diagram (Figure 2). This investigation has not enabled us to clearly separate the influence of vegetation and soil although the distribution of plots on the ordination diagram (Figure 2) suggests that both factors play an important role in determining ant community composition.

Ecological information on individual species of ants is generally inadequate to discuss individual distribution patterns observed here. However a number of comments may be made on selected species.

Pheidole latigena and *Rhytidoponera violacea*, species known to prey on the Jarrah leaf miner, *P. glyphopa*, are distributed throughout the Coastal Plain and Darling Plateau (Table 1). *P. glyphopa*, is common on the Coastal Plain in this region but rare in the Darling Plateau east of Perth (Mazanec 1978). The ubiquity of the major ant predators in this region suggests that they cannot be the limiting factor in leaf miner distribution.

Melophorus sp. 1 (ANIC) and *R. inornata*, significant agents influencing *Acacia* spp. seed distribution and survival (Shea *et al.* 1979), are also widespread in most study plots. This suggests that the phenomenon of ants burying *Acacia* seed observed by Shea *et al.* (1979) in the forests of the Darling Plateau is also likely to occur on the Coastal Plain.

Apart from the humid parts of Australia, Australian ant communities are usually dominated by various species of *Iridomyrmex* which influence the remainder of the ants present (e.g. Greenslade 1976). The dominance of this genus was also the case in the plots we investigated although selective pitfall trapping of certain species (e.g. *R. violacea* (Table 1)) tends to obscure this phenomenon. Our investigation indicates a change in dominant species across the two transects studied. *Iridomyrmex agilis* and *Iridomyrmex* sp. J.D.M. 9 were the dominant species from the coastal closed-scrub through to the banksia-sheoak-prickly bark tall woodland. The small purple form of *I. purpureus* was dominant on the insolated gravelly slopes of the Darling Scarp although the shade regime was too heavy for it to occur in the more dense forest of the Plateau. A further species, a member of the *I. conifer* gp., reached dominant status in certain areas including the banksia-sheoak-prickly bark tall-woodland and to the east. This species was, until recently, common in other parts of the Coastal Plain but has declined in recent years (R. P. McMillan 1980, pers. comm.).

As ants are dominant members of many Australian invertebrate communities, the distribution of ant species probably affects the distribution of many other animal taxa. Thus the trends observed in our study may reflect those of other zoological components of the ecosystem.

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The flora and vegetation of Barrow Island, Western Australia

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Abstract

Barrow Island is a limestone island 233 km^2 in area off the northwest coast of Western Australia. Its flora comprises both coastal and arid elements. Undisturbed vegetation may be classified into the following main types, listed in decreasing order of areal extent: *Triodia wiseana* hummock grassland on limestone uplands; *Triodia angusta* hummock grassland on watercourses and lowland loams; *Triodia pungens* hummock grassland on red sand; coastal complex, primarily *Spinifex longifolius* assemblage on white calcareous foredunes; short forb community on floodout flats; salt flat; and mangroves. These are mapped and described, a total of 29 subtypes being recognised. Vegetation patterns in undisturbed areas are controlled primarily by substrate, but fire, grazing and exposure to salt-laden winds are also involved.

Introduction

Barrow Island is a limestone island approximately 29 km by 11 km, 56 km from the West Australian coast between Onslow and Port Hedland (Fig. 1). Its vegetation is of significance for the following reasons. Firstly, it contains substantial areas of arid calcicole *Triodia* hummock grassland. There are detailed analyses of arid hummock grassland on inland siliceous sands (e.g. Wiedemann 1970, Fatchen and Barker 1979, Buckley 1981) but only broad descriptions of those on coastal calcareous sands (e.g. Sauer 1965, Burbidge 1971, Beard 1975). Secondly, Barrow Island is a Class A Reserve, and a knowledge of vegetation pattern is therefore significant for fauna conservation. Thirdly, Barrow Island was cut off from the mainland by rising sea-levels about 8 000 years ago. Are there endemic Barrow Island races of plant species as there are for some of the animals?

Lying at 115° 20′ E, 20° 45′ S, off the north-west shoulder of Western Australia, Barrow Island experiences a monsoonal northern climate (Gentilli 1972) moderated by its oceanic position. Prevailing winds are predominantly easterly in summer and south-westerly in winter. Summer temperature maxima exceed 40°C whilst winter maxima approximate 26°C. Mean annual rainfall is 200 mm, with peaks in February-March and May-June. Cyclones may occur between November and March: one in March 1964 deposited 330 mm rain in 12 hours (Butler and Cox 1975). Creeks and claypans fill only during the wet season. Heavy dews are also common.

The island consists of Tertiary limestones—the Upper Eocene Giralia Calcarenite and the lower Miocene Trealla Limestone—overlain by Quaternary dune limestone, alluvium and coastal sand (Kriewaldt 1964, Parry 1967). The Tertiary rocks are folded into an anticline. The southern end of the island is low as a result of faulting (the Barrow Island Fault), and the northern end as a result of the northern plunge of the anticline, together with minor faulting. The central section is wedge-shaped in cross-section, sloping from high coastal cliffs and steeply dissected uplands in the west to low cliffs and coastal plains in the east. The subsurface geology was outlined by Crank (1973).

Previous studies of Barrow Island vegetation may be summarised as follows. Serventy and Marshall (1964) noted *Triodia* hummock grassland as the dominant vegetation and listed 34 plant species during a zoological survey in 1958. Goodall (1969) constructed partial distribution maps in 1964 for 93 named species; Burbidge and Main (1971), reporting on a visit in 1969, collected 32 plant species and described the vegetation only as "tussock grassland dominated by *Triodia*", as did Main and Yadav (1971). Butler (1970) recognised 6 zones or habitat types, summarised in Table 1, with stands of *Erythrina vespertilio* and *Eucalyptus patellaris* as subtypes. This classification was used by Beard (1975) and Sedgwick (1978). Sedgwick and Butler also made brief descriptions of the vegetation at 80 points on the island, each located randomly within a 3 km grid square (Sedgwick 1976, Appendix E).

Table 1

Summary of previous vegetation classification (Butler 1970)

No.	Zone	Substrate	Characteristic species
1	Foredune	white sand	*Spinifex longifolius*
2	Red dunes	red sand	*Triodia angusta*, *Acacia coriacea*
3	Ridges	limestone	*Triodia wiseana*
4	Pans	clay	*Paspalidium tabulatum*
5	Creekbeds	red earths	*Triodia angusta*
6	Mangrove	tidal muds	*Avicennia marina*

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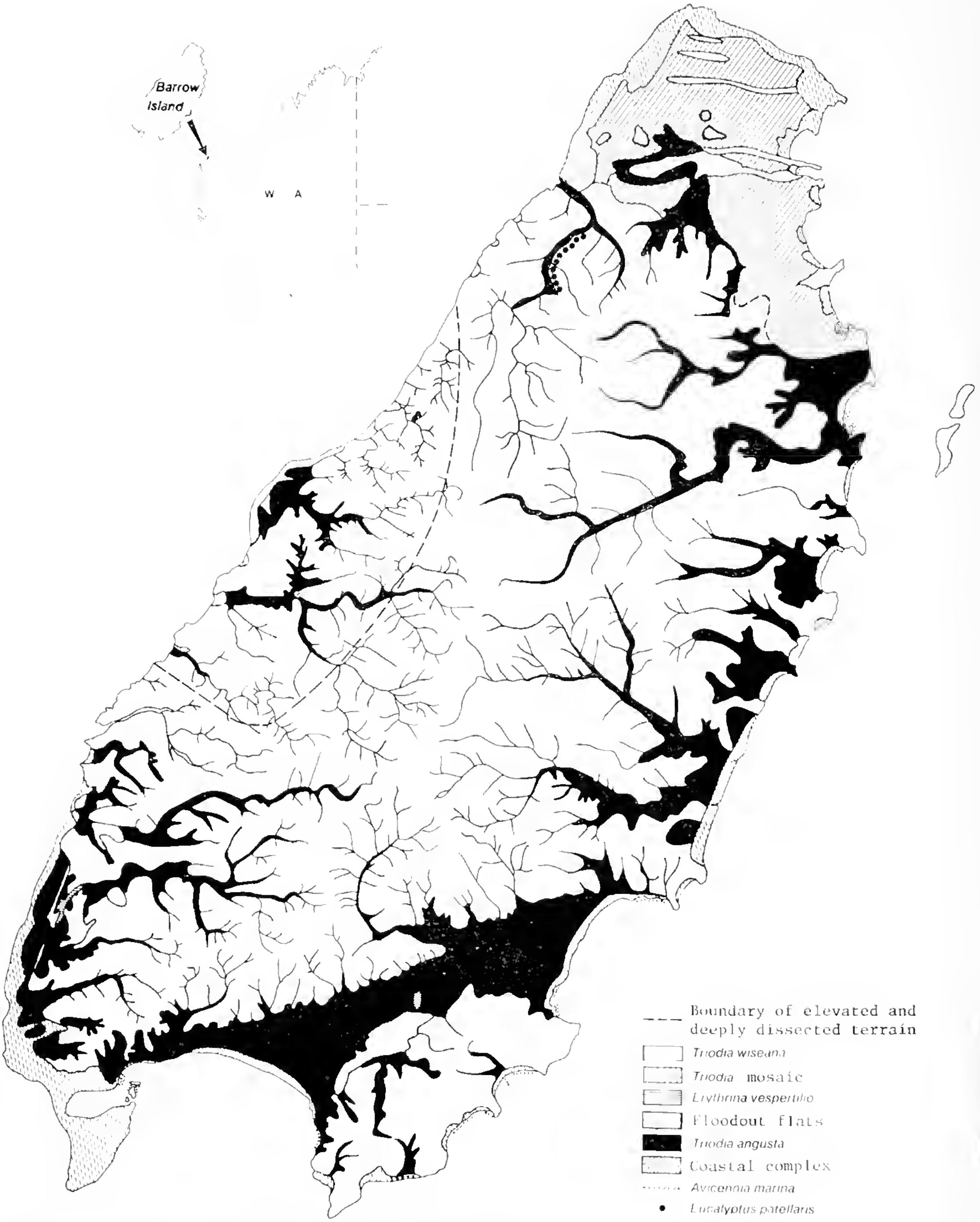

Figure 1.—Distribution of main vegetation units described in text.

Analysis of vegetation pattern in a large and relatively complex area such as Barrow Island must proceed in a series of successive approximations (Poore 1962). A single numerical analysis of vegetation data from random or blocked-random sample sites, for example, can only reveal the broader patterns (Buckley 1983). More precise descriptions require further analyses, with sampling patterns based on the results of previous approximations. I therefore used the classification given in Table 1 as a first approximation or first-degree classification. My aims were as follows. Firstly, I tested the validity of the first-degree classification by examining floristic separation between its 6 units. Secondly, I attempted to refine it to a second-degree classification. Thirdly, I mapped the distribution of the major units. Fourthly, I examined the relations between vegetation and factors such as soils, fauna and fire regime, in so far as time permitted, and attempted to pinpoint problems deserving investigation in the future.

Methods

1. Tests of first-degree classification. Firstly, I compiled floristic censuses for ten 1 m x 1 m, ten 5 m x 5 m and five 25 m x 25 m quadrats in each of units 1-5 as listed in Table 1, plus the *Erythrina vespertilio* subunit and a *Halosarcia* salt flat, and compared the overall floristic assemblage and the species-area relations in each unit to test floristic separation between units. Secondly, I analysed vegetation changes across the boundaries between the units, by laying out transects of contiguous 5 m x 5 m quadrats perpendicular to the boundaries, and scoring the presence or absence of each species in each quadrat. The resulting matrices were clustered by unconstrained hierarchical polythetic agglomeration and monothetic division, using the error sum of squares and euclidean distance in each case, followed by relocation, and the characteristic species of each cluster identified from their binary frequency ratios.

2. Second-degree classification. Using results from the above, I constructed a second-degree classification subjectively.

3. Vegetation mapping. The distributions of the major vegetation units were mapped from 1:20 000 vertical colour aerial photographs and a colour photomosaic of the entire island and 1:10 000 false-colour infrared vertical air photocoverage of selected portions, supported by extensive ground survey. The distributions of shrubs restricted to limited regions of the *Triodia wiseana* limestone upland vegetation were also mapped by ground survey.

4. Relation to environment. Soil texture was assessed subjectively in the field. Soil fertility was assessed by taking soil samples at intervals along transect lines, and from bulldozed pits where available, and measuring their pH, salinity, total N (micro- Kjehldahl method), and extractable P (1% bicarbonate extract). Other factors were assessed from historical records (e.g. fires), or subjectively (e.g. exposure, guano input).

Results

Flora

A complete floristic list is given in Appendix 1, which also shows the main habitat of each species using the first-degree classification given in Table 1. It comprises 218 species supported by voucher specimens, and a further 39 species mentioned in previous published or unpublished reports but no longer traceable to voucher specimens.

Transects

Profiles and cluster diagrams for the five transects are given in Figs 2 and 3. Cluster groups produced by monothetic division were similar or identical to those produced by polythetic agglomeration. Dendrograms are not reproduced here but are available from the author on request.

Transect 1 was taken across a valley cut by a deep river bed, its ends being in *Triodia wiseana* on limestone ridges, and its centre in *T. angusta* on deeper valley soils (Fig. 2). The two main clusters coincide with the *T. wiseana* and *T. angusta* areas as recognised on the ground, verifying that different floristic assemblages are associated with the two different *Triodia* species and that terrain classification on the basis of the dominant *Triodia* species represents a classification into recognisable and distinct plant communities. The characteristic species of the *T. wiseana* assemblage are: *Diplopeltis eriocarpa, Dodonaea lanceolata, Scaevola cunninghamii, Codonocarpus cotinifolius, Petalostyles labicheoides, Hannafordia quadrivalvis,* and *Acacia gregorii*. Only the first two of these are entirely confined to the *T. wiseana* quadrats, but all are relatively abundant, so that their greater frequency in the *T. wiseana* cluster has very high statistical significance, measured from the hypergeometric distribution as described by Buckley (1981).

Many of the species characterising the *T. angusta* assemblage grew only in the centre of the valley, and despite being quite abundant there, were consequently recorded in only one or two quadrats of the transect: namely, *Adriana tomentosa, Indigofera monophylla, Pterigeron bubakii, Solanum lasiophyllum, Dysphania plantaginella* and *Paspalidium tabulatum*. Three further species, *Centipeda minima, Cymbopogon procerus* and *Tephrosia rosea*, were also confined to the *T. angusta* assemblage: they were recorded in 5, 4 and 3 quadrats respectively. The other characteristic species of the *T. angusta* assemblage were *Stylobasium spathulatum, Calandrina balonensis* and *Chrysogonum trichodesmoides*.

The third cluster shown for this transect comprises quadrats associated with the road verge, the river bed, and old tracks along the southern side of the valley. Six species have high binary frequency ratios in this cluster: *Chamaesyce atoto, Trichodesma zeylanicum, Acanthocarpus preissii, Corchorus sidioides, Hannafordia quadrivalvis* and *Stylobasium spathulatum*. Of these six, the first two species are representative of disturbed ground only, whilst the next three are also common on the limestone slopes, and the last on the valley soils. Further division separates

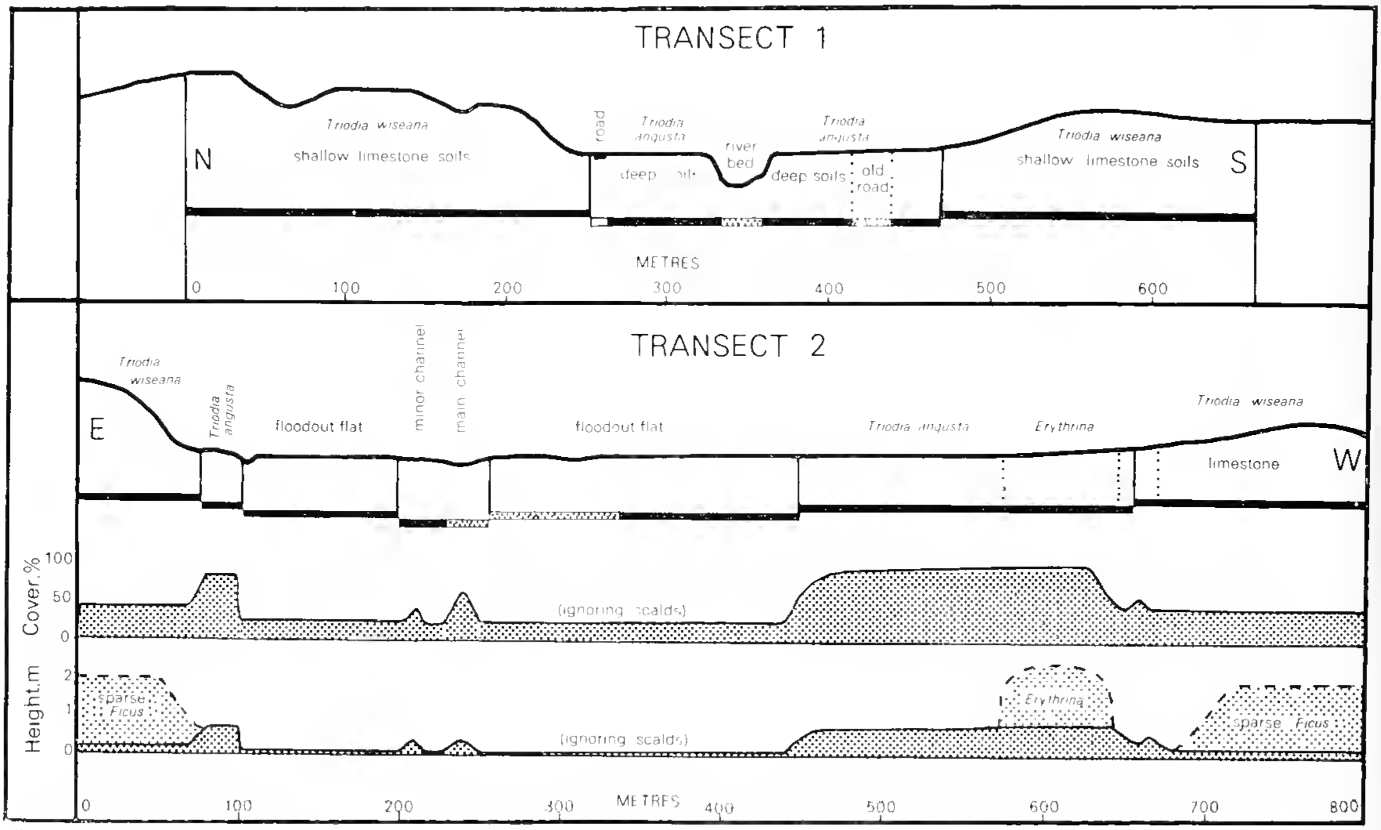

Figure 2.—Vegetation transects 1 and 2. Approximate topographic profiles are shown as heavy lines. Floristic clusters (see text) are plotted as horizontal bars, each cluster on a different horizontal line. Shaded areas within bars represent subdivisions of main clusters. Thus in transect 1 the *Triodia angusta* valley cluster is comprised of three sub-groups occupying respectively the deep valley soils, the riverbed, and ground disturbed by tracks. In transect 2, the western half of the floodout-flat cluster is subdivided at the next finer stage, as is the central-channel cluster. Total aerial cover and vegetation cover are also shown for transect 2, with the ground and shrub layer distinguished by shading density in the latter case. Cover and height are not shown for transect 1 since both main clusters are hummock grassland of closely comparable structure.

the *T. wiseana* cluster into a mosaic of three sub-units, associated only indistinctly with small-scale topography. At the boundaries between the *Triodia angusta* and *T. wiseana* zones there are regions where both occur together. These are grouped with the *T. angusta* quadrats on the basis of overall floristics: 97% of quadrats containing *T. angusta* (with or without *T. wiseana*) are in the *T. angusta* cluster, the corresponding figure for *T. wiseana* being only 77%; 95% of the 'mixed' quadrats are grouped with *T. angusta*.

The second transect runs across the largest floodout flat on the island, starting on a ridge on its inland side (Fig. 2). Clusters based on overall floristics coincide very precisely with vegetation types recognised on the ground. Limestone hills at the eastern and western ends bear low open *Triodia wiseana* hummock grassland, and the flat is fringed by a band of very dense *T. angusta*, accompanied on the western margin by *Erythrina vespertilio*. The boundary between the *T. wiseana* and *T. angusta* is much sharper than in transect 1. A flood channel runs down the centre of the flat; where crossed by the transect, it consists of a shallow eastern section and a deeper western channel. Immediately west of the flood channel there is a relatively bare area of flat with numerous scalds. All these features are reflected in the cluster groupings in Fig. 3. Seven species are confined to the *T. wiseana* community: *Polycarpaea longiflora*, *Caladrinia balonensis*, *Indigofera colutea*, *Ficus platypoda*, *F. opposita*, *Enneapogon oblongus* and *Chamaesyce australis*. *Paspalidium tabulatum* and *Ptilotus obovatus* are also common between spinifex hummocks. *Abutilon exonemum* and *Capparis spinosa* are common in both *T. wiseana* and *T. angusta* but not on the flat; *Chrysopogon fallax* and *Eulalia fulva* protrude from the *T. angusta* hummocks, though not present in the transect. The floodout flat bears an assemblage of small forbs, notably *Heliotropium undulatum*, *Stackhousia elata*, *Sida fibulifera*, *Sporobolus australasicus*, *Centipeda minima*, *Centaurium erythraea*, *Chamaesyce atoto*, *Dichanthium affine*, *Dysphania plantaginella*, *Eragrostis xerophila* and *Haloragis gossei*. Scalded areas are more depauperate, *Pterigeron bubakii*, *Eragrostis xerophila and Centaurium erythraea* being the main species; the central flood channels support a lush growth of the forbs mentioned above, together with *Pterocaulon sphacelatum*, *Morgania glabra*, *Malvastrum spicatum*, *Cleome viscosa*, *Triumfetta leptacantha* and *Trichodesma zeylanicum*, some of these being more common in the eastern channel and others in the western.

Half of the hummocks in the easternmost fringe of the western *T. angusta* belt were dead in September 1980, and a quarter of those in the centre of the belt; this might have been the result of flooding, but since most of the remaining hummocks had brown centres under thin green skins it could indicate

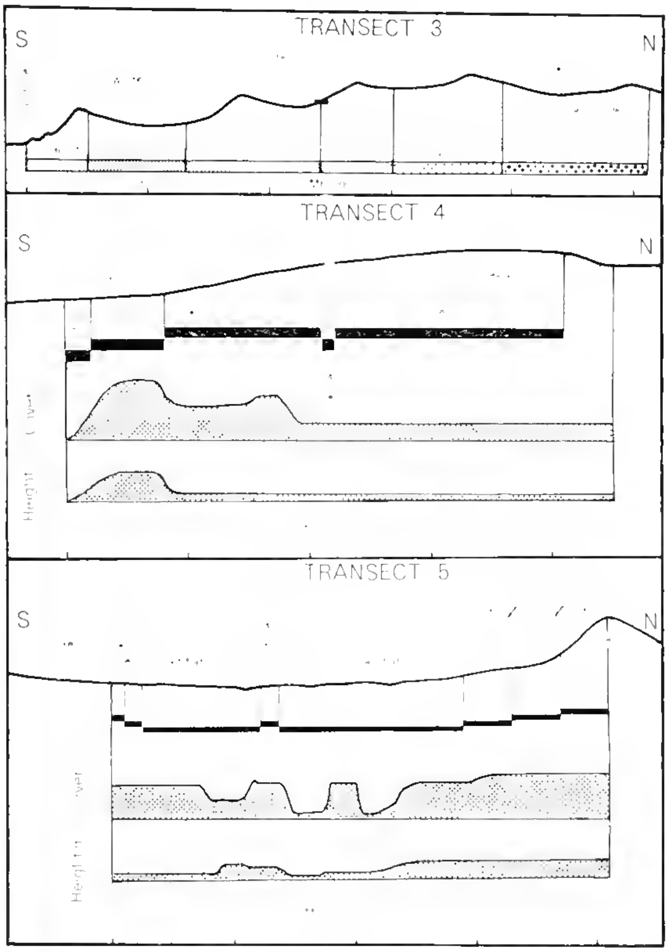

Figure 3.—Vegetation transects 3, 4 and 5. Key as for Figure 2. The vegetation of Transect 3 is much more uniform than that of the other 4 transects; it can be subdivided satisfactorily, but at a lower dissimilarity level. The 6 clusters represent sections of a continuous gradient within a single main vegetation type, rather than the sharply demarcated communities characteristic of the other transects, and have therefore been shown as subdivisions of a single bar.

that the stand was overmature. The ground under the trees was bare save for occasional seedings of *Triodia* and *Abutilon exonemum*, abundant *Erythrina* seedlings 10-40 cm high, and an open cover of *Malvastrum spicatum*, *Nicotiana occidentalis*, *Eragrostis xerophila*, *Trichodesma zeylanicum*, *Cleome viscosa*, *Haloragis gossei*, and *Pterigeron bubakii*, which were otherwise restricted to the sparse inter-hummock spaces.

The third and fourth transects contrast sandy and rocky coasts at the southern end of the island. Transect 3 runs from a sandy strandline and associated *Spinifex longifolius* on the white-sand foredune ridge, across an area of coastal *Acacia coriacea* on cream calcareous dunes a few metres high, to the edge of *Triodia pungens* hummock grassland on gently undulating subcoastal pink calcareous sands (Fig. 3). Structure being determined by the dominant species, the primary field classification is into *Spinifex*, *A. coriacea* and *T. pungens* zones. The vegetation of this transect is much more homogenous than that of the other 4, and if the same dissimilarity coefficient is used as a stopping value in the clustering process, the entire transect would be included in a single cluster. The cluster dendrogram showed a gradual floristic change along the transect, however, and the *A. coriacea* zone can be subdivided on the basis of overall floristics, with distinct and non-overlapping quadrat groups on each ridge. This gradual floristic change may reflect the sequence of ridge soils; inspection of the raw data and binary frequency ratios indicates that floristic differences between them are confined to a gradual increase in species richness on the ridges further inland, with the sequential appearance of *Rhagodia obovata*, *Triodia angusta*, *Heliotropium undulatum*, *Adriana tomentosa*, *Chamaesyce myrtoides*, *Olearia axillaris*, *Nicotiana occidentalis*, *Dysphania plantaginella* and *Triodia pungens*. The fusion dendrogram indicates that these four groups are very similar floristically; the inland *T. pungens* zone is distinct though not disjunct floristically, whilst the strandline assemblage has the greatest floristic separation from the rest of the transect. *Spinifex longifolius* and *Atriplex semilunaris* are restricted to quadrats on the seaward side of the first ridge, also characterised by the loose-sand species *Ptilotus villosiflorus* and *Chamaesyce australis*, and the halophyte *Frankenia pauciflora*.

Transect 4 commences on a narrow beach of limestone pebbles and runs through a narrow band of *Spinifex* on shallow sand, a tall dense belt of *Triodia angusta* with *Stylobasium spathulatum* and *Acacia bivenosa*, and up a short slope, covered by low open *Triodia pungens*, to a limestone ridge bearing a mixed *T. wiseana-T. pungens* assemblage (Fig. 3). The limestone cap and slopes are floristically similar, the main difference being the presence of *T. wiseana* on the cap only. Rather than separating slopes and cap, further division into four clusters picks out the two quadrats at the edge of the cap; these lack *T. pungens* and most of the associated species, instead containing *Dodonaea lanceolata*, *Capparis spinosa*, *Rhynchosia minima* and *Boerhaavia diffusa*. Two relatively abundant species, *Diplopeltis eriocarpa* and *Nicotiana occidentalis*, are confined to the *T. wiseana-T. pungens* assemblage on limestone, as are six further species, notably *Jasminum calcareum*, *Ficus platypoda* and *Chenopodium carinatum*. *Olearia axillaris*, *Frankenia pauciflora* and *Stylobasium spathulatum* are confined to the *Triodia angusta* belt, which is also characterised by *Acacia bivenosa* and *Myoporum acuminatum*. *Rhagodia obovata* is the main species associated with *Spinifex longifolius* in this transect, whilst *Enchylaena tomentosa* and *Ptilotus villosiflorus* are also common on the rubble beach itself.

The fifth transect crosses a salt flat near the northeastern coast. The flat lies between two limestone ridges, and the transect starts at the base of the southern ridge, close to the edge of the flat, and continues to the top of the northern ridge (Fig. 2). Four clusters are separated: the *Triodia wiseana* community on the limestone ridges; a mixed *Triodia* assemblage on the lower limestone flanks; a "fringe" group comprising quadrats at the edges of the salt flat together with a few on a slightly raised limestone area within it; and the main saltflat community, comprising 60% of the total. The

Triodia wiseana community is characterised, as elsewhere, by *Polycarpaea longiflora*, *Heliotropium ovalifolium*, *Cymbopogon procerus*, *Pterocaulon sphacelatum* and *Solanum lasiophyllum*. *Scaevola cunninghamii*, *Ficus platypoda* and *Sida corrugata*, each recorded only once, are also confined to the ridges. The mixed *Triodia* assemblage, besides containing all three *Triodia* spp., is characterised by *Cymbopogon procerus*, *Trichodesma zeylanicum*, and *Sclerolaena spinosa*; the "fringe" quadrats lack *T. wiseana* and are characterised by *Sclerolaena spinosa* and *Nicotiana occidentalis*. On the main salt flat *Sclerolaena* is replaced by *Neobassia astrocarpa*, *Frankenia pauciflora*, *Threlkeldia diffusa* and *Limonium salicorniaceum*. In addition, there is a consistent microtopographic pattern, with the succulent halophytes *Halosarcia halocnemoides* and *H. indica* ssp. *leiostachya* in slight salty depressions, and *Sporobolus virginicus*, *Dysphania plantaginella* and *Synaptantha tillaeacea* on slightly higher areas.

Results of the transect analyses may therefore be summarised as follows. Transect 1 demonstrates that the distinction between *Triodia wiseana* and *T. angusta* vegetation types is supported by overall floristic differences. Comparison of transects 1, 2, 4 and 5 shows that there is a variety of mixed-*Triodia* assemblages with a variety of associated species, which cannot satisfactorily be included with any of the single-*Triodia* communities. Transect 2 again confirms the *T. wiseana*-*T. angusta* separation and demonstrates that the floodout forb-flat is floristically as well as structurally distinct from the hummock grasslands. It also shows that the *Erythrina* woodland is not a separate community, but merely a hummock grassland with *Erythrina* overstorey. The third and fourth transects contrast vegetation pattern on white-sand and limestone-rubble coastlines, and the fifth describes a distinct salt flat assemblage.

Overall, the transects demonstrate clear floristic separation between the units of the first-degree classification, which is therefore supported. There is floristic overlap between the mixed *Triodia* assemblages and the three single-*Triodia* communities; between the understorey of old *Avicennia* stands on sand, and the salt-flat assemblage; between the assemblages of coastal and inland limestone; and between disturbed ground and surrounding undisturbed vegetation.

Maps.

The main vegetation units are mapped in Fig. 1. The subunits are not mapped. Coastal and subcoastal sand assemblages (*Spinifex longifolius*, *Acacia coriacea*, coastal *Triodia angusta* and *T. pungens*) are mapped as a single unit owing to constraints of scale. Within the *T. wiseana* limestone uplands, a number of shrub species are confined to particular regions. A similar situation applies in the *T. angusta* lowlands. The distributions of 10 such species are mapped in Figs. 4 and 5. The distributions of *Hakea suberea* and *Gossypium robinsonii* were also mapped; both are scattered but widespread and have therefore not been shown here.

Figure 4.—Distribution of *Acacia pyrifolia, Cassia pruinosa, Codonocarpus cotinifolius, Eucalyptus patellaris, Melaleuca cardiophylla* and *Passiflora foetida*.

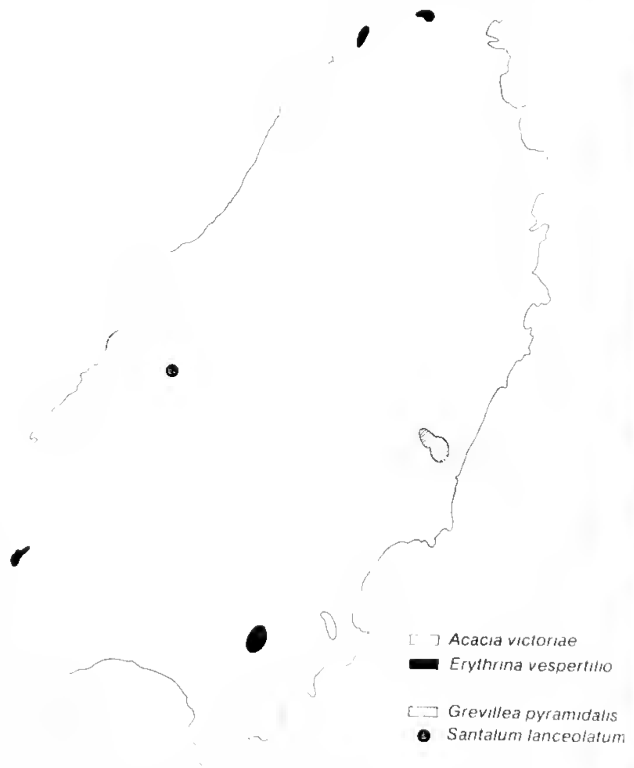

Figure 5.—Distribution of *Acacia victoriae, Erythrina vespertilio, Grevillea pyramidalis* and *Santalum lanceolatum*.

Second-degree classification.

I propose the following second-degree classification:

1. Limestone uplands dominated by *Triodia wiseana*

(a) higher ridges and plateaux with caprock, in centre and west of island. Open *T. wiseana* cover, 0.3 m high. Associated species: *Ficus platypoda, Pittosporum phylliraeoides, Acacia pyrifolia* (Fig. 4), *A. gregorii, Enneapogon oblongus.*

(b) lower ridges and slopes, with limestone rubble. *Ficus platypoda, Codonocarpus cotinifolius, Grevillea pyramidalis, Cassia pruinosa, Pittosporum phylliraeoides, Melaleuca cardiophylla* in certain areas (Fig. 4). *Indigofera monophylla, Diplopeltis eriocarpa, Corchorus sidioides, C. parviflorus* and *Polycarpaea longiflora* often associated.

(c) steep gullies with *Mallotus nesophilus* and *Goodenia microptera* in patches (centre and west); limestone solution hollows with *Mallotus, Cyperus cunninghamii, Plumbago zeylanica* and *Nicotiana occidentalis.*

(d) *Eucalyptus patellaris* stands. One of these is in a creekbed ("Valley of the Giants") and the other on a high western ridge (Figs 1, 5).

2. Areas dominated by *Triodia angusta:* watercourses and lowlands

a. watercourse lines in upland areas, bearing narrow lines of *T. angusta* cutting through the *T. wiseana* on slopes and ridges.

b. broad areas of dense *T. angusta* on flat bottoms of main valleys, on deep soils derived from slopewash debris. Clumps to 1 m height x 2 m diameter, 70-90% cover. *Gossypium robinsonii* often associated.

c. extensive lowland plains to east and south of island (Fig. 1), characterised by an *Acacia bivenosa* overstorey.

d. subcoastal fringe in some areas (e.g. south coast) where a belt of *T. angusta,* often with intermittent *Acacia coriacea* overstorey, lies between coastal *Spinifex* and a belt of *Triodia pungens* slightly further inland.

e. *T. angusta* with *Erythrina vespertilio* overstorey; a number of small stands (Fig. 5).

f. *T. angusta* with *Acacia victoriae* overstorey; a single stand on old red sands associated with fossil shells of the bivalve mollusc *Anadara* (Fig. 5).

3. Mixed *Triodia* assemblages

These do not form ecologically separate units, but are either ecotonal, in the case of (a) and (b), or in the case of (c) a mosaic controlled by small-scale soil pattern. They are listed together for convenience only.

(a) cemented conglomerate (old valley fill) at margins of present valleys. Dense *T. wiseana* with some *T. angusta.*

(b) similar areas but with less cemented or deeper soils; *T. angusta* stands with isolated *T. wiseana..*

(c) a large area of *T. pungens / T. angusta / T. wiseana* mosaic in the northeast corner of the island (Fig. 1). *T. wiseana* is confined to ridges, and is more abundant toward the western side of this region. Coastal sandy areas bear *T. angusta,* as do watercourses; the intervening red sands or blown red sands on limestone carry *T. pungens.*

4. Coastal sand assemblages

a. strandline: *Ipomoea pescaprae, Salsola kali.*

b. white aeolian foredune areas: open vegetation dominated by *Spinifex longifolius* and also characterised by *Ptilotus villosiflorus* and *Cynanchum floribundum.*

c. *Acacia coriacea-Triodia angusta* belt on cream to pink sands behind *Spinifex* zone, on the inland sides of the white-sand foredunes. *A. coriacea* also grows in association with *Spinifex* (assemblage b) and *T. pungens* (assemblage d) but less densely and consistently.

d. *Triodia pungens* on red sands inland from foredunes. This includes low red dunes, often with *A. coriacea* overstorey, and narrow red sand flats inland. This community is also characterised by *Scaevola cunninghamii.*

5. Coastal rock assemblages

a. limestone or conglomerate cliffs, scarps and headlands bearing *Triodia wiseana,* and also characterised by *Sarcostemma australe* and *Capparis spinosa.*

b. exposed cliffs to the southwest, covered with blown sand and bearing *T. angusta* and *Frankenia pauciflora.*

c. exposed headlands and visors; bare or with sparse *Frankenia* cover.

d. conglomerate—pebble beaches (e.g. the northern margin of Bandicoot Bay) with a narrow strandline zone of *Frankenia pauciflora* and *Spinifex longifolius* backed by *Acacia bivenosa* and *Stylobasium spathulatum* over *Triodia angusta.*

e. low limestone areas bearing *Frankenia, Sclerolaena, Neobassia* and *Halosarcia* species.

6. Mangroves: *Avicennia marina*

a. pure stands of *Avicennia* in mud pockets in limestone and rocky beaches.

b. Old *Avicennia* stands swamped by sand, with ground cover of halophytes toward inland margin: *Neobassia astrocarpa, Sclerolaena spinosa, Halosarcia* spp., *Frankenia pauciflora, Threlkeldia diffusa, Enchylaena tomentosa* and *Sporobolus virginicus.*

7. Floodout flats

Red sands, red clayey sands and sandy red earths with patchy scalds and flood channels, bearing diverse assemblage of small forbs, with very occasional *Triodia angusta* and shrubs. Characteristic species include *Centaurium erythraea, Sporobolus australasicus, Morgania glabra, Evolvulus alsinoides, Pterigeron bubakii, Malvastrum spicatum, Heliotropium undulatum, Nicotiana occidentalis* and *Pterocaulon sphacelatum,* the last five being denser and taller in floodout channels to the virtual exclusion of other species.

8. Salt flats

Limited areas near mouths of intermitent sandy watercourses, rendered salty by seawater percolation and salt spray deposition. Halophytes and succulents: *Halosarcia indica* ssp. *leiostachya, H. halocnemoides, Sclerolaena spinosa, Neobassia astrocarpa, Threlkeldia diffusa, Frankenia pauciflora.*

9. Disturbed areas

(a) road verges, well sites, etc. Characteristic species (all native): *Diplopeltis eriocarpa, Trichodesma zeylanicum, Cymbopogon procerus, C. ambiguus, Heliotropium undulatum, Adriana tomentosa, Tephrosia* *rosea*, *Cassia notabilis*, *Pterigeron bubakii*, *Petalostyles labicheoides*. This secondary cover is denser in *T. angusta* lowlands, where all the above species are present, than on *T. wiseana* uplands where *Cymbopogon* is common along verges but the other species are much sparser.

(b) WAPET camp and offices: lawn of introduced *Cenchrus ciliaris* and *Cynodon dactylon* at camp, and planted trees of the introduced *Eucalyptus camaldulensis*, *E. torquata*, and *E. gomphocephala* in addition to planted natives such as *E. patellaris*, *Erythrina vespertilio* and *Pittosporum phylliraeoides*.

(c) disturbance in coastal assemblages is minimal, and floristics approximate those of surrounding areas.

Relation to substrate.

As indicated in the section above, each main vegetation unit is associated with a particular substrate, distinguishable on the basis of topography, texture and salinity. Results presented below show that there are also differences in pH and fertility, as measured by total nitrogen and extractable phosphorus content. (Total P was also measured for 7 samples, and the proportion extractable/total P found to be remarkably constant, with a mean of 0.162 and standard error 0.011). Comparison of the soils from different substrate units is hindered by variation with topography and depth within some units; in particular, the variation in weathering and soil formation on limestone areas, and the ridge sequences in the calcareous coastal sands. These were checked as follows.

Soils from two bulldozed exposures under *Triodia wiseana* (profiles A, B), and shallow soils from three additional limestone ridges are compared in Table 2. Sample C represents material from under a limestone slab on the northern ridge of transect 1; sample D the thin layer of blown sand covering the limestone ridge at the inland end of transect 4, under *T. wiseana* and *T. pungens*; and sample E the detrital soil between limestone blocks on the high western Trealla limestone plateu, in an area of *Triodia wiseana* and *Acacia pyrifolia*. Overall, the shallow "topsoils" have significantly lower extractable phosphorus than the deeper "subsoil" materials from between or below massive shattered limestone blocks or coarse limestone rubble ($p < 0.01$). The high plateau sample (E) has lower extractable phosphorus content than any other island soil except the floodout-flat clayey sand, and is slightly less alkaline than the other limestone ridge soils. Ridge topsoils C and E have relatively high nitrogen contents, but not the dark humic topsoils from profiles A and B; sample C contains detrital material from an ant nest, and perhaps also sample E. There is a gradual decrease in pH inland across the white calcareous ridges of transect 3 (Table 3), and the strandline sand is low in total N, but there are no significant differences in total N or extractable P between the ridges.

Table 2

Triodia wiseana soil profiles: pH, total nitrogen, and extractable phosphorus

Profile	Depth m	Soil type	pH	Total N ppm	extr. P ppm
A	0·05	dark humic topsoil	7·25	570	289
A	1·3	interstitial material	7·79	690	407
A	1·5	red homog. subsoil	7·80	550	354
B	0·05	topsoil	7·60	500	190
B	1·2	rubble "subsoil"	7·73	620	470
B	1·2	rubble "subsoil"	7·85	490	505
C	0·10	dk. red-brn sandy loam	7·50	2 200	180
D	0·05	blown sand on limestone	7·75	160	273
E	0·05	skeletal soil between limestone blocks	7·18	1 100	80

Table 3

Dune sands: pH, total nitrogen and extractable phosphorus. Each value is the mean of three samples.

Location	Soil type	pH	total N ppm	extr. P ppm
Transect 3, above strandline	white calc. sand	8·88	100	337
Transect 3, 25 m inland	white calc. sand	8·50	130	437
Transect 3, 100 m inland	cream calc. sand	8·57	170	343
Transect 3, 160 m inland	pink calc. sand	8·41	160	405
Transect 3, 250 m inland	pink calc. sand	8·27	160	312
Bandicoot Bay neck, high dune	white calc. sand	8·70	150	584

Table 4

Soil pH and fertility of main substrate units: means (m) and standard deviations (s). N and P units are ppm.

Unit	n	pH		total N		extr. P	
		m	s	m	s	m	s
floodout flat	2	7·63	·40	455	64	52	4
limestone topsoil	2	7·42	·25	535	50	240	70
limestone, subsoil	4	7·79	·05	588	87	434	67
limestone, rubble	2	7·71	·01	150	0	293	67
red sand	1	7·75		400		635	
white sands	5	8·61	·18	142	28	421	100
salt flat	1	9·30		240	....	160	....

Overall differences between main substrate types are shown in Table 4. T-tests show that the mean pH of the white sands is significantly higher than that of the limestone soils ($p < 0.001$) and significantly less than that of the salt flat ($p < 0.001$); the mean pH of the floodout flat differs significantly only from that of the salt flat. Mean N content of the white calcareous sands is significantly less than that of the salt flat ($p < 0.05$), red sand ($p < 0.001$), and limestone ($p < 0.001$); sample numbers are insufficient to show whether the salt flat N is significantly lower than that of the floodout flat. The limestone areas have highest soil N. Differences in extractable P are not statistically significant save for the low levels in the floodout soils.

Comparisons between soils occupied by different *Triodia* species are hampered by the variety of substrates occupied by each in mixed or marginal communities. *Triodia angusta* grows on both valley soils and coastal white sands. *T. pungens* is generally confined to red or pink sands but these range from the deep red sands at the northern end of transect 3 to the shallower red sands over limestone in the northern *Triodia* mosaic (Fig. 4) and the extremely thin cover of windblown red sand on the limestone ridge in transect 4. The range of variation in *T. wiseana* soils has already been described.

In conclusion, the soil analyses performed are sufficient to show that differences in soil pH and fertility parallel textural differences between major substrate units in some cases but not all. Considerably more detailed study would be required to establish patterns between subunits.

It was not possible to study the factors controlling shrub distribution (Figs. 4 and 5) in any detail, but the pattern for those associated with *T. wiseana* appears to be as follows. The highest western and northern regions with a greater percentage cover of limestone caprock have no shrubs or trees other than *Ficus platypoda*, occasional *Pittosporum phylliraeoids* and a single stand of *Eucalyptus patellaris*. Remaining areas tend to carry *Acacia pyrifolia* on the highest and most open ridges with caprock, *Cassia pruinosa* on similar but more restricted areas, and *Codonocarpus cotinifolius*, *Grevillea pyramidalis*, *Melaleuca cardiophylla*, *Acacia bivenosa* and *A. gregorii* on the broken limestone gravel of lower ridges and slopes.

Discussion

Effects of fire and grazing

As with *Triodia* hummock grasslands in general, the inland vegetation of Barrow Island burns readily but regenerates from seed, from rootstocks, or by epicaudal shoot production. The frequency of natural fires is unknown, since the island has been fired by man since its first European discovery.

It was burnt end-to-end by Captain Jarman in 1865, and a large fire burnt 75% of the island in 1961 (Cox 1977). Subsequently there have been a number of smaller fires. Burbidge and Main (1969) visited the island in November 1969 and compared the vegetation regenerating on areas burnt respectively 5 weeks, 3 months, 4 years and 7 years previously. In general, with modifications depending on substrate, the secondary succession after fire was started by *Triodia* spp., particularly *T. pungens*; shrubs such as *Petalostyles labicheoides*, *Acacia bivenosa*, *A. coriacea*, *A. gregorii*, *Stylobasium spathulatum*, *Adriana tomentosa* and *Corchorus parviflorus*, which regenerate from the rootstocks; and herbs of disturbed ground such as *Trichodesma zeylanicum* and *Heliotropium ovalifolium*. The additional species *Codonocarpus continifolius*, *Diplopeltis eriocarpa*, *Triumfetta appendiculata*, *Hannafordia quadrivalvis*, *Cynanchum floribundum*, *Clerodendrum tomentosum*, *Scaevola cunninghamii*, *Olearia axillaris* and *Pterocaulon sphacelatus* were recorded only in the oldest burnt area.

In contrast to the rapid regeneration of burnt vegetation, areas where plant cover (and topsoil) were removed mechanically during the early phases of island utilisation have revegetated very slowly, if at all. Cleared areas forming part of the WAPET regeneration program, where the subsoil is ripped, the topsoil replaced, and wet-season flood erosion prevented, have regenerated more rapidly. They are seeded naturally, initially by herbs such as *Heliotropium ovalifolium* and *H. undulatum*, *Paspalidium tabulatum*, *Pterigeron bubakii* and *P. macrocephalus*, *Trichodesma zeyanicum*, *Solanum diversiflorum*, *S. lasiophyllum*, *Chamaesyce* spp., *Pterocaulon sphacelatum* and *Chrysogonum trichodesmoides*, and shrubs such as *Diplopeltis eriocarpa*, *Stylobasium spathulatum*, *Adriana tomentosa*, *Tephrosea rosea*, *Petalostyles labicheoides*, *Indigofera monophylla*, *Corchorus parviflorus* and *Cassia notabilis*. This colonising vegetation is subsequently replaced by *Triodia angusta*.

Plants regenerating after fire or clearance are grazed preferentially by the island's various marsupials and rodents (Butler 1970). Whilst the hare wallabies, *Lagorchestes conspicillatus conspicillatus*, eat mainly *Triodia* spp., the biggadas, *Macropus robustus isabellinus*, concentrate opportunistically on smaller forbs and for this reason are generally most abundant on floodout flats after rain. They are also common in the hummock grasslands, however, eating *Triodia* flowering heads or young leaves during dry periods. Their selective grazing probably accounts for the close association of, e.g. *Pittosporum phylliraeoides* and *Jasminum calcareum* with clumps of *Ficus platypoda*: seedlings germinating outside the fig clumps are eaten, and only those protected or concealed can reach maturity. Selective grazing probably also excludes a number of species from Barrow Island. The most conspicuous of these is *Ptilotus exaltatus*, which is abundant on neighbouring islands, such as Double Island and the Lowendal Islands, that are too small to support macropod populations. The same may apply to a number of species which, though found on Barrow Island, are much less common there than on the smaller islets: *Sesuvium portulacastrum*, *Tribulus terrestris*, *Atriplex semilunaris*, *Setaria dielsii*, *Commelina ensifolia*, *Ipomoea pescaprae*, *Indigofera trita*, *Portulaca intraterranea* and *P. pilosa*, though dietary studies are as yet inadequate to assess the grazing pressure on these species, and the greater exposure and presence of seabird colonies on the islets may also be significant.

The plant communities as animal habitats

The main vegetation types listed earlier represent distinct habitat types for mammals (Butler 1970) and birds (Sedgwick 1976), but the subtypes do not seem to be significant. The low *Triodia* hummocks (< 400 mm) on the western side of the island are a poorer habitat for birds than the taller *Triodia* and associated shrubs to the east, but the *Ficus*, *Erythrina* and *Eucalyptus* trees are apparently of little significance (Sedgwick 1979). Foredune areas, mangroves and coastal headlands are important nest sites for the bar-shouldered dove and osprey. Smith (1976) divided the island's 38 reptile species into those confined to rocky areas, those confined to sands, and those found on both: Butler (1970) gave more detailed reptile habitat notes. Perry (1972) found that of the island's 25 termite species, 20 were grass harvesters found in the various *Triodia* habitats, and 5 were wood eaters occupying old mangrove logs. No termites were present in the coastal foredunes.

Floristic relations with the mainland

Different elements of the Barrow Island flora have different origins. Most species occupy similar habitats on island and mainland (cf. Sauer 1965). *Canavalia maritima*, *Capparis spinosa*, *Avicennia marina*, *Ipomoea pescaprae*, *Cassytha filiformis*, *Sporobolus virginicus*, *Sesuvium portulacastrum*, *Chamaesyce atoto* and *Salsola kali* are part of the cosmopolitan seaborne Indo-Malayan strand flora (cf. Schimper 1891). Of the Australian species, *Spinifex longifolius*, *Euphorbia tannensis* ssp. *eremophila*, *Chamaesyce australis*, *Tribulus* spp., *Tinospora smilacina* and *Myoporum acuminatum* are widespread along tropical Australian coasts, and *Olearia axillaris* and *Scaevola crassifolia* are widespread on the southern temperate coastal sands.

A large element of the Barrow Island flora is Eremaean (Gardner 1944, Burbidge 1960), species such as *Crotalaria novaehollandiae*, *Cynanchum floribundum*, *Enchylaena tomentosa*, *Haloragis gossei*, *Petalostyles labicheoides*, *Portulaca oleracea*, *Ptilotus obovatus*, *Rhagodia obovata*, *Santalum lanceolatum*, *Sarcostemma australe*, *Sida corrugata*, *Sida fibulifera*, *Themeda australis*, *Trichodesma zeyanicum*, *Triodia pungens* and *Triraphis mollis* being widespread in the arid zone in a range of habitats.

Finally, several naturalised or adventive alien plants have been recorded on Barrow Island. *Solanum nigrum*, *Cryptostemma calendula*, and a *Sonchus* sp. have reached the island but were eradicated. There is a single plant of *Acacia grasbyi* at the WAPET camp, possibly introduced by barshouldered doves in the mid seventies. In addition, *Cenchrus ciliaris* and *Cynodon dactylon* have been introduced as lawn grasses but have not spread, and a few introduced eucalypt species have been planted around the WAPET camp and offices.

Barrow Island is separated from the mainland to the southeast by a channel 12 m deep, bordered by shoals and islands. Hence, given the Holocene sealevel history outlined by Thom and Chappell (1978), the island would have been isolated from the mainland between 7500 and 8000 BP. Since this time, gene flow between island and mainland has been negligible for terrestrial animals and probably low for plants. Barrow Island has endemic races of four mammals, and an endemic form of a fifth (Butler 1970), and at least five of the reptiles differ from mainland populations (Smith 1976). There have been no taxonomic studies of possible endemic forms in Barrow Island plant populations: Serventy and Marshall (1974) considered that Barrow Island *Lechenaultia divaricata* specimens had larger flowers than Central Australian ones, and peculiarities in size or succulence were noted for a few species during the present study, but both succulence and flower size may respond directly to rainfall, and Serventy and Marshall's visit in 1958 was preceded by good rains. Plants of *Nicotiana occidentalis*, *Chamaesyce australis*, *Calandrinia balonensis* and *Portulaca intraterranea* on the smaller islets are more succulent than those on Barrow Island itself; this could be due to the greater salinity, lower grazing pressure, or higher phosphorus input from seabird guano on the smaller islets.

Additional factors influencing plant distribution

Some coastal vegetation types are apparently modified by exposure to salt-laden winds. Limestone headlands on the Barrow Island coast, and small limestone islets offshore, bear *Triodia angusta* or *T. pungens*, though *T. wiseana* is the dominant species on inland limestones. This substitution is particularly evident in more exposed sites where the *Triodia* hummocks often show evidence of wind and salt-pruning, growing in approximately shore-parallel lines whose dead and partially eroded upwind edges shield the living material on the island side. On Barrow Island this substitution could be accounted for in terms of substrate control in those cases where the headlands are covered thinly by windblown sands, but such an explanation does not hold on other headlands or on the islands, and salt exposure therefore seems a more likely reason.

Seabird nesting colonies are more significant to the vegetation on the smaller islets than on Barrow Island itself, though even on Barrow Island osprey and sea-eagle nests are often surrounded by a narrow ring of 'weedy' species such as *Salsola kali* and *Nicotiana occidentalis*. Small rock islands with tern nesting sites (e.g. Pasco Island, Prince Island) are often densely covered by *Salsola kali*, *Setaria dielsii*, *Amaranthus viridis*, *Nicotiana* spp. and *Cleome viscosa*, probably in response to increased soil nitrogen and phosphorus. Cormorant colonies, in contrast, remain largely denuded for several years after use, one on a small Lowendal islet containing only dead *Pittosporum phylliraeoides*, separated by a marginal ring of partly dead specimens from the healthy trees outside the colony. Cormorant colonies are generally at the outer limits of vegetation on these small rocky islands and the plants are already under stress.

The importance of herbivorous insects other than termites is unknown except in a few cases. The most conspicuous of these is the consumption of *Capparis spinosa* by larvae of the Caper White butterfly, which feed and pupate almost exclusively on this plant, though *Boerhavia* seems to be attacked in the absence or complete defoliation of *Capparis*. Such defoliation is particularly severe on the small offshore islets.

It is possible that dynamic successional factors are as important as substrate in controlling the relative distributions of *Triodia angusta* and *T. pungens* in some areas. River valleys bear *T. angusta* and the large red sand flats largely *T. pungens*. On the coasts a narrow belt of *T. angusta* on partly stabilised cream sands separates the *Spinifex* assemblage of the mobile white foredunes from *T. pungens* on the stabilised inland dune slopes and red sands behind. Similarly, the mosaic of *T. angusta*, *T. pungens* and *T. wiseana* in the northern quarter of the island reflects a substrate mosaic. Small-scale *Triodia* pattern in the coastal complexes, however, could be accounted for only by a fine balance of substrate type, hydrology and exposure, or perhaps by the interaction of substrate factors with dynamic factors such as drought or fire. This requires further investigation.

Conclusions

The dominant vegetation on Barrow Island is *Triodia* hummock grassland, ringed by a complex of coastal vegetation types and broken in places by floodout flats. In all, nine vegetation units comprising 29 subunits were recognised and the main units mapped and described. Actual ground vegetation patterns are of course more complex than this hierarchical classification, but it is believed to be an accurate and useful descriptive system which represents a considerable advance over earlier studies. The island's flora is a subset of the local mainland flora and comprises coastal elements, notably one derived from the Indo-Malayan strandline flora, and inland elements derived from the Australian Eremaean. The distribution of the island's main vegetation types is controlled primarily by substrate, including soil modification by calcium carbonate solution and redeposition, but fire, grazing and salt-wind exposure are also involved.

Recent and continuing anthropogenic vegetation modification has produced a disjunct "disturbed ground" unit, composed entirely of native plants, which succeeds in time to *Triodia angusta* hummock grassland. Where disturbance occurs in the *T. wiseana* limestone uplands, replacement by *T. angusta* is likely to be permanent, but to date this appears to be the only permanent vegetation modification caused by oil extraction and associated activities, and the small relative changes in the areas of the two habitat types are unlikely to have influenced the fauna. This state of affairs, however, is contingent upon current management practices: namely, restricting the anthropogenically disturbed area in any given terrain unit at any given time to less than that proportion of its total area which is likely to be disturbed by natural agents such as fire or cyclones; maintaining the populations of grazing macropods within their original bounds; and enhancing regrowth by ripping, topsoil replacement and flood control. Similarly, the continued absence of alien plants other than those planted around the camp and offices is contingent upon the quarantine contraints on incoming materials and people; the absence of seed-dispersing stock; the maintenance of high marsupial populations, which eat the introduced species; and continual active checks and eradication of any aliens which reach the island.

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Appendix 1

Key

† Collected by RCB during October 1980 and held at Herbarium Australiense.

* Collected by W. H. Butler previously and held in Barrow Island Herbarium. A total of 213 species are supported by voucher specimens. The remaining species are no longer traceable to voucher specimens, and some at least are likely to be misidentifications.

[1] new record for Barrow Island group.
[2] a single plant, now extinct.
[3] well-watered hollows only.
[4] in island's only brackish waterhole.
[5] only recorded from small islands around Barrow Island.
[6] introduced species.

Habitats

W *Triodia wiseana* assemblages of limestone uplands.
A *Triodia angusta* assemblages of valley fill and lowlands.
R red sands.
C coastal white sands.
B rocky coasts.
F floodout areas.
S salt flats.
M mangroves.
D disturbed ground, or planted specimens.

Collection Numbers

Collection numbers are those of RCB. Those in the first column are held by W. H. Butler (P.O Box C1580, Perth). Those in the second column are held by the Herbarium Australiense.

Nomenclature

Plant names are as Green, J. W., 1981, *Census of the Vascular Plants of Western Australia*. publ. Dept. Agriculture, South Perth.

	Habitat	WHB No.	Herbarium Australiense No.
Abutilon crispum	RD		
†*_Abutilon exonemum_	RD	6681 6813 7033	6681 6686 6813 6817 6924 7009 7033
Abutilon fraseri	RD		
† _Abutilon leucopetalum_[1]	R	7232	7231
†*_Acacia bivenosa_	WARCFD	7210	6790 7210
†*_Acacia coriacea_	CR		6680 7246
†*_Acacia grasbyi_	D	6696	6696
†*_Acacia gregorii_	WA		6655
†*_Acacia pyrifolia_	W		6939
†*_Acacia victoriae_	FR	6952	6951 6952
†*_Acanthocarpus preissii_	WR	6784	6784
†*_Adriana tomentosa_	D	6763	6763
Alternanthera sp.			
Amaranthus pallidiflorus			
† _Amaranthus viridis_[1]	CB	6821 6961	6683 6836 6884 6961 6962
Arctotheca calendula[6]	D		
Aristida browniana			
†*_Aristida contorta_	R	6910	6910
† _Atalaya hemiglauca_[1]	WR	6862	6862 6866
† _Atriplex isatidea_	C		6742
†*_Atriplex semilunaris_	CB	7043 7077	7044 7078 7080
†*_Avicennia marina_	M		
*_Boerhavia chinensis_	CBR		
†*_Boerhavia diffusa_	CBR	6601	6625 6880 7059
† _Boerhavia repandra_	CB		6645 6650 7011
† _Bonamia rosea_	R	6916 6932	6603 6664 6673 6917 6936
† _Bothriochloa bladhii_[1]	W	6895	6895
† _Bulbostylis barbata_[1]	C	7203	7203
† _Calandrinia balonensis_			
†*_Calandrinia polyandra_	WA	6746 6815	6746 6815
†*_Canavalia rosea_	CB		6879
†*_Capparis spinosa_	WB		6798
† _Capparis_ sp.[1, 5] (RB 7155)	B	7155	7155
†*_Cassia glutinosa_	WD		
†*_Cassia notabilis_	WRD	6658	6658 6931
† _Cassia oligophylla_	W		
†*_Cassia pruinosa_	W	6635 6937	6635 6640 6661 6937
Cassia venusta			
† _Cassytha filiformis_[1]	CB	7050 7102	7050 7051 7102
†*_Cenchrus ciliaris_[6]	D		
† _Centaurium erythraea_[1]	F	6695 6719	6695 6719
†*_Centipeda minima_	F	6805	6805 6726 6765
† _Chamaesyce atoto_	C	6688 6903 7092	6688 6826 6901 6902 6904 6956 7092 7094
† _Chamaesyce_ sp. aff. _atoto_	WCB	6794 7148	6841 6923 7079 7148 7159
†*_Chamaesyce australis_	WCB	6756	6731 6831 6833
† _Chamaesyce myrtoides_	C	6688 7083 7093	6832 6690 7062 7081 7083 7116
†*_Chenopodium carinatum_	RCD	6769	6624 6752 6827 6840
†*_Chrysogonum trichodesmoides_	WRD	6745	6745
†*_Chrysopogon fallax_	ARB		
†*_Cleome viscosa_	BD	6700	6700
†*_Clerodendrum tomentosum_	AR	6928	6615 6628 6643 6928 7220
*_Clianthus formosus_	AR		
†*_Codonocarpus cotinifolius_	AD	6941	6941
†*_Commelina ensifolia_	WB		

	Habitat	WHB No.	Herbarium Australiense No.
Commelina lanceolata			
† *Convolvulus* sp.[1] (RB 7250)	B		7250
†* *Corchorus parviflorus*	WARBD	7132	7132
† *Corchorus sidioides*[1]	WARB	6938	6732 6751 6793
†* *Corchorus walcottii*	AD	6638	6623 6647 6734 6870
†* *Cordia subcordata*	C		7221
† *Corynotheca acanthoclada*[1]	W	7202	7202 7222
† *Crotolaria medicaginea*[1, 5]	B	7258	7258
* *Crotolaria novae-hollandiae*	CD		
Crotolaria trifoliastrum			
Cuscuta australis			
† *Cymbopogon ambiguus*	WD		6760 6947
Cymbopogon bombycinus			
†* *Cymbopogon procerus*	WD	6947	6946 6947 6760
†* *Cynanchum floribundum*	CR	6654	6662
† *Cynodon dactylon*[6]	D	6740 6798	6740 6741 6749 6798 6848
†* *Cyperus cunninghamii*[1]	WB	6605 6627	6627 6651 6858 6943
† *Cyperus squarrosus*	F	6737	6737
†* *Dactyloctenium radulans*	BD	7128	7128
†* *Dichanthium affine*	F	6714	6705 6714
† *Dicladanthera forrestii* [1, 5]	B	7129 7130 7142	7129 7130 7131
† *Dicladanthera* sp. (RB 6863)	W	6863	6863
†* *Diplopeltis eriocarpa*	WAD		6744
†* *Dodonaea lanceolata*	WA	6613	6613
Dolichandrone heterophylla			
* *Duboisia hopwoodii*			
† *Dysphania inflata*[1]	FB		
† *Dysphania plantaginella*	FB	6706	6706 6685
†* *Dysphania rhadinostachya*	RCD	6721	6753
† *Enchylaena tomentosa*	SM	6960 7234	6960 7042
Enneapogon caerulescens			
†* *Enneapogon oblongus*	WFB	6891 7226	6800 6801 6891 6968 7225
† *Enneapogon polyphyllus*[1]	FB	7242	7230 7242
†* *Eragrostis basedowii*	FB		
† *Eragrostis cumingii*[1]	F		6725
†* *Eragrostis dielsii*	FB	7261	7031 7261 7262
†* *Eragrostis falcata*	F	7058	7056 7057
†* *Eragrostis xerophila*	FB		
†* *Eriachne flaccida*	F	6737	6737 6810
†* *Eriachne mucronata*	WA		
†* *Erythrina vespertilio*	A		
* *Eucalyptus camaldulensis*[6]	D		
* *Eucalyptus gomphocephala*[6]	D		
†* *Eucaluptus patellaris*	WA		
* *Eucalyptus torquata*[6]	D		
†* *Eulalia fulva*	AR		
†* *Euphorbia tannensis* ssp. *eremophila*	RC	7001 7002	6837 7001 7002 7003 7005 7012 7098 7099 7111
† *Evolvulus alsinoides*	F	7237	7238
† *Ficus opposita*[1]	W	6802	6802
†* *Ficus platypoda*	W	6621 6776	6776 7022
† *Ficus* sp.			6616
* *Fimbristylis schultzii*	F		
†* *Flaveria australasica*	WCB	7068	6657
†* *Frankenia pauciflora*	BSM	6733 7060	6729 6733 6949 6950 7069
†* *Gnaphalium luteo-album*	WF		
†* *Gomphrena conferta*	SB	7029 7030	7030 7125
†* *Goodenia microptera*	WB	6896	6785 6896 6921 7054
Gossypium australe			
†* *Gossypium robinsonii*	A	6940	6940
† *Gnaphalium* sp.	RB	6652	6652
†* *Grevillea pyramidalis*	W		
†* *Hakea suberea*	W		
†* *Haloragis gossei*	D	6712	6712 6749
†* *Halosarcia halocnemoides*	SM	6780	6772
†* *Halosarcia indica* ssp. *leiostachya*	SM	6781	6773
†* *Hannafordia quadrivalvis*	WAR	6619 6626	6619 6626 6632
Heliotropium conocarpum			
Heliotropium crispatum			
Heliotropium cunninghamii			
†* *Heliotropium ovalifolium*	WARD	6611 6792	6618 6670 6771 6792
†* *Heliotropium undulatum*	WARD	6850 6867	6637 6689 6755
† *Heliotropium* sp.[1] (RB 6866)			6866
† *Heliotropium* sp.[1] (RB 7037)		7037	7037 7090
Hemichroa diandra			
* *Hibiscus sturtii* var. *campylochamys*	W		
† *Indigofera boviperda*[1]	B		
† *Indigofera colutea*	WF	6814	6686 6814 7256
† *Indigofera enneaphylla*			
†* *Indigofera georgei*	WA		
†* *Indigofera linifolia*	AR	7013	7014 7233
†* *Indigofera monophylla*	WAD	6877	6602 6612 6629 6639 6787
† *Indigofera trita*[1]	B	7036	7036 7060 6914

	Habitat	WHB No.	Herbarium Australiense No.
† *Indigofera* sp. (RB 6723)			6723
**Indigofera* sp.			
†**Ipomoea brasiliensis*	C		
Iseilema eremaeum			
†**Jasminum calcareum*	W	6739	6739 6828 7153
† *Jasminum* sp. (RB 7144)		7145	7144 7146
Keraudrenia sp.			
† *Launaea sarmentosa*[1], [5]	C	7117	7118 7123
† *Lawrencia* sp. (RB 7136)		7137 7147	7135 7136 7137 7147
Lechenaultia divaricata			
† *Lepidium* sp. (RB 7139)		7139	7139 7140 7141
†**Limonium salicorniaceum*	S	6778 7035	6676 6778 7034 7035
Loranthus sp. (Amyema ? RB)			
† *Lotus australis*[1]	W	6881	6881
†**Mallotus nesophilus*[3]	W	6897	6857 6897
†**Malvastrum americanum*	WAFBD	6709	6607 6609 6610 6709 6959
† *Marsdenia cinerascens*[1]	B	6969	6967 6969
**Marsilea* sp.	F		
†**Melaleuca cardiophylla*	W	6922	6922
†**Melhania oblongifolia*	B	7133 7134 7157	6604 7073 7074 7075 7114 7120 7121 7126 7133 7134 7157 7263
**Mimulus gracilis*	F		
†**Morgania glabra*[1]	F	6727	6727 6809
†**Mukia maderaspatana*	WD		6918
†**Myoporum acuminatum*	RC	6929	6641
†**Neobassia astrocarpa*	SB	6740	6722 6740 6873
†**Nicotiana benthamiana*[3]	WB	6856	6856 6942 7267
†**Nicotiana occidentalis*	WARCBD	6696	6614 6691 6702 6812 6915
†**Oldenlandia crouchiana*			
†**Olearia axillaris*	C	6843	6820 6855
**Olearia revoluta*	C		
†**Panicum australiense*	W	7158	7152
Paspalidium clementii			
Paspalidium gracile			
†**Paspalidium tabulatum*	WRBF	6737 6768 6788 6912	6677 6764 6912 7028
†**Passiflora foetida*	WB		
†**Petalostylis labicheoides*	RD	6791	6759
†**Phyllanthus maderaspatensis*	W	6899 7241	6899 6900 6905 6906 6935 7241
†**Pittosporum phylliraeoides*	W	6860	6865 6887 6894 7154
†**Pluchea rubelliflora*	WRD	6854	6854 7206
†**Pluchea squarrosa*	WRD	6911	6911
†**Pluchea tetranthera*	WRD	6852 6953 6958	6852 6953 6958
†**Plumbago zeylanica*[3]	WB	6620	6620 6644
†**Polycarpaea longiflora*	WRD		6631 6663
**Polymeria ambigua*	WA		
Polymeria calycina			
Portulaca australis			
† *Portulaca intraterranea*[1]	B	7107 7207	7095 7106 7107 7208
Portulaca oleracea			
**Portulaca pilosa*	B	7053 7255	7052 7088 7112 7225
†**Psoralea lachnostachys*	ARD	6760	6754 6762
†**Psoralea leucantha*	WAD	6736	6642 6736
† *Pterigeron adscendens*	RD	7205	7204 7205
†**Pterigeron bubakii*	ARD	6698	6684 6698 6717 6957
†**Pterigeron decurrens*	RD		
†**Pterigeron macrocephalus*	RD	7257	7257
†**Pterocaulon sphacelatum*	RD		6796
Pterocaulon sphaeranthoides			
†**Ptilotus clementii*	WAD	6682	6861 6945
†**Ptilotus exaltatus*	RB	7006	7004 7032
**Ptilotus fusiformis*	R		
†**Ptilotus obovatus*	WAD	6804 6715	6606 6634 6697 6715 6876 6890
†**Ptilotus villosiflorus*	C	6735	6735
†**Rhagodia dioica*	C		
†**Rhagodia obovata*	C	7104	6819 6830 7037 7091 7096 7097 7103 7104
**Rhizophora stylosa*[2]	M		
†**Rhynchosia minima*	WB	6889 7151	6660 6825 6849 6908 6919 6920 7110 7122
†**Ruellia primulacea*	WB	6885 6907	6885 7007 7008 7045 7046 7047 7048 7072
†**Ruppia maritima*[4]			6869 6972
†**Salsola kali*	RCD		
† *Samolus repens*	WB	6933 7259	6913 6933 7259 7260
Santalum lanceolatum			
†**Santalum spicatum*	A	6864	6864
†**Sarcostemma australe*	WB		6782
† *Scaevola* sp. cf. *aemula*	D		6888
† *Scaevola crassifolia*	C	7100	7100 7101
† *Scaevola cunninghamii*	WRCB	6608 6653 6666	6646 6653 6666 6785 6842
†**Scaevola decipiens*	RF	6622	6617 6622
**Scaevola glandulifera*	WB		

	Habitat	WHB No.	Herbarium Australianese No.
Scaevola globulifera	WRCB		
**Scaevola nitida*	C		
†**Scaevola spinesceus*	RCB	6675 7015	6675 6678 7026 7063 7223
**Scaevola* sp.			
**Scirpus dissachanthus*[3]	W		
Scirpus marginatus			
Sclerolaena convexula			
†**Sclerolaena spinosa*	CRBSM	6783	6711 6750 6770 6775 6777 6779 6871 7224 7268
**Sclerolaena uniflora*			
Sesbania bispinosa			
†**Sesuvium portulacastrum*	MB	6965	6965
†**Setaria dielsii*	CB	6963 7753	
**Setaria verticillata*			6963 6964 7019 7020 7021 7023 7024 7113
† *Sida calyxhymenia*[1]	C	7236	7235
†**Sida corrugata*	WB	6875	7245 7143
†**Sida echinocarpa*	D	6853	6853
†**Sida fibulifera*[1]	RF	6701	6710
†**Solanum cleistogamum*	WB	6687 7228	6720 7227 7228 7239 7243
†**Solanum diversiflorum*	RD	6633	6633 6636 6713 6718
† *Solanum esuriale*[1]	B	7156	7138 7160
Solanum horridum			
†**Solanum lasiophyllum*	WARD	6738	6738
**Solanum nigrum*[6]	D		
† *Solanum phlomoides*			
Solanum quadriloculatum			
Sonchus sp.[6]	D		
*†*Sorghum plumosum*	A	6716	6692 6808 7149
†**Spinifex longifolius*	C	6822	6822 6823
†**Sporobolus australasicus*	F	6704	6694 6699
†**Sporobolus virginicus*	MCB	6648 6693	6667 6708 7115
† *Stackhousia elata*[1]	D	6659	6730
Stackhousia muricata			
Stemodia grossa			
†**Stylobasium spathulatum*	AD	6703	6753
†**Swainsona kingii*	ABD	7086	7085 7086 7087
†**Swainsona pterostylis*	RCD	6656	6649 6665 6671
†**Synaptantha tillaeacea*	RF	6874 7229	6874 7027 7061 7079 7229
†**Tephrosia eriocarpa*	WAD	6668	6668 6955
†**Tephrosia rosea*	WAD	6818	6818 6721 6789
Themeda australis			
†**Threlkeldia diffusa*	BSM	6954	6743 6872 6954 7018
†**Tinospora smilacina*	B		6859
Tribulus occidentalis	B		
† *Tribulus terrestris*[1]	B		7064 7065 7066
†**Trichodesma zeylanicum*	WARCFD		6774
†**Triodia angusta*	A	6838	6708 6747 6971
†**Triodia pungens*	R		
†**Triodia wiseana*	W	6909	6757
†**Triumfetta appendiculata*	WA		6669
†**Triumfetta leptacantha*	WA	6807	6672
†**Triumfetta micracantha*	WA	6882	6797 6868 6882
†**Triraphis mollis*	B	6892 7082	6892 7067 7089 7254
†**Vittadinia hispidula*	R	6786	6786
**Vittadinia* sp.			
† *Wahlenbergia* sp.[1] (RB 6816)	F	6766	6766 6816
†**Waltheria indica*	B		

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Ecological features of an outlying stand of jarrah (*Eucalyptus marginata*) at Jilakin Rock, Western Australia

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Abstract

Features of a biogeographically significant stand of jarrah, about 115 km east of the nearest jarrah forest, are described. The stand represents a relict of formerly wider distribution. In 1981 129 individuals were located of which 43% had been killed by wildfire in 1967. No seedlings or saplings were found: the smallest tree found alive was of diameter 6.3 m. The largest trees in the stand reached 150 cm in diameter, similar to that in low quality jarrah forest. The stand is protected by its inclusion in an A class reserve. Future management of the stand will need to minimise the risk of wildfire.

Introduction

Jarrah, *Eucalyptus marginata* Donn ex Sm., is the dominant tree species of south-western Australia. It is found in the Darling Range more or less continuously west of a line from near New Norcia, Northam, York, Dryandra, Williams, along the Albany Highway to Cranbrook, within the Stirling Ranges and east to Beaufort Inlet (Beard 1976, 1979a,b,c; 1980a,b; Smith 1974). Churchill (1968) found several populations of jarrah isolated from the main range, though some result simply from the above described eastern boundary fragmenting into isolates of jarrah (see particularly Beard 1979c, 1980b; Smith 1974 and Lange 1960). The two most truly isolated populations are at Mt. Lesueur and Jilakin Rock. Both are separated from the main range of jarrah by about 115 km. The population at Mt. Lesueur occurs on lateritic soils around mesas and consists entirely of individuals of mallee from 2-3 m in height. That at Jilakin Rock comprises trees reaching a maximum height of about 24 m.

Although the occurrence of jarrah at Jilakin Rock has been on the public record for over 60 years (O'Connor 1918, Arboris 1933), there has been no scientific study made of the population. The aim of this paper is to describe the extent, population size and dimensions of the trees of the jarrah stand at Jilakin Rock; to compare the dimensions of these trees with those in low quality jarrah forest to the west; and to discuss the origin of the stand and its conservation status.

Table 1

Climatic data for Kulin and Lake Grace, climatic stations nearest Jilakin Rock.

Kulin (elevation 300 m)

	J	F	M	A	M	J	J	A	S	O	N	D	Y	No. Years
Kulin (elevation 300 m)														
Mean rainfall (mm)	11	17	23	24	51	61	56	43	29	22	15	12	364	59 60
Median rainfall (mm)	4	5	14	18	46	58	54	39	29	18	8	7	368	59 60
No. rain days	2	3	3	5	10	13	15	12	8	7	4	2	84	37-42
Lake Grace (elevation 288 m)														
Mean max. temp. (°C)	32·2	31·4	28·1	23·2	19·7	16·3	15·6	16·1	18·7	22·6	26·0	30·4	23·4	17
Mean min. temp. (°C)	14·8	14·7	13·4	11·0	7·8	6·7	5·5	4·8	6·0	8·3	10·5	13·2	9·7	17

Environment

Jilakin Rock is a large granitic dome nearly 340 m above sea level, or some 60 m above the surrounding plain (Fig. 1). It is situated 400 m west of Jilakin Lake and 16 km east of Kulin. Soils around the rock are sandy.

Rainfall data for Kulin Post Office are listed in Table 1. Temperature data are not available for Kulin. The nearest station is at Lake Grace, 50 km south of Jilakin Rock (Table 1).

Near the eastern margin of the jarrah forest, Baker's Hill, Narrogin and Kojonup have an average annual rainfall of 618, 507 and 546 mm respectively, considerably more than at Kulin. Mean maximum temperatures of the hottest month (January) range from 29.4 to 31.5°C at the eastern margin of the jarrah forest. Mean minimum temperature of the coldest month (August) varies from 5.0—6.0°C. Thus temperatures experienced at Lake Grace differ little from those near the eastern boundary of the jarrah forest.

Location and habitat of jarrah at Jilakin Rock

Jilakin Rock is surrounded by samphire vegetation to the east, around Jilakin Lake, and elsewhere shrubland and woodland almost 20 m in height. The jarrah population occurs amongst a compact stand of some large individuals of jam *Acacia acuminata* Benth., rock she-oak *Allocasuarina huegeliana* (Miq.) L. Johnson and York gum *Eucalyptus loxophleba* Benth. only on the fringe of the northern side of Jilkin Rock and along a small ephemeral watercourse running from the base of the rock for about 80 m (Fig. 1).

Fourteen trees were found in private property (Loc. 7759) along this watercourse. A road about 10 m wide crosses this creek, so it is likely that 5-10 trees were removed in the road-making. All remaining trees occur in Loc. 10087, part of A class reserve 15385. The approximate extent of the population is shown in Fig. 1. Clearly the distribution of jarrah downslope from Jilakin Rock is closely related to extra run off. The trees are naturally irrigated (Beard 1980a). None of the other granite bosses near Jilakin Rock (Fig. 1) have jarrah trees at their bases.

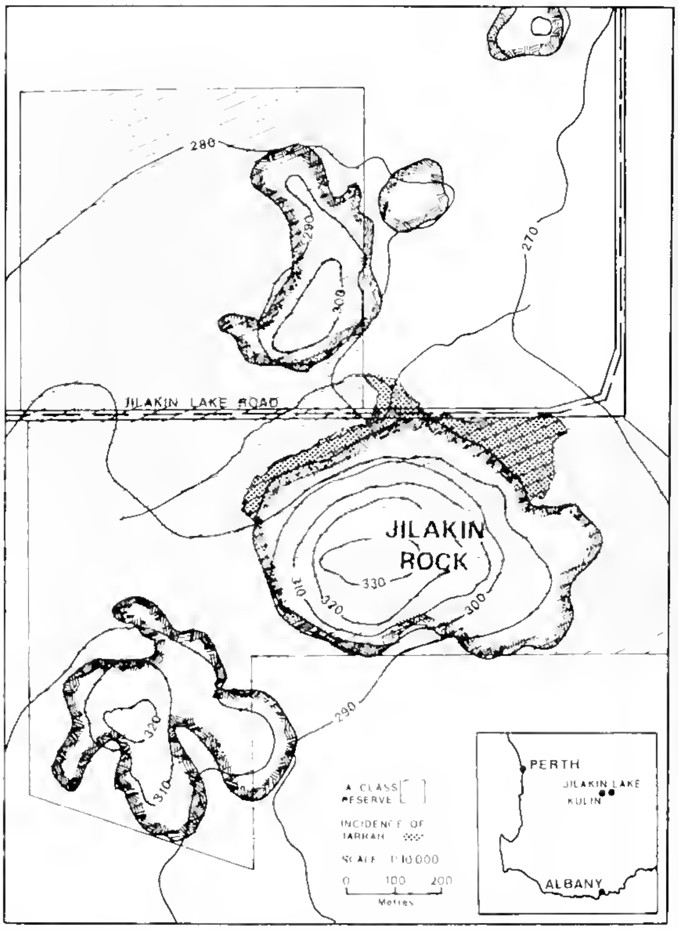

Figure 1.—The distribution of jarrah at Jilakin Rock.

Table 2

Frequency distribution of diameter* of the jarrah population at Jilakin Rock.

Diameter overbark 1·3 m above ground (cm)	No. alive	No. dead	% dead within each diameter class†	% dead of total dead
6·3– 9·9	4	3	43	5
10– 19·9	15	19	56	35
20– 29·9	11	17	61	31
30– 39·9	16	9	36	16
40– 49·9	12	1	8	2
50– 59·9	....	1	....	2
60– 69·9	4	....	....	....
70– 79·9	3	1	....	2
80– 89·9	....	1	....	2
90– 99·9	....	....	....	....
100–109·9	....	....	....	....
110–119·9	....	....	....	....
120–129·9	....	....	....	....
130–139·9	....	1	....	2
140–149·9	1	....	....	....
Not measured	8	2	20	4
Totals	74	55	43	101

* Diameter of largest stem per lignotuber.

† Calculated only if sample size of diameter class >5.

Table 3

Frequency (%) distributions of diameter of jarrah stands in low quality forest and at Jilakin Rock

Locality	Site-vegetation type*	Plot size (ha)	No. trees	Diameter overbark (cm)														
				10–20	20–30	30–40	40–50	50–60	60–70	70–80	80–90	90–100	100–110	110–120	120–130	130–140	140–150	150–160
Coondle	HZ	4·05	352		30·4	19·0	15·3	15·3	9·4	6·0	2·6	0·6	0·6	0·3	0·3	0·3	....	....
Beraking	HZ	4·05	398		27·6	12·6	15·5	13·9	8·5	9·3	7·3	1·3	2·8	0·8	0·3	0·3	....	....
Beraking	Z	0·41	75		53·3	21·3	10·7	2·7	2·7	1·3	4·0		2·7		1·3	....	....	
Dale	HM	0·41	44		29·5	36·4	25·0	4·5	2·3				2·3			....	....	
Dale	H	0·41	38		28·9	18·4	13·2	7·9	7·9	13·2	2·6	5·3	2·6		....	....	....	
Cooke	ZP	0·41	41		22·0	22·0	24·4	7·3	12·2	2·4	7·3	2·4			....	....	....	
Clare	Z/HZ	2·63	229		11·8	13·5	17·9	19·7	13·5	7·4	5·7	6·1	1·7	1·3	0·4	0·4		0·4
Leona	Z	0·41	41		63·4	19·5	7·3	4·9			2·4	2·4				....	....	
Bell	ZM	0·20	37	51·4	13·5	10·8	13·5	5·4	2·7	2·7			....			....		....
Yourdamung	F	0·40	32	18·8	18·8		9·4	9·4	9·4	15·6	9·4		....	6·3	....	....	3·1	
Surface	Z	0·40	48	8·3	4·2	10·4	18·8	10·4	29·2	8·3	4·2	4·2	....	2·1	....		....	
Jilakin Rock	NA	NA	112	30·4	25·0	22·3	11·6	0·9	3·6	3·6	0·9	....	....	....	....	0·9	0·9	....
Jilakin Rock	NA	NA	78	....	35·9	32·1	16·7	1·3	5·1	5·1	1·3	....	....	....	....	1·3	1·3	....

NA—Not Applicable. *After Havel (1975)

Number and size of individual trees

In October 1981 I measured the diameter at 1.3 m above ground of nearly all of the jarrah trees at Jilakin Rock. Most consisted of multiple stems coming from a common lignotuber, in which case I always measured the stem of largest diameter at breast height. In a few cases where trees had fire scars or were otherwise damaged at breast height I measured diameter 1.6 m or 1.9 m above ground level. In all, 129 trees were located, of which 119 were measured as just described.

Nearly half of the trees were dead. As all of these had charcoal present on bark, I conclude that fire was responsible for the deaths (Table 2). Fire scars and other damage caused by fire were noted on half of the 20 trees with diameter exceeding 40 cm. According to B. A. Parker, occupier of adjacent Locations 7759 and 6319, there has been one fire only in the jarrah stand since he settled at Jilakin in 1921. This was in 1967 (Greble 1979).

No seedlings or advance growth (small saplings < 1.3 m high) were present in 1981 and none of the trees was in bud, flower or fruit. This was in marked contrast to November 1932 when A. C. Harris (unpublished data) recorded the trees seeding heavily. He also noted a dense crop of young seedlings as well as dense clumps of sapling-pole size trees. It is unlikely that the area was grazed between 1932 and 1981 because surrounding farms are fenced.

Comparisons with low quality jarrah forest

A considerable body of information is available for low quality jarrah forest. Height of mature codominant trees rarely exceeds 25 m, being usually less than 20 m (Havel 1975, Abbott and Loneragan 1983). The frequency distribution of diameters is generally of the form of a negative exponential (Table 3). Most of the plots when measured were uncut, but for those that had been cut over diameters of stumps (adjusted to 1.3 m above ground) have been included. As the lower limit for diameter was either 10 cm or more often 20 cm, the Jilakin data have been calculated for both criteria. For stems above 10 cm or 20 cm, the diameter distribution of the Jilakin jarrah stand is typical of much of the low quality jarrah forest.

However, the absence of seedlings and advance growth from the Jilakin population is quite different from the low quality forest where seedlings and saplings are abundant (pers. obs.).

A study of the growth rate of the Jilakin jarrahs has not been made. Several plots in the nearest jarrah forest, Dryandra State Forest, were established in 1976 and remeasured in 1981. These yield an annual increase in diameter underbark of 0.12 cm, although the sample size of eleven trees is very small. Notwithstanding that, a rate of 0.12 cm yr^{-1} agrees well with the figure of 0.11 cm yr^{-1} derived from a more widely based study of growth rate of jarrah in low quality forest (Abbott and Loneragan 1983). On this basis, over the period 1910-1981 jarrah trees at Jilakin Rock would have increased their diameter underbark on average by only 8 cm.

Origin of the stand

Three different origins of the stand have been proposed. The first and least likely is an aboriginal myth and is detailed by Arboris (1933). A. C. Harris in 1929 (unpubl.) suggested that seeds of jarrah had been carried to Jilakin Rock accidentally by aborigines "either in skins, or perhaps in their hair". Jilakin Rock was once a meeting place for aborigines who penetrated inland during each winter, returning to the coast each summer as water became scarce. The scientifically most favoured explanation is due to Churchill (1968). Changes in climate, particularly over the last 10 000 years, resulted in the eastern boundary of the jarrah forest fluctuating. In a period wetter than the present this boundary would have extended as far east as Jilakin Rock. One difficulty with this view is that no other granite rocks between Jilakin Rock and the present eastern margin of jarrah forest are known to support adjoining populations of jarrah.

Conservation status of the stand

The jarrah population at Jilakin Rock is part of A class reserve 15385 for parklands and water. Cutting of timber is prohibited. It was gazetted in 1914 after the occurrence of the stand was drawn to the attention of the Surveyor-General. Two of the largest sound trees were cut down before then, probably in 1910 as Loc. 7759 adjacent to the jarrah stand was fenced in October 1909.

Wildfires present a threat. Agricultural land surrounds the stand, resulting in the presence of many weeds. The wildfire of 1967 killed 57% of all stems less than 30 cm in diameter. Thus it is the smaller size classes that are most vulnerable to wildfire. The stand probably should be managed by regular burning with low intensity fires, as is the bulk of the jarrah forest, so as to minimize the risk of wildfire.

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Epidermal characteristics of some Western Australian wandoo-woodland species for studies of herbivore diets

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Abstract

Characteristics of the epidermis of plant tissues can provide sufficient differences for separation at least at the generic taxonomic level. The comparisons of known samples with residual fragments of leaf cuticles in faeces provides a non-lethal method of determining the diets of herbivores. This current paper describes the methods employed to establish a voucher series for plants at the Yalanbee Experimental Station for a study of the food resources of the western grey kangaroo.

Three preparation techniques were compared on the wandoo-woodland plant specimens. The chromic acid/nitric acid digestion method gave the best results for most Western Australian native species. For the more mesic native shrub species and the introduced and native grass species, the acetic acid digestion method proved more successful in providing clean specimens of these species within cuticles. Imprint methods generally provided prints of inadequate detail for use in identifying the residual fragments from the faecal remains.

A diagnostic key using epidermal characteristics provided a method to extend the techniques of faecal fragment identification to use by non-specialised technical assistants.

Introduction

Studies of the diets of herbivores date from at least the mid-eighteenth century when, according to Tribe (1950), Linnaeus reported on the preference shown by farm animals for certain plant species. For almost the next two centuries the techniques used for the study of herbivore diets were dominated by those used for domestic animals in enclosed situations. Most of these techniques had practical limitations or were impossible to apply to open grazing and other less intensive farming practices. A developing interest in the food preferences of game and other non-domesticated animals led to new techniques for the study of food habits. One of these techniques was the identification of fragments of leaf epidermis from faeces (Baumgartner and Martin 1939, Dusi 1949). Except for vascular bundles, fibrous strengthening material and cutinized epidermal tissue, little plant material remains recognizable in faecal material (Phillipson 1952). Only the cuticle and its epidermal imprint has sufficient characteristics to be identified as belonging to a specific species.

The literature on dietary studies utilizing epidermal characters has been accumulating over the past 40 years (Dusi 1949, Stewart 1965, Kok and Van der Schijff 1973) and detailed accounts of the characteristics of the epidermal structures of monocotyledons (Metcalfe 1960, Clifford and Watson 1977) and dicotyledons (Metcalfe and Chalk 1950) have provided extensive background information. However, it was not until Storr (1961), Kiley (1966) and Stewart (1965, 1967) that the full potential of faecal analysis was realised in determining the feeding habits of wild and rare animals. Studies of the dietary preference of Australian macropods are limited (Kirkpatrick 1965, Griffiths and Barker 1966, Griffiths *et al.* 1974, Davis and Ellis 1979) and such studies in Western Australia are restricted to those of Storr (1961, 1964) on the quokka. Faecal analysis was used to gain further knowledge about the diet of the western grey kangaroo at the CSIRO Yalanbee Experimental Station in the wandoo (*Eucalyptus wandoo* Blakely) woodland-pasture landscapes near Bakers Hill. This method was the only practical option available, because the animals of the experimental station were part of a population dynamics study and could not therefore be killed to determine dietary resources through analysis of stomach contents. Because no previous work on the diet of the grey kangaroo had been attempted in the wandoo woodland, epidermal tissue vouchers had to be initially developed. The following report describes the development of methods for the preparation of plant epidermi, the nomenclature of epidermal characteristics for the series of voucher specimens, and the diagnostic key used in the western grey kangaroo dietary study (Halford *et al.* 1984.)

Epidermal tissue preparation

A number of techniques have been developed to prepare epidermal tissue for microscopic analysis. Once high-quality voucher specimens are available, the subsequent identification of epidermal fragments in animal faeces is made possible. These preparation techniques can basically be categorised into direct and indirect methods. Direct methods usually involve the removal of the leaf surface from the remainder of the plant material by bacterial disintegration, mechanical scraping, peeling or chemical maceration. Bacterial disintegration of the tissue (Louw *et al.* 1949, Skoss 1955) involves the breakdown of the tissue below the cuticle using certain microorganisms which digest the material with an enzyme complex of cellulases, hemicellulases and pectinases. Following a period of time the cuticle is mechanically lifted from the partially digested tissue. The major difficulty of the method is the time (often 14 days) required to obtain material and the specialized media requirements and anaerobic growing conditions for the bacteria.

Epidermal peeling (Dusi 1949) and mechanical scraping (Metcalfe 1960, Clarke 1960) involve the removal of the epidermal layer directly, as one might remove the peel of a ripe plum, or by gradually scraping the leaf tissue from the cuticle. These methods are time-consuming and difficult to apply where the epidermis is thin and closely associated with fibrous material, or where the leaves are ridged and furrowed, as in many Australian sclerophylls. The chemical maceration techniques utilize a variety of solutions to macerate tissue in order to free the cuticular layer membrane. Discussion and literature references for many macerating techniques are available (e.g. Sinclair and Sharma 1971). Generally these methods use mixtures and various concentrations of several weak acids, or hydrogen peroxide and a base as potassium hydroxide. Most of these methods are adequate in clearing the cuticle fragments from any remaining mesophyll or fibrous material, but the concentration of solutions, timing of various digestion periods and subsequent stain techniques often vary with the type of leaf material to be prepared. The major advantage of the direct method is that they can give a clear representation of the cuticle; however, the procedures may be time-consuming.

The indirect methods involve applications of liquid plastics or latexes which, upon drying to a thin, transparent film, can be peeled off and examined under a microscope. The materials used include Duco cement (William 1973), acrylic plastics (Horanic and Gardner 1967), cellulose acetates, Bennett and Furmidge 1956), polyvinyl alcohol (Mueller *et al.* 1954), mucilage and latex (Shah and Gopal 1969), and silicone rubber (Idle 1969). Indirect methods are generally much quicker and simpler to apply than the direct methods, but the quality of the epidermal reproduction is usually inferior.

Materials and methods

Three methods were examined to ascertain the most successful method for species of the wandoo-woodland vegetation. These included the indirect method of Horanic and Gardner (1967) and the direct methods of Storr (1961) and Jain (1976). In the Horanic and Gardner method, a 6:6 mixture of Rhoplex AC-33 acrylic polymer emulsion was initially applied to the surface of the leaf and allowed to dry for 10 minutes. Two additional coats using full-strength Rhoplex were applied at 10 minute intervals and allowed to dry for 40 minutes. The emulsion was then removed and transferred to a microscope slide. Generally the imprints did not give adequate representation of the epidermi of a large number of the sclerophylls. It was unable to show any detail of ridged or deeply furrowed leaf surfaces and abaxial surfaces of leaves with revolute margins. The preparation was difficult to apply to terete leaves because the resulting film was curved and difficult to view under the light microscope or photograph.

Applying the method or Storr (1961), leaves were cut into 5 mm squares or, if leaves were small, they were trimmed along one edge to facilitate epidermal removal. The material was placed in a solution of equal parts 10% chromic acid and 10% nitric acid and carefully boiled in a fume hood until epidermal separation occurred. A dilute KOH solution was used to rinse the tissue before the cuticles were removed from remaining fibre and vascular tissue. Pieces of the epidermis were transferred through a graded series of ethanol from 10-95%, then stained with 0.1% gentian violet in 95% ethanol. Staining time varied with the material and ranged from 30 sec. to to 24 h. The stained tissue was transferred to absolute ethanol and mounted in euparal. Storr's technique gave good results for a broad range of the Western Australian species, excepting those species which had thin cuticles, where features were difficult to distinguish.

Using the method of Jain (1976), material was cut into 5 mm squares and allowed to stand in a 30% glacial acetic acid in water solution at 80°C for 24 h. The material was then washed with water, cleared of remaining fibrous tissue and dehydrated through the series of ethanol solutions to 95%, and stained in 0.1% gentian violet in 95% ethanol before mounting in euparal. Jain's method did not thoroughly clear the epidermis of the more sclerotic leaves, such as *Hakea trifurcata* and *Acacia celastrifolia*. It did, however, prove to be very successful in producing clean epidermi from grasses and the native species with more mesic leaves such as *Phyllanthus calycinus*.

Microphotographs of the best preparations were made at low magnification (30x). The photographs were taken with a Zeiss photo-microscope using Microfile Pan film.

To analyze the faecal material, a dried pellet was gently boiled for 15 min in a solution of equal parts 10% chromic acid and 10% nitric acid. After maceration, the material was filtered and rinsed several times with a dilute KOH solution, then stained with a 0.5% solution of gentian violet in 95% ethanol for 48 h. The stained fragments were mounted onto microscope slides in euparal. The fragment material could then be compared to the vouchers of suspected diet plants to determine the food resources actually ingested.

Epidermial character nomenclature

The epidermis of leaves has a number of characteristics which are useful in identification and classification of plants. In the field of palaeobotany, microscopic features of the epidermis (as they are reflected in the cuticle), have long been recognized as an aid in the study of fossil leaves (Bornemann 1856 cited by Dilcher 1974). Stace (1965) has shown how leaf epidermal features can be used to support other taxonomic aids, especially in the classification of the Combretaceae. More recently, Bongers (1973) used epidermal character in the taxonomy of the Winteraceae. Also epidermal characters have been applied as a safeguard against fraudulence in commercial stock feed (Parkinson and Fielding 1930 cited by Martin 1955), and police departments have found the epidermis useful in plant identification (Dilcher 1974). Useful epidermal characters used in the identification of fragmentary material include: cell orientation, stoma complexes, dermal appendex, and other epidermal cells.

Cell orientation

Storr (1961) in his faecal analysis work found the orientation of the epidermal cells to be a very useful diagnostic feature. The distinctive orientation of the epidermal cells along the longitudinal axis of the leaf is commonly observed in monocotyledons (Fig 1a), and is rare among dicotyledons where these cells are more irregularly distributed (Fig 1b). This basic pattern difference readily discriminates between these two large groups and can be beneficial in distinguishing relative proportions of grazing and browsing material eaten by herbivores.

Stoma complexes

The appearance of the stomata, especially with reference to the nature and orientation of neighbouring cells, is a frequently used taxonomic character (Metcalfe and Chalk 1950, Van Cotthem 1970). Dilcher (1974) has provided a series of terms relevant to the stomatal cell complexes which have proven helpful in the identification of epidermal tissue fragments (Fig. 1). The stomata complex of monocotyledons are commonly of the paracytic type. However, types such as tetracytic and anocytic have also been observed (Metcalfe 1961, Stebbins and Khush 1961). An added feature of the stomata complexes in monocotyledons is the shape of the subsidiary cells. These cells range from triangular to parallel-sided forms through intermediates to dome-shaped cells (Metcalfe and Chalk 1950). A species usually has a mixture of domes with either triangular or parallel-sided types, but it is very unusual to find triangular and parallel-sided types together (Clifford and Watson 1977).

In dicotyledons, the more common stomata complex types are anomocytic, anisocytic, paracytic and diacytic. Storr (1961) suggested that the first three are the most commonly observed types in Australian species. Potential variation does exist and Metcalfe (1960) warns that stomatal types of more than one kind sometimes occur together on the same leaf surface, or stomatal complexes on the upper and lower surfaces may not be alike.

Storr (1961) also suggests that stomata pore orientation may be useful as a diagnostic feature, but this appears to be of restricted use.

Dermal Appendages

All outgrowths of the epidermis are categorized under the term 'dermal appendage'. There is an enormous diversity of external appendages in the dicotyledons, but this is not exhibited as extensively in the monocotyledons (Metcalfe 1960). Radford *et al.* (1974) summarizes the types of epidermal appendages under three main headings including 'simple' trichomes which can be uniseriate or multiseriate, compound trichomes of several forms and glandular trichomes. The features of length, size and density of the trichomes are more liable to vary with environment than the occurrence of different kinds (Sharma 1975). These characters should be avoided because of their questionable value for identifying epidermal fragments of different species. The presence or absence, however, can be of assistance. Gray *et al.* (1969) have demonstrated that the presence or absence of hairs between two closely related varieties of *Danthonia* was not environmentally induced, as the hairs were found to persist under a variety of controlled environments and transplant studies.

Other epidermal cells

The epidermal areas between the leaf veins (intercostal) and the tissue over the veins (costal) in monocotyledons sometimes have two cell types distinguishable by their size. Much elongated cells called 'long cells' tend to occur in intercostal regions, while more equidimensional cells called 'short cells' tend to occur only in the costal regions. In some grasses such as *Bromus* the short cells are absent (Metcalfe 1960). In others, such as *Coelachne* and *Mibora*, the distinctions tend to break down, which reduces their value as diagnostic features. Short cells also may contain a silica body or walls which give a cork reaction and the number occurring together or the arrangement may be of diagnostic value. The walls of the long cells of grasses can vary from straight and clear to very sinuous and clearly pitted. Also, the relative length and breadth can be of some value, but is subject to considerable variation.

The cells of dicotyledons are less regular than those found in the monocotyledons. The abaxial surface in some dicotyledons may be completely devoid of trichomes or stomata. There is generally, however, sufficient difference in the cells of different species to be of potential taxonomic value when looking at a limited number of species, as in faecal analysis study at the Yalanbee Experimental Station (Halford *et al.* 1984).

Intraspecific variation

It is important to differentiate environmentally modifiable features from those controlled genetically. Esau (1960) has noted that features such as the number of stomata per unit area, and whether guard cells are raised or lowered when compared to other epidermal cells, are so variable that they are of little taxonomic value. Characteristics such as a stomata frequency, epidermal cell frequencies and trichome densities generally vary with growing conditions. On the other hand, characteristics such as the type of stomatal complexes, distribution pattern of trichomes and types of trichomes tend not to vary with the environmental conditions and are, therefore, of greater value as diagnostic features in studies examining dietary preferences.

Wandoo-woodland vouchers

Of these species of the natural woodland regions and the pastures of the Yalanbee Experimental Station, slides of 60 species were produced of suitable quality for comparisons to the fragmentary material from the faeces of the grey kangaroos resident in the area. The voucher slides, enlarged photographs and descriptions of the important epidermal features of these species were used to prepare the diagnostic key to the more common species found in the faecal samples (Table 1).

All monocotyledons from the study area had stomatal apertures along the longitudinal axis of the leaf. Examples of Australian natives were *Neurachne alopecuroides*, *Lepidosperma tenue* and *Loxocarya flexuosa*. The introduced Mediterranean grasses of the pasture area also exhibited this pattern. Although this feature was rarer in the dicotyledons, it was observed in *Calothamnus sanguineus*, *Adenanthos cygnorum*, *Astroloma pallidum* and *Stackhousia hueglii*. In *Casuarina* the stomatal aperture was perpendicular to the long axis of the needle. No other dicotyledon showed regular orientation of the stomatal apertures.

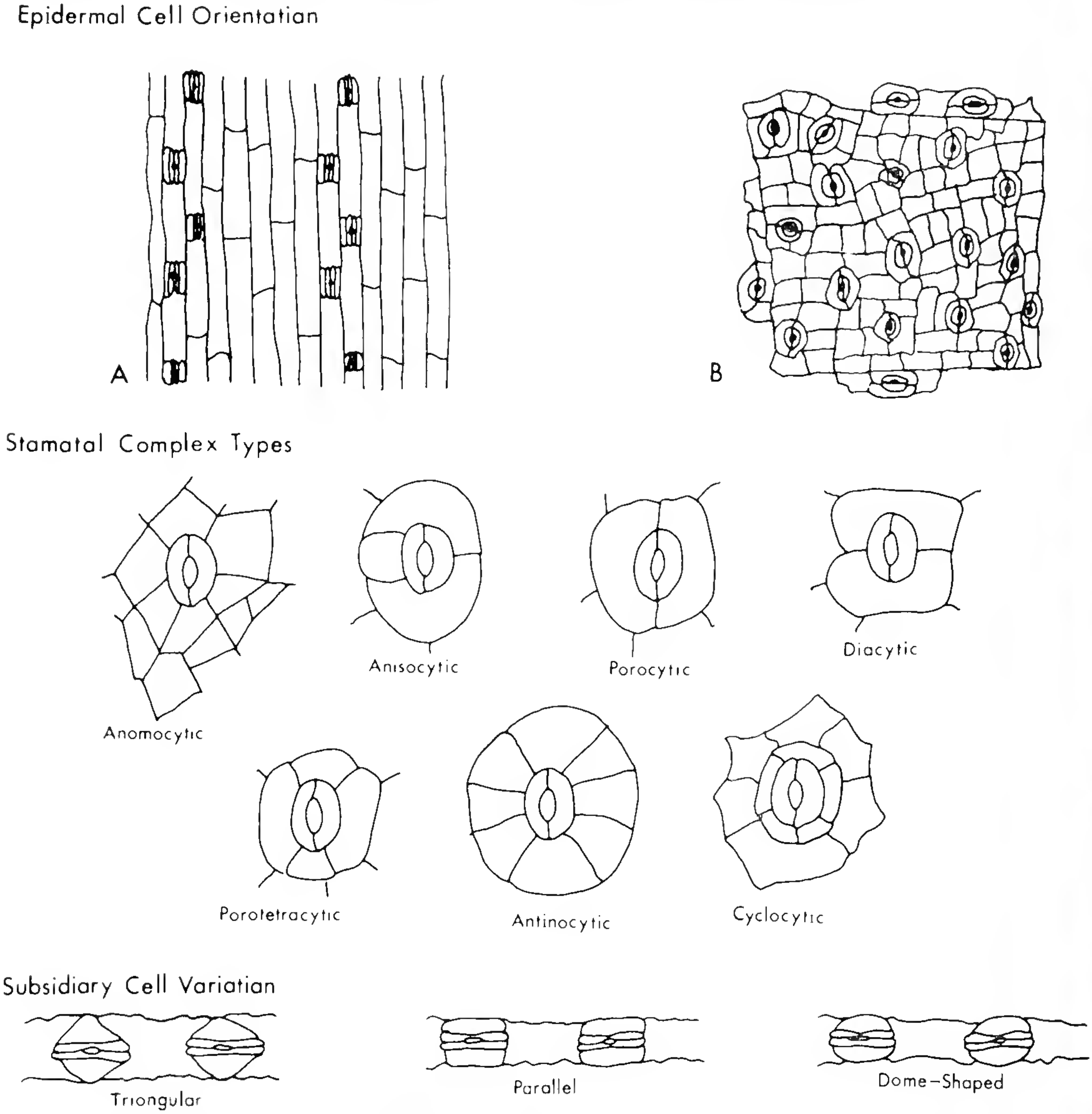


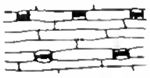
Figure 1.—Epidermal tissue variation. Epidermal cell orientation in: (A) a monocotyledon (*Bromus rigidus*) shownig longitudinal orientation of epidermal cells and (B) a dicotyledon (*Acacia celastrifolia*) showing irregular orientation. Stomatal complex type nomenclature of angiosperm leaves (after Radford *et al.* 1974) and subsidiary cell variation of monocotyledons (after Metcalfe 1960).

The nature and orientation of the subsidiary cells of the stomata proved to be especially diagnostic in the separation of the dicotyledonous species at the Yalanbee Experimental Station. The anomocytic stomatal arrangement, where cells surrounding the stomata are indistinguishable from normal epidermal cells, was found in *Hibbertia hypericoides*, *H. montana*, *Astroloma pallidum* and *Olearia rudis*. The anisocytic arrangement of three distinct subsidiary cells enclosing the stomata was observed in *Boronia crenulata*, *Hemigenia canescens* and *H. pimelifolia*. The paracytic arrangement of two

Table 1.

Key to the identification of selected native species in the Yalanbee Experiment Station woodland region using epidermal characteristics.

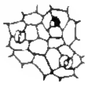
A. Epidermal cells longitudinally orientated



B. Epidermal cells rectangular (length:width ratio >> 1 : 1) .... *Conostylis setigera*

BB. Epidermal cells more-or-less isodiametric (length:width ratio ≃1:1) .... *Loxocarya flexuosa*

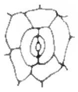
AA. Epidermal cells usually irregular in orientation



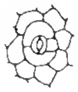
B. Trichomes or hair present

C. Trichomes scattered

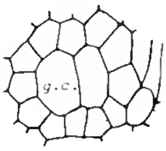
D. Stomatal cell complexes paracytic



...... or anisocytic ......



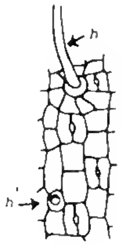
E. Epidermis with glandular cells (g.c.) surrounded by ring of typical epidermal cells ....



..... *Leptospermum erubescens*

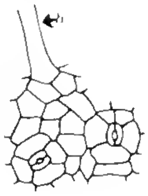
EE. Epidermis lacking glandular cells

F. Stomatal complexes in ± linear arrangement, hairs (h) easily broken (h′) during preparation.........



. *Adenanthos cygnorum*

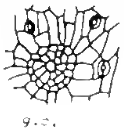
FF. Stomatal complexes irregular in arrangement, hairs robust and persistent ....



.... *Boronia crenulata*

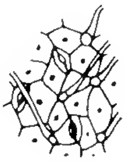
DD. Obviously subsidiary cells absent (i.e. anomocytic) (NB. *Calothamnus sanguineus* may show paracytic forms also)

E. Glandular cells present.....



.... *Calothamnus sanguineus*

EE. Glandular cells absent, epidermal cells with papillose projection common ....

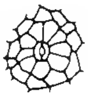


.... *Oxylobium parvifolium*

CC. Trichomes clustered in circular depressions within the intercostal regions ....

.... *Dryandra* spp.

BB. TRICHOMES ABSENT

C. STOMATAL CELL COMPLEXES ANTINOCYTIC ....  .... *HAKEA* SPP.

CC. STOMATAL CELL COMPLEXS NOT ACTINOCYTIC

D. STOMATAL COMPLEXES ARRANGED IN DEFINITE BANDS

E. STOMATAL BANDS < 2X WIDTH OF COSTAL REGIONS,
STOMATA IN ONLY A FEW LINES .... *ASTROLOMA PALLIDUM*

EE. STOMATAL BANDS > 2X WIDTH OF COSTAL REGION,
IN NUMEROUS LINES ....*CONOSPERMUM GLUMACEUM*

DD. STOMATA COMPLEXES NOT IN BANDS

E. STOMATAL CELL COMPLEXES CELLS ANOMOCYTIC OR ANISOCYTIC (SEE BELOW)

F. SUBSIDIARY CELLS ANOMOCYTIC 

G. GUARD CELLS SUNKEN .... *HOVEA CHORIZEMIFOLIA*

GG. GUARD CELLS NOT SUNKEN .... *GOMPHOLOBIUM MARGINATUM*

FF. GUARD CELL COMPLEXES ANISOCYTIC 

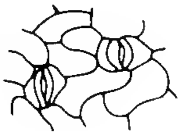
G. GUARD CELLS SUNKEN .... *DAVIESIA CORDATA*

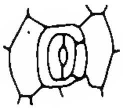
GG. GUARD CELLS NOT SUNKEN .... *ANTHOCERCIS LITTOREA*

EE. STOMATAL COMPLEXES PARACYTIC 

F. SUBSIDIARY CELLS ± EQUAL IN SIZE

G. EPIDERMAL CELL WALLS ± STRAIGHT, GUARD CELLS
± SQUARES IN OUTLINE ....  ... *GASTROLOBIUM* SPP.

GG. EPIDERMAL CELL WALLS ROUNDED OR SLIGHTLY
UNDULATING, SUBSIDIARY CELLS ± TRIANGLAR...  . *SYNAPHAEA PETIOLARIS*

FF. SUBSIDIARY CELLS UNEQUAL IN SIZE ....  .... *ACACIA CELASTRIFOLIA* subsidiary cells parallel to the long axis of the stomata was recorded in all species of the genus *Gastrolobium* and all of the monocotyledon species studied. *Adenanthos cygnorum*, and all species of *Casuarina* also had the paracytic arrangement. All species of the genus *Hakea* examined had the antinocytic arrangement of stomata surrounded by radially elongated subsidiary cells. *Calothamnus sanguineus* was found to have a combination of anomocytic and paracytic types. In other species, such as *Grevillea pilulifera* and all the *Dryandra* species prepared, the stomata were not discernible, due to a dense mat of trichomes covering the stomata.

Stomatal distribution in the plants of the Yalanbee Experimental Station study site also provided a diagnostic character. A regular distribution of the stomata over the epidermal surface was observed in *Acacia celastrifolia*, *Calothamnus sanguineus*, *Adenanthos cygnorum* and *Hakea undulata*. Certain species had stomata arranged in distinct repeated patterns. This included the stomata of *Lepidosperma tenue*, *L. scabrum* and *L. angustatum* where the stomata were arranged in rows oriented along the longitudinal axis. In most of the species of the grasses, the stomata occurred in well-defined longitudinal bands in the intercostal zones. Each intercostal zone included one or more stomatal band depending on the species.

Stomata in some species tended to be associated with epidermal pits and furrows. The stomata of the *Dryandra* species studied were confined to depressions on the abaxial surface of leaves. The stomata of leaves of *Lomandra caespitosa* and *L. effusa* and the stems of *Opercularia vaginata*, *Casuarina humilis*, *C. heugeliana* and *Dampiera lavandulacea* were limited to longitudinal grooves.

Trichomes occurred in many of the species sampled from the wandoo woodland. Simple unicellular trichomes were present in *Boronia crenulata*, *Melaleuca holosericea*, *Leptospermum erubescens*, and *Hemigenia canescens*. *Adenanthos cygnorum* had simple unicellular trichomes but was distinguished by a large, flat basal cell to the trichome. *Hibbertia hypericoides* had sessile stellate hairs and *Hemigenia canescens* had glandular and bicellular hairs. All of the species of *Dryandra* in the study had lociform trichomes densely covering the abaxial surface. *Calothamnus sanguineus* had setaceous trichomes, but these tended to break down during preparation of the epidermi. Several species had papillose projections from the epidermal cells. These included *Gastrolobium calycinum* and all of the species of *Casuarina examined*. The grasses tended to have mostly unicellular trichomes, which were not valuable in the identification of individual species.

Shape of the epidermal cells was helpful in distinguishing monocotyledons from dicotyledons. The cells of the monocotyledons were typically rectangular, with the length parallel to the longitudinal axis of the leaf. Some intermixed of the monocotyledons, however, were square. The dicotyledons varied from the isodiametrical cells as in *Dryandra sessilis* to more rectangular cells as in *Opercularia vaginata*. Irregular shaped cells in *Calothamnus* and occasional paired cells separated by a sinuous wall in *Calothamnus* and *Leptospermum* were diagnostic. *Loxocarya flexuosa*, *Astroloma pallidum* and some of the grasses were also distinguishable from other species by sinuous epidermal cell walls. Other plants had typically straight walls with varying degrees of curvature at the corners.

In general, most of the plant epidermi from the Yalanbee Experimental Station study area had enough difference to allow identification to genera. However, within some genera, such as *Hakea*, the identification of epidermal fragments to a single species was not always possible. Even so, through careful preparation of faecal material and voucher specimens, it has been possible to develop a basis for studying the dietary preferences of the western grey kangaroo in the wandoo woodland-pasture landscapes of the Yalanbee Experimental Station. With the aid of the key it is possible to examine material rapidly and identify the common species being grazed.

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Diet of the western grey kangaroo (*Macropus fuliginosus* Desm.) in a mixed pasture-woodland habitat of Western Australia

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Abstract

The late autumn/early winter diet of western grey kangaroo living in a landscape of native wandoo open forest surrounded by pasture grasslands was assessed using faecal analysis. Eventhough some animals were observed regularly feeding in the pastures at night, a considerable number of native woodland species appeared in their diet in addition to the exotic pasture species. Thirty-one taxa of native plants were recorded from grey-kangaroo faeces. Of the native species, *Conostylis setigera*, *Opercularia vaginata*, *Bossiaea eriocarpa* and *Casuarina* spp. were the most frequently encountered in the faecal preparations. The frequency of pasture grasses appearing in the faecal material increased following the first winter rains which resulted in good pasture growth. Apparently kangaroos travel considerable distances to graze or browse on favoured species. Higher nitrogen content of certain favoured native species is hypothesized as contributing to this preference.

Introduction

European settlement of Australia has had a profound effect on the members of the Macropodidae. Some species have been driven to extinction, while others have increased in numbers due to favourable habitat changes (Calaby 1971). Changes in vegetation due to grazing stock have generally improved the habitat for the red kangaroo (*Megaleia rufa* Desm.) in many parts of its range and populations have greatly increased in numbers (Frith 1964, Newsome 1965). The western grey kangaroo (*Macropus fuliginosus* Desm.) and eastern grey kangaroo (*Macropus giganteus* Shaw) have disappeared from heavily settled areas but their numbers can be high in some pastoral districts.

At present the large macropods are variously viewed as pests whose population size should be controlled, objects of aesthetic pleasure and should be protected, or a valuable wildlife resource worthy of exploitation and conservation. Each of these views requires the development of a suitable management programme. To accomplish the aims of any management programme, there must be some manipulation of the environment or the animal population (Main 1968). The first step in the research programme to establish a management plan data base is to understand the relationship between the organism and its environment. Social organisation, habitat choice, food habits and the ecophysiology of the organisms are just some of the areas which need to be considered.

The ecology of a resident population of western grey kangaroo in a mixed landscape of native woodland and pastoral lands on the CSIRO Yalanbee Experimental Station at Bakers Hill, Western Australia is currently being studied (G. Arnold, pers. comm).

The grey kangaroos at the Yalanbee Experiment Station spend much of the day in a 90 ha area of native woodland. Spotlighting and a system of camera and electric-eye monitored fence openings indicate that numerous kangaroos feed in the pasture lands adjacent to the native woodland (G. Arnold, unpublished data). However, little is known of their feeding behaviour in the native woodland area. Objectives of this current study were to document the natural vegetation of the grey kangaroo residence area at the Yalanbee Experiment Station and to determine information on the kinds of food resources the animals are exploiting.

Study site

The Yalanbee Experiment Station at Bakers Hill, Western Australia (31°45'S, 116°27'E) lies 90 km north-east of Perth and 26 km south-east of Northam. The climate is Mediterranean with mild wet winters and hot dry summers. Twenty year averages from the station indicate a mean annual precipitation of 625 mm, with the highest mean monthly values occurring in June and July, both at 86 mm. Average maximum temperatures range from 17°C to 34°C in July and January, respectively. Summer daily maxima over 40°C are common. Mean monthly minima range from 17°C in January to 4°C in July.

Topographic relief of the study area is low, with a range of approximately 150 m (Fig. 1a). Soils in the study area include the Yalanbee, Kauring and Malebelling soil series (Fig. 1b). Yalanbee soils ocupy the highest landscape positions and are predominantly yellowish-brown ironstone gravels. Kauring soils are shallow, overlying granitic rocks which are exposed in some areas. Malebelling soils consist of light-brown gritty loamy sand with some ironstone gravels toward the base over yellow and reddish-brown mottled sandy-clay loam with rock fragments.

Vegetation

The Yalanbee Experiment Station lies within the Wandoo Woodland vegetational region (Gardner 1942). The regional dominant is *Eucalyptus wandoo*. Depending on habitat conditions, *E. accedens*, *E. marginata*, *E. calophylla* and *Casuarina huegeliana* can also be common species of the woodland canopy stratum. Ground traverses provided a subjective impression of the vegetation of the native woodland at the station and helped locate representative stands for intensive sampling.

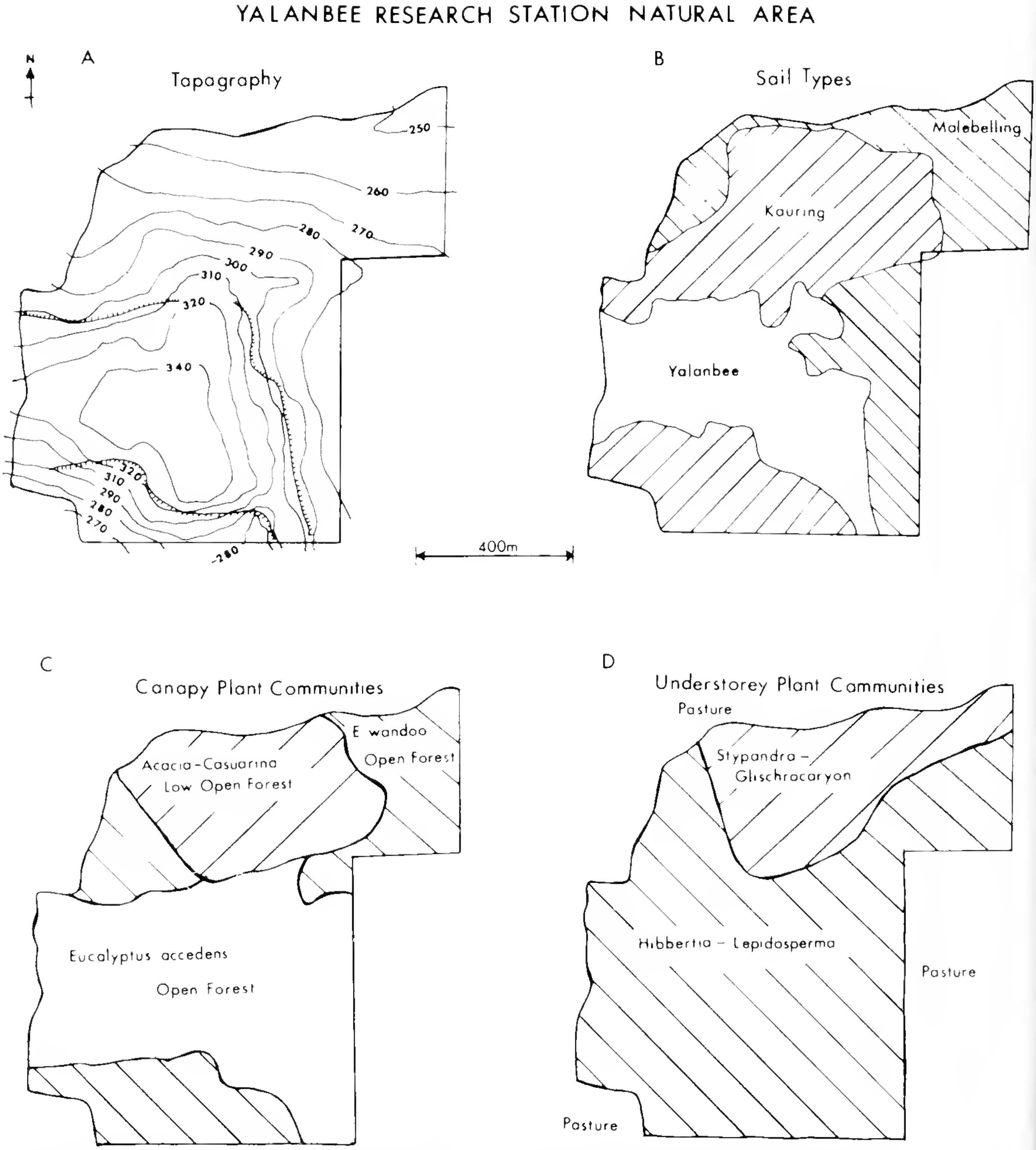

Figure 1.—Yalanbee Research Station Natural Area. (A) Topography shown by 5 m elevational contours. Breakaway slope margin is also shown. (B) Soil types of the study area after Dimmoch (unpublished data). (C) Canopy vegetational communities. (D) Understorey vegetation communities.

The tree stratum was sampled using 23 sites of 10 x 10 m. Within each site all trees (diameter at breast height (dbh) > 4 cm; height > 2 m) were identified to species and the dbh measured. A canopy density value for the site was obtained as the mean of four readings on a crown-cover densiometer (Lemmon 1956). The mean of the relative density and relative basal area provided species importance values for the primary stand by species data matrix.

The understorey stratum was sampled at 25 sites distributed throughout the natural woodland area. At each site a line transect of sixteen 1 m^2 quadrats provided an estimate of species cover and frequency. An understorey importance value for each species was calculated by summing the mean cover and frequency percentages and dividing by two. The vegetation data was subjected to several ordination techniques using the Ordiflex Program Package of Gauch (1973) and a polythetic agglomerative classification system (Gilbert and Walls 1966) using percentage similarity (Bray and Curtis 1957). Mapping divisions were constructed objectively from the results of the data analysis. By locating the sites on aerial photographs and using apparent photographic similarity, physiognomic features, geomorphological data and further field observation, the vegetation maps were developed. The canopy plant communities were named for the dominant species and the structural classifications of Specht (1970). Understorey plant communities were named for their most important species, even though the two species were only a part of very diverse assemblages of species.

Canopy Communities

The three communities designated were 1) Powderbark (*Eucalyptus accedens*) open forest, 2) Wandoo (*E. wandoo*) open forest, and 3) *Acacia-Casuarina* (*Acacia acuminata-Casuarina huegeliana*) low open forest (Fig. 1c). The Powderbark open forest was dominated by *E. accedens* and occurred on the old lateritic plateau and the eastern break-away slope. Other tree species in the community were *Dryandra sessilis, E. wandoo, E. marginata* and *E. calophylla. D. sessilis and E. marginata* were restricted to areas of the lateritic plateau. The average canopy cover of the community was 38% and the mean height of the trees was 42 m.

The Wandoo open forest community named for the dominant species, *E. wandoo,* was found in three areas of the native vegetation. These occurred on the southern steep break-away slopes, the north-eastern more gradual slopes and the nearly flat north-western corner region. Other occasional associates of *E. wandoo* in this community were *Acacia acuminata, E. calophylla, C. huegeliana* and *E. accedens.* Canopy cover averaged 46% and the mean height of the trees was 39 m.

The *Acacia-Casuarina* low open forest was co-dominated by *Acacia acuminata* and *Casuarina huegeliana.* The community was confined to the northern slopes and restricted to the soils which were shallow and overlying granitic parent material. Other tree species in the community were *E. accedens, E. calophylla* and *E. wandoo.* Mean canopy cover was 33%, but the range of between 5% and nearly 100% gives a better representation of the discontinuous nature of the distribution of thickets of *Acacia* and *Casuarina.* Average tree height was 7 m.

Understorey Communities

Unlike the separation into three apparent communities found in the canopy, only two distinct types of understorey were delineated in the analysis of the data from the understorey vegetation sampling data. The extreme heterogeneity of the understorey vegetation presented difficulties and even the samples within the same major group have only limited similarity. The two very broad classification groups were designated as the *Hibbertia-Lepidosperma* community, and the *Stypandra-Glischrocaryon* community.

The *Hibbertia-Lepidosperma* community covered the majority of the area except the north-central region (Fig. 1d). *Hibbertia hypericoides, Lepidosperma tenue, L. scabrum,* and *Conostylis setigera* were common throughout the area (Table 1). *Hakea lissocarpa, Acacia celastrifolia, Calothamnus sanguineus, Adenanthos cygnorum* and *Gastrolobium trilobium* were dominants in restricted areas of the community. The understorey layer generally ranged from 0.5 m to 1.5 m in height. Percentage cover ranged from areas almost denuded of understorey species on the break-away slopes to 75% in areas on the lateritic plateau.

The *Stypandra-Glischrocaryon* community was restricted to soils of granitic origin within the areas of *Acacia-Casuarina low open forest. Stypandra imbricata* and *Glischrocaryon aureum* were common through this region (Table 1). Other common species were *Opercularia vaginata, Trymalium ledifolium, Scaevola fasciculata, Xanthorrhoea preissii* and *Neurachne alopecuroidea.* The shrub height rarely exceeded 1 m except for the occasional *X. preissii.* Presenting the data for the two understorey communities as mean cover values and frequency percentages (Table 1) provides information on plants available to the grey kangaroo for food.

Kangaroo diet

Spot-lighting surveys reveal that grey kangaroo at the Yalanbee Experiment Station do feed in the pastoral areas adjacent to the native woodland (G. Arnold, unpublished data). These survey techniques cannot be used effectively, however, to observe the animals feeding in the heavy scrub of the native bushland areas. An important aspect of the current study was to discover what plants the grey kangaroo utilized in their diets and to determine if the diet changed markedly when the winter rains made green feed more readily available. As the population dynamics of the group were also under study, direct analysis of rumen contents of culled animals was not possible. Indirect methods using identification of faecal pellet plant fragments and records of grazed plant species provided the best alternatives.

Table 1

Mean percentage cover values and frequency percentages for species determined from the sites classified into the *Stypandra-Glischrocaryon* and *Hibbertia-Lepidosperma* communities. Abbreviations are: for Order, Monocotyledonae (M) and Dicotyledonae (D); and for Life Form, Shrub (S), and Herbaceous Perennial (H). All non-legume species found in less than 3 % of quadrats grouped as "minor" species.

Species	Order	Family	Life Form	*Stypandra-Glischrocaryon*		*Hibbertia-Lepidosperma*	
				Cover	Freq.	Cover	Freq.
Stypandra imbricata	M	Liliaceae	S	3·20	47·5		
Glischrocaryon aurea	D	Haloragaceae	S	2·50	41·2	0·11	3·4
Scaevola fasciculata	D	Goodeniaceae	S	3·00	40·0		
Neurachne alopecuroides	M	Poaceae	H	1·10	57·5	0·57	20·0
Phyllanthus calycinus	D	Euphorbiaceae	S	0·60	31·4	0·56	13·8
Trymalium ledifolium	D	Rhamnaceae	S	6·40	31·3	0·47	4·0
Opercularia vaginata	D	Rubiaceae	H	2·30	25·0	0·31	4·7
Stackhousia pubescens	D	Stackhousiaceae	S	0·40	18·8		
Bossiaea eriocarpa	D	Papilionaceae	S	0·80	16·2	0·38	10·6
Anthocercis littorea	D	Solanaceae	S	1·30	11·2		
Lomandra caespitosa	M	Liliaceae	S	0·20	10·0	0·06	5·9
Acacia acuminata	D	Mimosaceae	S	0·38	3·8		
Gompholobium preissii	D	Papilionaceae	S	0·06	6·2	0·09	3·8
Xanthorrhoea preissii	M	Liliaceae	S	0·20	1·2	1·36	5·3
Lomandra hermaphrodita	M	Liliaceae	H	0·06	1·2	0·14	5·9
3 Minor Dicot spp.	D			0·06			
26 Minor Dicot spp.	D					2·75	
8 Minor Monocot spp.	M					0·28	
Adenanthos cygnorum	D	Proteaceae	S			0·69	3·0
Hakea ruscifolia	D	Proteaceae	S			0·48	3·1
Lepidosperma angustatum	M	Cyperaceae	H			0·11	3·4
Trymalium angustifolium	D	Rhamnaceae	S			0·56	3·6
Stylidium brunoneanum	D	Stylidiaceae	H			0·06	3·8
Baeckea camphorosmae	D	Myrtaceae	S			0·30	3·8
Hakea ambigua	D	Proteaceae	S			0·83	3·8
Dryandra sessilis	D	Proteaceae	S			0·54	3·8
Dryandra carenacea	D	Proteaceae	S			1·18	4·1
Acacia celastrifolia	D	Mimosaceae	S			0·72	4·7
Casuarina humilis	D	Casuarinaceae	S			0·83	4·7
Hakea incrassata	D	Proteaceae	S			0·55	5·0
Lasiopetalum molle	D	Sterculiaceae	S			0·13	5·3
Borya nitida	M	Liliaceae	S			0·78	5·3
Gastrolobium trilobium	D	Papilionaceae	S			2·02	5·6
Petrophile striata	D	Proteaceae	S			1·23	6·6
Hakea undulatum	D	Proteaceae	S			0·63	6·3
Lepidobolus sp.	M	Restionaceae	H			0·92	6·6
Leptospermum erubescens	D	Cyperaceae	H			0·85	6·9
Tetraria octandra	M	Cyperaceae	H			0·57	7·2
Calothamnus sanguineus	D	Myrtaceae	S			2·22	7·8
Dampiera lavandulacea	D	Goodeniaceae	S			0·19	8·4
Dryandra nivea	D	Proteaceae	S			1·04	8·7
Acacia pulchella	D	Mimosaceae	S			0·53	9·1
Melaleuca holosericea	D	Myrtaceae	S			2·53	9·7
Hakea trifurcata	D	Proteaceae	S			2·74	10·0
Calytrix brachyphylla	D	Myrtaceae	S			0·65	12·8
Lepidospermum tenue	M	Cyperaceae	H			0·63	14·7
Hibbertia montana	D	Dilleniaceae	S	0·25	3·8	0·78	15·9
Jacksonia restioides	D	Papilionaceae	S			1·42	15·6
Hemigenia canescens	D	Lamiaceae	S			1·16	15·6
Loxocarya flexuosa	M	Restionaceae	H	0·71	7·5	1·71	20·0
Hakea lissocarpha	D	Proteaceae	S			2·90	21·6
Lepidospermum scabrum	M	Cyperaceae	H	0·06	1·2	1·19	21·8
Conostylis setigera	M	Haemodoraceae	S	0·10	6·2	1·52	34·1
Hibbertia hypericoides	D	Dilleniaceae	S			5·72	48·1

The epidermis of leaves has a number of characteristics which are useful in the identification and classification of plant species. They also have the advantage that most of the cuticular and epidermal tissue remain undigested in the passage through the digestive systems of animals. Cuticular material can also be identified in animal stomach contents and faeces. (Stewart 1967, 1971, Stewart and Stewart 1970). No study of epidermal characteristics of species of the Wandoo Woodland, however, was available for identifying epidermal fragments in the faecal pellets of the grey kangaroo. An initial period was, therefore, necessary to prepare a series of reference slides of epidermal material from plants known from the woodland and pasture areas of the Yalanbee Experiment Station (Halford *et al.* 1984.)

Epidermis Reference Collection

Reference slides of suitable quality were produced of 60 of the 140 species identified in the native vegetation area and adjacent pasture using the techniques of Storr (1961) and Jain (1976). The relative merits of each of these techniques are discussed in a previous paper (Halford *et al.* 1984). In those species which have leaves or phyllodes which are reduced or absent, the epidermal features of stem material were used for descriptive purposes. Also in a few cases there was some difficulty in finding sufficient species-specific epidermal characters to differentiate members within one genera. There was, however, little difficulty in separating generic groups on the basis of epidermal characters alone.

Faecal Material Preparation

Microscopic observation of the untreated faecal material did not provide sufficient clarity of the epidermal fragments for identification. A modification of Storr's (1961) preparation was, therefore, used to clear epidermal material from residual fibre fragments. Such acid digestion procedures have presented problems in animal diet analyses previously (e.g. Griffiths and Barker 1966) but it was felt that the ability to identify plant species in the faecal pellet was enhanced to a far greater extent than the potential to lose species from the dietary list due to complete digestion of soft epidermal tissue by this method. Each faecal pellet was split into two equal portions. One portion was stored to allow for possible re-analysis. The other portion was placed in a 20 ml solution of equal parts of 10% chromic acid and 10% nitric acid and gently boiled for 15 min. After maceration, the material was allowed to cool, rinsed with a very dilute solution of KOH. The material was then suspended in a 0.5% solution of gentian violet in 95% alcohol. After staining for 48 h, the material was passed through a 0.5 mm sieve and both the fractions re-suspended. Samples of each were placed on microscope slides and mounted in euparal. The separation of these fractions generally assisted in the visual clarity of the slides. The slides were examined at a magnification of 70 x. All fragments lying in the field of view along fifteen transects of the length of the slide were examined, compared to the collection of reference preparations, and identified. In a series of observations on subsamples of pellets, it was determined that after five slides from the same pellet, very few new species were recognised. Subsequently, therefore, the list of species from a single pellet was determined from five subsample slides.

Field Collections

Faeces were collected in areas of the two understorey communities and from adjacent pastures where kangaroos were observed. Faecal samples were obtained on April 4 and May 15, 1979. Two additional sets of samples were collected from the two native vegetation areas on June 6 and June 25, 1979. On May 21st. 25 mm of rain fell at the Experimental Station. This rainfall was followed by another 15 mm in the six days to the end of the month. These rains provided the first effective growing period of the season and produced good growth of annuals in the pastures and areas around the granite outcrops of the *Stypandra-Glischrocaryon* community. Faecal samples were not collected on the last two dates from the pasture areas because of the thick regrowth of the pasture grasses. Only recently deposited faeces were collected during each sampling. This was achieved by noting that newly deposited material had a shiny mucus layer. The shiny appearance was lost within one week. Faecal pellets were collected by traversing the sites systematically. From each deposit of faeces, two pellets were taken for analysis. The remaining faeces were removed and kept separately to ensure that duplication of sampling did not occur. However, this collection method did not necessarily avoid sampling more than once from the same kangaroo. The number of faecal pellets collected in the field samples ranged from 26 to 42 pellets. Samples returned from the field sites were oven-dried at 80 C for 24 h and stored at room temperature until analysis.

Field Grazing Observations

During the course of the study a list of plants which appeared to be grazed by the larger herbivores was compiled. These were easily distinguished from those grazed by insects but it was not possible to differentiate between the grazing of grey kangaroo, brush wallaby and rabbits, the only large herbivores in the area. There were 32 taxa of native plants observed to be grazed in the areas of native bush (Table 2). The herbaceous perennials and annuals which appeared after the rains were often heavily grazed, especially around the granite outcrops of the *Stypandra-Glischrocaryon* area.

Species Recorded from Faecal Pellets

Thirty-one species of native plants were recorded from grey-kangaroo faeces collected at Yalanbee (Fig. 2). The exotic grasses *Bromus rubens, B. rigidus, Avena sativa* and *Triticum* sp. constituted the group referred to as "pasture grasses". These grasses were not easily separated by their epidermal patterns and to avoid misidentification, no attempt was made to distinguish between the species in the faecal samples. Other plants of the pasture area, which included several species each of *Lupinus* and *Trifolium*, and *Arctotheca calendula*, were not found in the faecal collections. Of the natives, the most commonly identified species was *Conostylis setigera*, a tufted perennial monocotyledon, occurring in 60% of all pellets analysed during the survey. *Opercularia vaginata* and *Bossiaea eriocarpa* occurred in over 40% of pellets analysed. *Adenanthos cygnorum*, and two taxa which were difficult to separate, a *Hakea* sp. and *Casuarina* sp, were also frequently observed in the faecal samples. Of the species observed in the faeces, 29% were monocotyledons and the remaining 71% were dicotyledons. When compared to 22% monocotyledon—78% dicotyledon percentages for the field sample ratio, it appears the grey kangaroo show some favour for the monocotyledons but further study needs to be done to verify this possibility.

When the data from the summer collections from the different understorey communities were compared there were some notable differences, (Fig. 2). *Acacia celastrifolia*, a plant restricted to the *Hibbertia-Lepidosperma* community, was common in the samples from this area and absent from the *Stypandra-Glischrocaryon* region. *Acacia celastrifolia* was also found in faecal pellets collected in the pasture areas adjacent to the *Hibbertia-Lepidosperma* region. *Calothamnus sanguineus, Adenanthos cygnorum* and the grouping of the several *Hakea* species were identified from all the collection areas but were more frequent in the faecal samples from the *Hibbertia-Lepidosperma* zone and the pasture areas. The pasture grasses and *Conostylis setigera* were common in the faecal collections from all sites. *Opercularia vaginata* and *Bossiaea eriocarpa* were very common in the two native vegetation sites, but were less frequent in the samples from the pasture.

Table 2

Species of the native woodland showing signs of grazing by large herbivores and confirmed in faecal pellet analyses. Asterisk (*) denotes those species grazed after the first effective rains. See Table 1 for abbreviations.

Species	Order	Family	Life form	Grazed	Faeces
Acacia celastrifolia	D	Leguminosae	S	..	X
Adenanthos cygnorum	D	Proteaceae	S	X	X
Anthocercis littorea	D	Solanaceae	S	X	
Bossiaea eriocarpa	D	Leguminosae	S	X	X
*Burchardia multiflora**	M	Liliaceae	H	X	
Calothamnus sanguineus	D	Myrtaceae	S	X	X
Casuarina spp.	D	Casuarinaceae	S	...	X
Conostylis setigera	M	Haemodoraceae	H	X	X
Dampiera lavandulacea	D	Goodeniaceae	S	X	X
Daviesia juncea	D	Leguminosae	S	X	X
Daviesea decurrens	D	Leguminosae	S		X
*Dianella revoluta**	M	Liliaceae	H	X	
Dichopogon sp.*	M	Liliaceae	H	X	
Drosera spp.*	D	Droseraceae	H	X	
Dryandra carduacea	D	Proteaceae	S	X	X
Gastrolobium trilobium	D	Leguminosae	S	X	X
Gastrolobium calycinum	D	Leguminosae	S	X	X
Glischrocaryon aureum	D	Haloragaceae	S	X	X
Gompholobium preissii	D	Leguminosae	S		X
Gyrostemon subnudus	D	Phytolacaceae	S	X	.
Hakea ambigua	D	Proteaceae	S		X
Hakea trifurcata	D	Proteaceae	S	X	X
Hakea undulata	D	Proteaceae	S		X
Jacksonia restioides	D	Leguminosae	S	X	X
Lasiopetalum molle	D	Steruliaceae	S	X	
Lepidosperma scabrum	M	Cyperaceae	H	X	X
Lomandra effusa	M	Liliaceae	H	X	X
Lomandra hermaphrodita	M	Liliaceae	H	X	X
Loxocarya flexuosa	M	Restionaceae	H		X
Mirbelia ramulosa	D	Leguminosae	S	X	X
*Neuracline alopecuroidea**	M	Poaceae	H	X	X
Native grasses (not flowering)*	M	Poaceae	H	X	..
Opercularia vaginata	D	Rubiaceae	H	X	X
Petrophile serruriae	D	Proteaceae	S	X	
Stylidium affine	D	Stylideaceae	H	X	...
Stypandra imbricata	M	Liliaceae	H	X	X
Tetraria octandra	M	Cyperaceae	H	X	....
Tetratheca confertifolia	D	Tremandraceae	S	X	....
Tribonanthes uniflora	M	Haemodoraceae	H	X	...
Xanthorrhoea preissii	M	Liliaceae	S	....	X

Change in the frequency of plant species present in the faeces following the onset of winter rains were apparent, despite the relatively small sample (Fig. 3). The percentage of pellets containing pasture grasses was higher following the initial winter rains and the consequently greater availability of the pasture grasses. *Conostylis setigera* remained a common constituent in the diet both before and after the beginning of the winter growing season. The frequency of occurrence of *Opercularia vaginata*, *Bossiaea eriocarpa* and *Casuarina* spp. decreased in the winter samples when compared to the pre-rainfall collections. *Gompholobium preissii* and *Phyllanthus calycinus* were only recorded in faecal samples collected during winter. Also, there was a drop from 24 taxa in the pellets sampled from collections before the rains, to 13 in the samples following the first rains.

Diet Preferences

Information on diet preference can be developed when the field frequency of a plant species in the native communities is compared to the frequency of occurrence in the samples of the diet. An index of diet preference was calculated using the frequency percentage of a species from all native understorey field samples combined divided by the frequency of occurrence of the species from all faecal pellets analysed. The resulting data was then somewhat subjectively classified into species which were 1) highly preferred, ratio > 3.00; 2) moderately preferred, ratio 2.00-3.00; 3) of low preference, ratio 1.00-2.00; and 4) of rare occurrence in diet, ratio < 1.00. It is apparent that the pasture grasses are an important component in the diet of the grey kangaroo at the Yalanbee Experimental Station, even though the animals must leave their resting areas to graze (Table 3). Of the native species, *Adenanthos cygnorum*, *Casuarina* spp. and *Opercularia vaginata* received the highest diet preference ratios. Other preferred native species were *Acacia celastrifolia*, *Hakea* spp., *Gastrolobium trilobium*, *Bossiaea eriocarpa* and *Calothamnus sanguineus*. *Conostylis setigera* was the most frequently encountered species in the faecal pellets. Its frequent field presence resulted in a rating subjectively placing it with moderately preferred species.

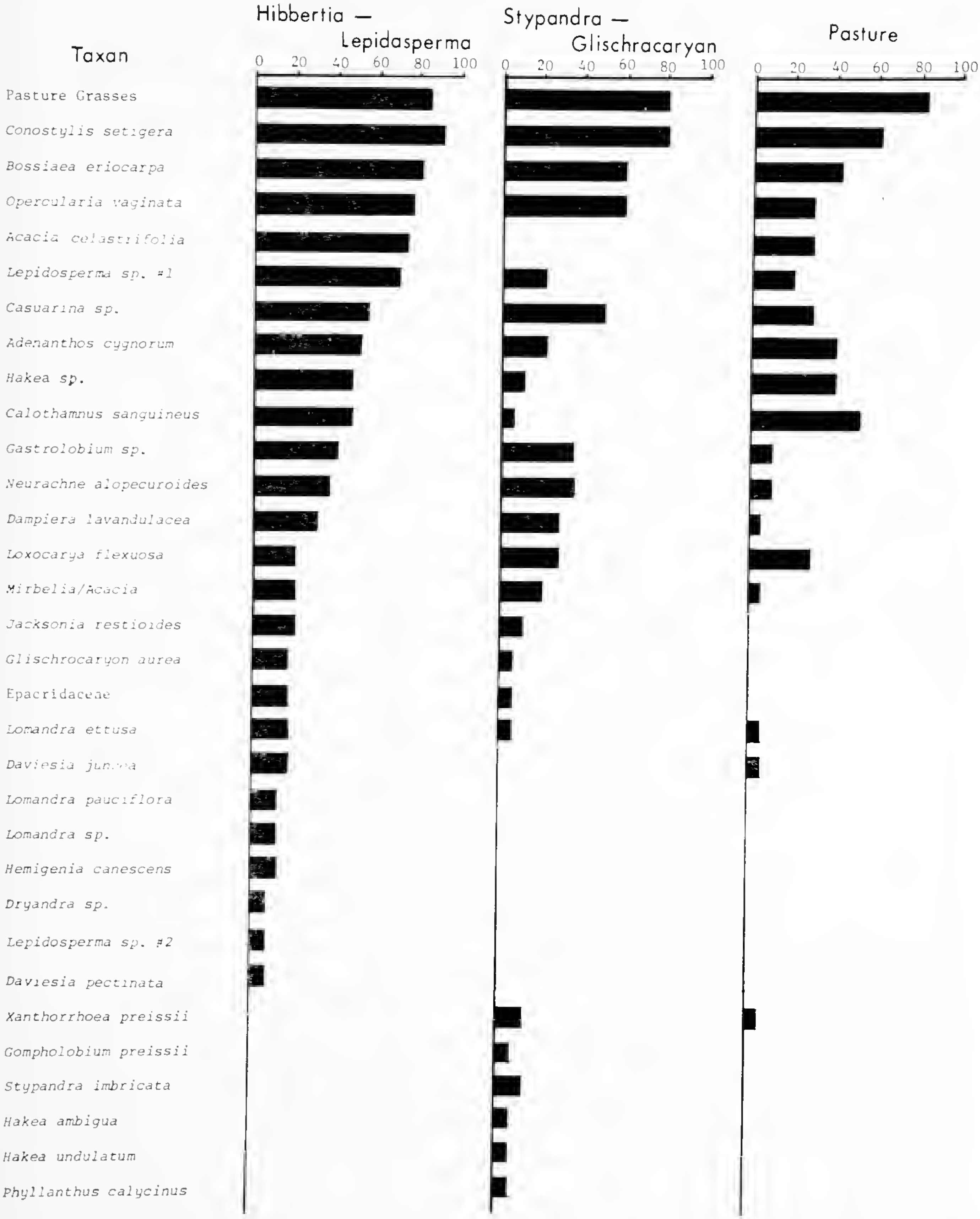

Figure 2.—Collection site variation in the diet of the grey kangaroo. Frequency of occurrence of plant species in faecal pellets collected in sites of pasture, the *Hibbertia-Lepidosperma* understorey community and the *Stypandra-Glischrocaryon* under-standard surveyor's measure.

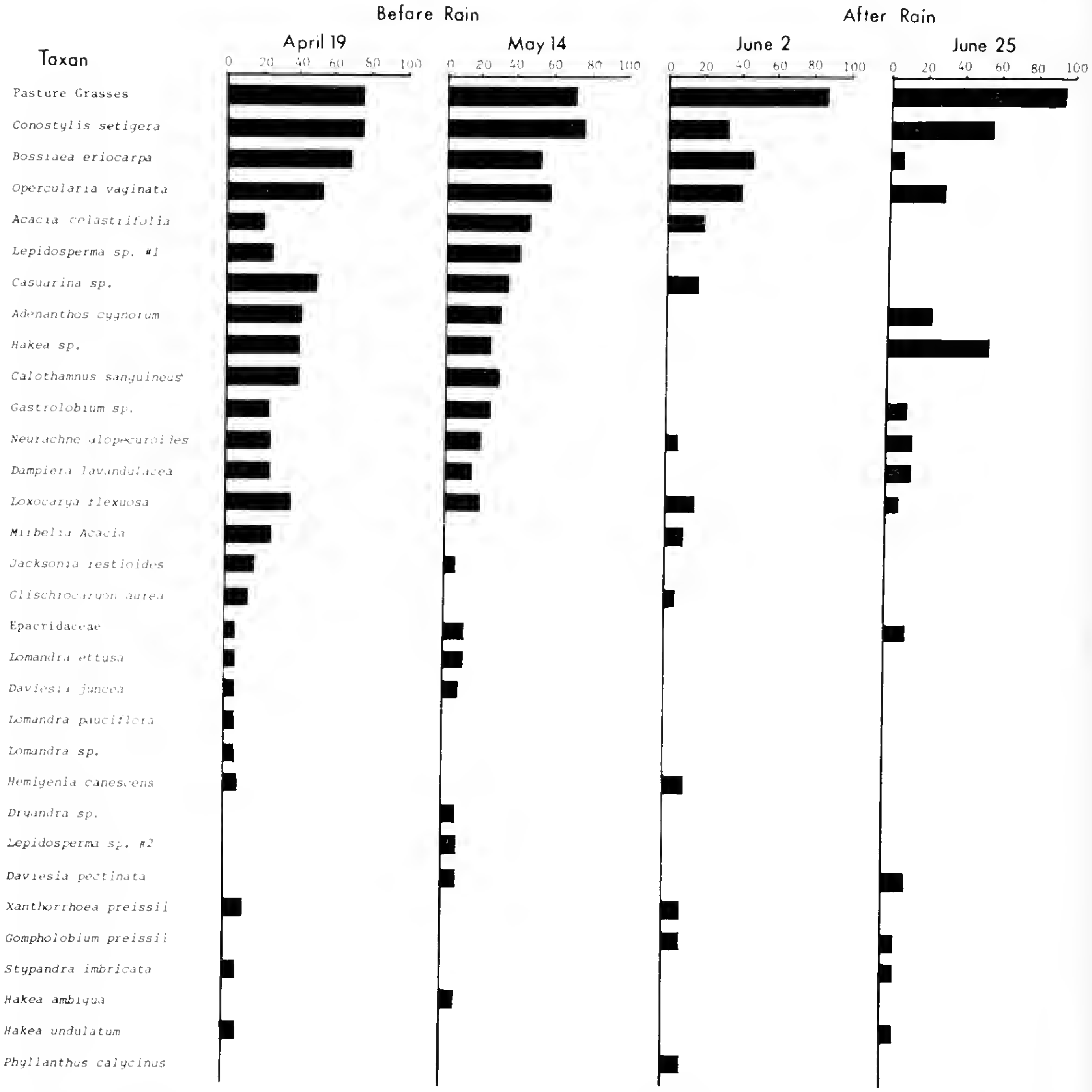

Figure 3.—Diet constituents of the grey kangaroo. Frequency of occurrence in faecal pellets collected on April 19 and May 14, 1979 before significant rainfall, and June 2 and June 25 during the period of good vegetational condition. Data from all collection sites were grouped.

Discussion

Grey kangaroos, like most large herbivores, consume a broad spectrum of plant species representing a range of plant life forms. The grey kangaroo in the native woodland-pasture landscape of the Yalanbee Experimental Station are consuming a mixture of native species in addition to the grasses of the pasture areas. A large number of native dicotyledons occur in the diet of the grey kangaroo in this study. Previous studies of the food habits of large macropods show they are predominantly grazers, with grasses the most important part of the diet. The eastern grey kangaroo was observed by Kirkpatrick (1965) to graze on native grasses and introduced pasture grasses in southern Queensland. Griffiths and Barker (1966) and Griffiths *et al.* (1974) also observed that most of the grazing of the eastern grey kangaroo was confined to the pasture grasses and that dicotyledons represented only a very small part of the diet. These studies, however, were carried out in open grasslands where the dicotyledons are only minor components.

Table 3

Diet preferences of western grey kangaroo at the Yalanbee Experimental Station determined as a ratio of the diet frequence and the field frequency. For diet preference categories, see text.

Species	Diet Frequency	Field Frequency	Preference Ratio	Diet Preference
Pasture Grasses	82·5	0·0	∞	High
Adenanthos cygnorum	28·2	2·4	11·8	High
Casuarina spp.*	27·5	3·8	7·2	High
Opercularia vaginata	43·8	6·2	7·1	High
Acacia celastrifolia	22·5	3·8	5·9	High
Hakea spp.*	32·5	7·8	4·2	High
Gastrolobium trilobum	18·8	4·5	4·1	High
Bossiaea eriocarpa	46·2	11·8	3·9	High
Calothamnus sanguineus	21·2	6·2	3·4	High
Daviesia juncea	3·8	1·5	2·5	Moderate
Dampiera lavandulacea	16·2	6·7	2·4	Moderate
Conostylis setigera	60·2	28·8	2·1	Moderate
Epacridaceae*	6·2	3·0	2·0	Moderate
Lepidosperma spp.*	18·8	11·7	1·6	Low
Daviesia decurrens	2·5	1·6	1·5	Low
Mirbelia/Acacia	10·0	8·0	1·2	Low
Loxocarya flexuosa	21·2	17·5	1·2	Low
Xanthorrhoea preissii	5·0	4·5	1·1	Low
Gompholobium preissii	3·8	4·3	0·9	Rare
Jacksonia restioides	7·5	12·5	0·6	Rare
Glischrocaryon aureum	6·2	11·0	0·6	Rare
Dryandra spp.*	12·5	4·4	0·6	Rare
Hakea undulata	2·5	5·0	0·5	Rare
Lomandra spp.*	3·0	6·7	0·4	Rare
Hakea ambigua	1·2	3·0	0·4	Rare
Hemigenia canescens	3·8	12·5	0·3	Rare
Stypandra imbricata	2·5	9·5	0·3	Rare
Phyllanthus calycinus	2·5	17·3	0·1	Rare

* Field frequencies of several species combined.

Studies on the yellow-footed rock wallaby in western New South Wales in rock outcrop areas, however, revealed that the dicotyledonous species were the dominant group in the diet of these animals (Dawson and Ellis 1979). In good vegetational conditions the largest component of the diet was composed of the small herbaceous ephemeral forbs. During drought conditions, the monocotyledons became a more important dietary component.

In our study, the proportion of monocotyledons to dicotyledons in the diet was nearly equal to the proportions in the habitat, although the preferences here also seem to make the monocotyledons slightly more favoured in the diets than in field sample values. It is apparent, however, that the western grey kangaroo in the Yalambee region is more of a browser than its eastern counterparts because a large percentage of the shrubby dicotyledons are included as dietary constituents.

Notable among the dicotyledons consumed were the legumes, *Bossiaea eriocarpa*, *Acacia celastrifolia*, *Gastrolobium* sp., *Mirbelia/Acacia*, *Jacksonia restioides*, *Daviesia juncea*, and *Gompholobium preissii*. *Casuarina* sp., also a species known to have symbiotic nitrogen fixation capacity, was also common in the dietary components. Although the nitrogen levels of the leaves of these taxa were not analyzed in this study, the hypothesis that the kangaroo may be showing a preference to these species because of the added nitrogen content is a strong possibility. Other constitutents of actively growing plants such as Ca, P, K and moisture may also influence kangaroo preference.

Also notable, although not major components of the diet, were *Gastrolobium* spp., *Stypandra imbricata* and *Glischrocaryon aureum*, three species known to poison domestic stock (Gardner and Bennett 1956). The western grey kangaroo and other native mammals from the south-west of Western Australia have the ability to detoxify the secondary plant compounds found in species of *Gastrolobium* and *Oxylobium* (Oliver *et al.* 1977). It would not be surprising, therefore, to discover the western grey kangaroos also have the ability to tolerate the toxins produced by *Stypandra imbricata* and *Glischrocaryon aureum*.

The diet of the western grey kangaroo at the Yalanbee Experimental Station had a seasonality related to the greater availability of the pasture grasses following the first winter rains. The pasture grasses, however, were still an important constituent of the diet during the drought period of summer when the amount of edible material on the pasture areas was limited. Although annual species showed signs of grazing in the granite outcrop areas, no fragments of these ephemerals appeared in the faecal sample preparations. This may be because the annuals are only a minor component in the diet and the sampling procedure was not extensive enough to detect these species, or that fragments of these herbaceous species did not survive the digestive system of the kangaroo or the process of preparation of the faeces for analysis.

Although the determination of the reasons for the seasonal change in diet was beyond the scope of the current study, the seasonal switch to a preponderance of pasture plants and other ephemerals may be due to their greater nutritional quality. Storr (1964) observed seasonal fluctuations in the quality of the forage available to the Quokka (*Setonix brachyurus* Quoy and Gaimard) on Rottnest Island with respect to nitrogen. During summer and autumn there was a lower level of nitrogen available in grasses and shrubs compared to winter, when these plants would be actively growing. Ealey and Main (1967) observed that rainfall induced new seasonal growth which was high in nitrogen content.

An interesting point also is why the kangraoo still consumes a relatively large amount of the hard, sclerophyllous vegetation when there appears to be other, seemingly more edible, plant material available. This could be that abrupt changes in diet may have severe effects on the micro-fauna of the pseudo-rumen digestive system (Hume 1978) and the continued consumption of native sclerophylls is for roughage to balance the large quantity of soft ephemerals consumed after the onset of the rainy season.

There was little difference in species composition of the faeces from different sites. Also, there were pasture grasses in the faeces from both native vegetation sites as well as in faeces from the pasture areas. It is apparent that considerable movement of the animals takes place. This is also emphasized by the presence of *Opercularia vaginata* in faecal collections from all areas, despite being nearly restricted to the granite outcrop areas of the north

True quantification of the diet of the grey kangaroo at Yalanbee Experimental Station will require a greater understanding of the effects the kangaroo digestive system has on the plant epidermal tissue. Crocker (1959) emphasises that although survival of the leaf cuticle in the faeces of sheep was related to cuticle thickness, some of the diagnostic characters of the thinnest cuticles were completely obliterated during digestion. Slater and Jones (1971) showed that clover fed to sheep may be undetectable in the faeces. Storr (1961) in his studies of diet of the Quokka found there was a good correlation between the relative portions of native perennial plants fed under confinement conditions and the portions of their relative cuticular area in the faeces, but had difficulty in assessing the effect of the kangaroo digestive system when annual vegetation was used because the epidermis of the annual plants did not survive the preparation technique of boiling acid. Although Prince (1976) provided some information on the digestive efficiency of the western grey kangaroo, further studies are necessary to assess the ability of this species to digest cuticular plant material.

The study reported here using faecal analyses has shown that the western grey kangaroo at the Experiment Station still consume considerable numbers of native species, even though presented with extensive areas of surrounding pasture. Further data will be required before a management programme for the numbers of kangaroo in the population can be contemplated.

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Disturbed Rb-Sr systems of the Archaean Duffer Formation, Eastern Pilbara Block, Western Australia

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Abstract

The Duffer Formation is a thick sequence of Archaean calc-alkaline felsic volcanics in the Pilbara Block. A zircon U-Pb age of 3 453 ± 16 Ma has recently been obtained from this unit (Pidgeon 1978a). However, most Duffer Formation volcanics have been altered and their Rb-Sr whole-rock systems disturbed, indicating ages of between 3 000 and 3 100 Ma. It is likely that a metamorphic event resulted in local isotopic homogenization of Sr at this time.

In this study detailed sampling and description of typical units within the Duffer Formation was carried out to enable the recognition of the least altered lithologies. Samples from McPhee Creek do not define a single isochron but seven samples give an age of 3 018 ± 75 Ma and an initial $^{87}Sr/^{86}Sr$ ratio of 0.701 5 ± 0.000 7, whereas samples from Spinaway Creek define an isochron of age 3 063 ± 114 Ma and initial ratio 0.703 0 ± 0.000 7. However five "least altered" volcanics from McPhee Creek gives an age of 3 471 ± 125 Ma and an initial ratio of 0.699 8 ± 0.000 9. This initial ratio indicates that Duffer Formation magmas were derived from a source with a mantle-like Sr isotopic composition.

Introduction

The origin of early Archaean felsic volcanics is of primary importance to the understanding of Archaean crustal evolution. In many areas of modern felsic igneous activity Rb-Sr trace element and isotopic data provide useful petrogenetic evidence. Unfortunately the mobility of Rb and Sr during hydrous alteration and low grade metamorphism frustrates the interpretation of data from many Precambrian volcanic terrains (e.g. Allsopp *et al.* 1968, Page 1978). This paper presents Rb-Sr whole-rock data obtained during a study of the Duffer Formation, an early Archaean sequence of calc-akaline felsic volcanics in the eastern Pilbara Block (Barley 1980, 1981a).

Recently a zircon U-Pb age of 3 453 ± 16 Ma (Pidgeon 1978a) and galena Pb model ages of between 3 400 and 3 500 Ma (Sangster and Brook 1977, Richards *et al.* 1981) have been obtained from units within the Duffer Formation. However, previous Rb-Sr whole-rock isotopic studies (Pidgeon 1978a, Jahn *et al.* 1981) indicate that post-magmatic alteration processes have involved widespread mobility of Rb and Sr and disturbance of Rb-Sr whole-rock systems. This is reflected by considerable scatter on isochron diagrams (plots of $^{87}Sr/^{86}Sr$ *vs* $^{87}Rb/^{86}Sr$), and regression analyses which indicate ages which are younger than those obtained from zircon and galena studies. Such "isochrons" possess anomalous initial $^{87}Sr/^{86}Sr$ ratios which are of little use in petrogenetic interpretations.

In this study, detailed description and sampling of typical units within the Duffer Formation was carried out to enable the recognition of the least altered lithologies. Analyses of several samples of least altered lithologies within individual units, when compared with analyses of altered lithologies from the same unit, provide an indication of the mobility of Rb and Sr during alteration and the effect this has on Rb-Sr whole-rock systems. The zircon U-Pb age obtained by Pidgeon (1978a) is used as a reference in evaluation of the Rb-Sr whole-rock data.

Area of study

The Pilbara Block is the smaller of the two Archaean crustal blocks in Western Australia. It contains about 56 000 km^2 of granitoid-greenstone terrain, in which metamorphosed volcanic and sedimentary sequences (greenstones) form synclinoria and domes which are separated by large ovoid or elongate batholiths of granitoid and gneiss (Fig 1).

In the eastern Pilbara Block the greenstone sequence is divided into the lower, dominantly volcanic, Warrawoona Group and the overlying sedimentary rocks of the Gorge Creek Group (Hickman 1981). The Warrawoona Group consists of sequences of mafic volcanics interlayered with cherty sediments and sequences of felsic volcanics. The Duffer Formation is a distinctive unit within the Warrawoona Group, composed dominantly of andesite and dacite. It is best developed in the Marble

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Bar Belt, the McPhee Dome and the Kelly Belt (Fig. 1). Studies of the Duffer Formation in the McPhee Dome and the Kelly Belt (Barley 1980, 1981a) indicate that it forms part of a calc-alkaline volcanic association. To the west of the Corunna Downs Batholith (Fig. 1) the Duffer Formation has been dated at 3 453 ± 16 Ma by zircon U-Pb techniques (Pidgeon 1978a). Similar galena Pb model ages of between 3 400 and 3 500 Ma (Sangster and Brook 1977, Richards *et al.* 1981) for the Big Stubby and Lennons Find volcanogenic Zn-Pb sulphide deposits (Fig. 1) support the view that the zircon age is a reliable age of formation.

Metamorphism of the greenstone sequence ranges from prehnite-pumpellyite to amphibolite facies and has been accompanied by varying degrees of strain. Recrystallization of greenstones during low grade metamorphism has resulted in extensive redistribution of many elements and in the formation of mesoscopic zones of alteration or metadomains rich in secondary mineral phases (Barley 1980). Alteration involved

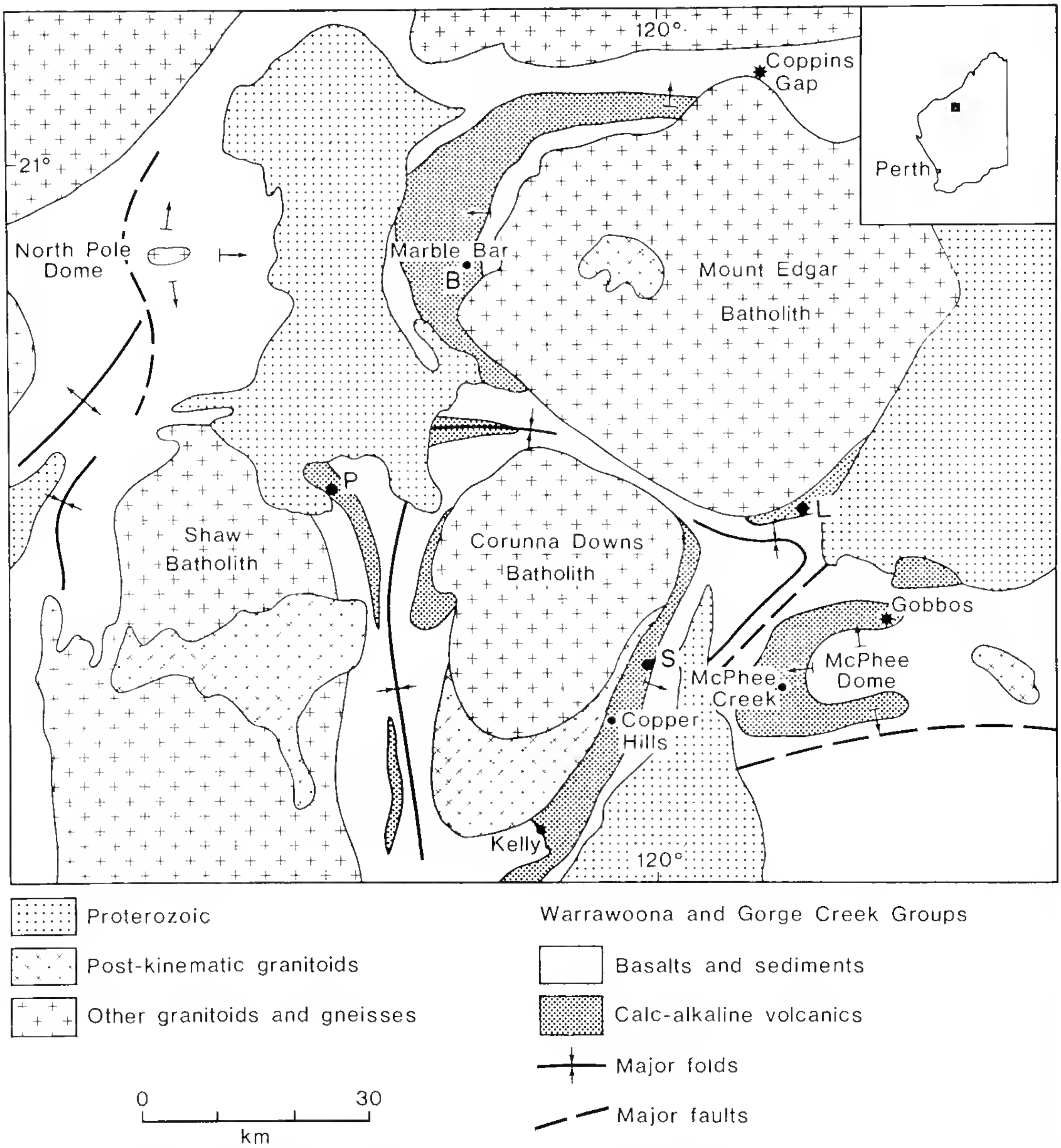

Figure 1. Geological map of part of the eastern Pilbara Block (after Hickman, 1975, Hickman and Lipple 1975) showing the locations and sample sites referred to in this paper. S = Spinaway Creek, B = Big Stubby, L = Lennons Find, P = Site of U-Pb in zircon study (Pidgeon 1978a). The calc-alkaline volcanic unit includes both the Duffer and Wyman Formations of Lipple (1975).

hydrothermal fluids and is strongest in porous rocks such as pyroclastic units and adjacent to fractures or veins. The centres of massive lava flows and some very large (>30 cm) fragments in pyroclastic units are commonly relatively unaltered, and in areas which have experienced only prehnite-pumpellyite or lower greenschist facies metamorphism may contain relict igneous mineral phases. The style of alteration is also related to the composition of parent rocks. Basaltic and andesitic rocks typically developed metadomains rich in Ca-Al silicate (epidote or pumpellyite depending on metamorphic grade), albite or chlorite and carbonate. On the other hand, Ca-Al silicate metadomains are relatively uncommon in rocks of dacitic and rhyolitic composition where more diffuse albite, sericite and sericite-carbonate alteration is prevalent. Heterogeneous alteration of this type is common in sequences of low grade metavolcanics (Smith 1968, Jolly 1980) and is thought to have occurred during burial. In the eastern Pilbara metadomains can be recognized in greenstones which have subsequently been deformed and metamorphosed to medium or high metamorphic grade (Barley 1981b).

Analytical methods

Depending on grain size, between 0.5 and 1.5 kg of each sample was crushed and approximately 200 g reduced to —200 mesh using a tungsten carbide mill. The experimental procedure for Rb-Sr analysis used in this laboratory are described by Lewis *et al.* (1975) and de Laeter and Abercrombie (1970). The value of ^{87}Sr/^{86}Sr for the NBS 987 standard measured during this study was 0.710 2 ± 0.000 1, normalized to a ^{88}Sr/^{86}Sr value of 8.375 2. The value of 1.42 x 10^{-11} yr^{-1} was used for the decay constant of ^{87}Rb. Rb-Sr data are given in Tables 1 and 2. All errors are at the 95 per cent (2σ) confidence limits. Regression analyses of the data were carried out using the program of McIntyre *et al.* (1966).

Table 1

Average Rb and Sr concentrations of least altered volcanics McPhee Dome and Kelly Belt.

	Mafic volcanics (Salgash Subgroup)	Felsic volcanics (Duffer Formation)
No. of samples	37	21
Mean Rb (ppm)	8	32
Range of Rb values (ppm)	1 to 35	4 to 73
Mean Sr (ppm)	113	301
Range of Sr values (ppm)	25 to 340	140 to 563
Average Rb/Sr ratio	0·06	0·11

A method of sampling altered volcanic sequences developed by R. E. Smith and co-workers (Smith 1968, Jolly 1980), which allows, evaluation of element movement during alteration has been used in this study. Alteration patterns in individual units were determined in the field and samples of each type of metadomain were taken, examined in thin section and classified on the basis of their secondary mineralogy (c.f. following discussion and Table 2).

As no samples which completely retained their original igneous mineralogy were found the following criteria (based on the examination of over 200 thin sections) were used when selecting samples of least altered metadomains for analysis:

1) that recognizable igneous textures are well preserved,
2) that secondary mineral phases are restricted to recognizable pseudomorphs after igneous minerals and that secondary mineral assemblages represent the approximate chemical composition of the igneous minerals replaced,
3) that samples contain no monomineralic aggregates of secondary minerals (e.g. epidote metadomains) and were collected as far as possible from inhomogeneities in outcrop, and
4) that samples contain no veins or cavities (e.g. amygdales) and contain less than 2% carbonate (visual estimate).

Where several samples classified as least altered metadomains from a single unit have been analysed, they show little variation in major and trace element contents. The assumption that the concentrations of most elements in least altered metadomains approximate original igneous compositions is also supported by smooth and generally tightly clustered trends on variation diagrams which are consistant with observed petrographic trends (Barley 1980).

For the purpose of this study the Duffer Formation was sampled at McPhee Creek in the McPhee Dome and at Spinaway Creek in the Kelly Belt (Fig. 1). Precise sample locations, descriptions of individual samples and major and trace element analyses are presented by Barley (1980).

Most of the McPhee Creek samples were taken from an outcrop of massive dacite. This unit is grey with diffuse patches (up to 20 cm in diameter) of pink, yellow and dark green coloured metadacite.

The grey metadomains are apparently least altered and show excellent preservation of igneous tectures with phenocrysts of plagioclase (some relict andesine-oligoclase) actinolite (replacing original pyroxene) and rare embayed quartz in a felted groundmass now composed of albite and epidote with minor chlorite and opaque oxides. Samples 86408, 86412 and 86426 are from grey least altered metadomains.

The contacts between grey and pink metadomains are generally quite diffuse (over 2 to 5 cm) and large areas of outcrop have a mottled grey and pink appearance. Pink metadomains contain abundant albite, sericite and carbonate, often partially retaining the textures and mineral assemblages evident in grey metadomains. Abundant carbonate (up to 10%) gives the pink metadomains their distinctive colour. Pink metadomains are enriched in Si, Al, K, Na and Rb relative to grey metadomains and are generally depleted in most other elements. Samples 86418 and 86419 are from pink albite and sericite-rich metadomains.

Yellow metadomains are more sharply defined with mineralogy and texture changing within less than a centimetre. The yellow metadomains are characterized by saccharoidal aggregates of epidote with minor quartz and carbonate. Original igneous

Table 2

Rb-Sr analytical data for Duffer Formation samples

(i) *McPhee Creek*

Sample	Rb (ppm)	Sr (ppm)	Rb/Sr	$^{87}Rb/^{86}Sr$	$^{87}Sr/^{86}Sr$	Sample Type
86424	13	340	0·040 ± 0·001	0·115 ± 0·002	0·70721 ± 0·00051	dacite, yellow metadomain
86435	17	230	0·070 ± 0·002	0·202 ± 0·005	0·71025 ± 0·00012	basalt, least altered metadomain
86412	14	183	0·084 ± 0·001	0·243 ± 0·003	0·71181 ± 0·00009	dacite, least altered metadomain
86408	35	330	0·104 ± 0·002	0·300 ± 0·006	0·71479 ± 0·00022	dacite, least altered metadomain
86409	43	240	0·185 ± 0·003	0·535 ± 0·008	0·72531 ± 0·00025	dacite, yellow metadomain
86426	73	300	0·244 ± 0·004	0·706 ± 0·009	0·73506 ± 0·00018	dacite, least altered metadomain
86413	48	147	0·331 ± 0·003	0·960 ± 0·01	0·74849 ± 0·00019	andesite, least altered metadomain
86419	125	290	0·435 ± 0·008	1·26 ± 0·01	0·75658 ± 0·00031	dacite, pink metadomain
86418	125	280	0·445 ± 0·008	1·29 ± 0·01	0·75815 ± 0·00033	dacite, pink metadomain

(ii) *Spinaway Creek*

Sample	Rb (ppm)	Sr (ppm)	Rb/Sr	$^{87}Rb/^{86}Sr$	$^{87}Sr/^{86}Sr$	Sample Type
86456	1·4	195	0·007 ± 0·0002	0·020 ± 0·0005	0·70378 ± 0·00015	basalt, least altered metadomain
86400	35	515	0·067 ± 0·0008	0·194 ± 0·0002	0·71182 ± 0·00019	dacite, least altered metadomain
86363	27	320	0·083 ± 0·001	0·240 ± 0·003	0·71398 ± 0·00016	dacite, least altered metadomain
86402	53	295	0·180 ± 0·002	0·521 ± 0·006	0·72609 ± 0·00021	dacite, least altered metadomain
86405	63	340	0·184 ± 0·002	0·532 ± 0·006	0·72628 ± 0·00025	dacite, least altered metadomain
86407	68	290	0·236 ± 0·003	0·684 ± 0·008	0·73375 ± 0·00022	dacite, least altered metadomain

NOTE: The Rb and Sr concentrations and Rb/Sr ratios have been determined by X-ray Fluorescence Spectrometry. We believe that the values are accurate to ± 5%. The Rb/Sr values do not correspond exactly with the ratios that would be derived from the separate Rb and Sr values listed.

textures are often completely destroyed. Small white patches (1 cm) within metadomains are rich in prehnite. Yellow metadomains are strongly enriched in Ca and depleted in most other elements with the exception of Al and Fe. Samples 86409 and 86424 are from grey metadomains which contain small (up to 2 cm) irregular yellow epidote-rich metadomains.

Sample 86413 is a grey metadomain from an outcrop of massive andesite and sample 86435 a relatively unaltered basalt from the Duffer Formation in McPhee Creek.

The Spinaway Creek samples were taken from the largest fragments (30-50 cm in diameter) in a subaqueous pyroclastic unit (described in Barley *et al.* 1979). With the exception of sample 86456 which is a least altered basalt from a unit overlying the Duffer Formation, all samples are dacites from grey metadomains with textures and mineralogies which are similar to those observed in least altered samples from McPhee Creek.

Results and discussion

Rb and Sr concentrations of volcanics in the McPhee Dome and Kelly Belt (Table 1) are similar to those from other Archaean volcanic sequences (e.g. Hallberg 1972, Hallberg *et al.* 1976, Jahn *et al.* 1974, Arth and Hanson 1975, Hawkesworth *et al.* 1975). Least altered Duffer Formation andesites and dacites have Rb contents which range from 4 to 73 ppm (mean 32 ppm) and Sr contents which range from 140 to 563 ppm (mean 301 ppm) with a mean Rb/Sr ratio of 0.11. Rb-Sr whole-rock data are given in Table 2.

Samples from McPhee Creek do not define a single isochron (Figure 2). Seven samples, including the altered metadomains, form a linear array with MSWD = 1.9. A model 3 isochron fit to these data indicates an age of 3 018 ± 75 Ma with an initial $^{87}Sr/^{86}Sr$ ratio of 0.701 5 ± 0.000 7. The five least altered samples give an age of 3 471 ± 125 Ma, an initial ratio of 0.699 8 ± 0.000 9 with a MSWD of 0.92 This age is similar to that obtained from a zircon U-Pb study of the Duffer Formation by Pidgeon (1978a). The initial ratio of 0.699 8 is close to that obtained from other suites of Archaean volcanics and to the value believed to be characteristic of the upper mantle during the early Archaean, (Jahn and Shih 1974, Moorbath 1975, Hart and Brooks 1977). Magmas erupted with initial $^{87}Sr/^{86}Sr$ ratios close to 0.700 0 at this time could have been derived from the upper mantle or by remelting of a short-lived source of low Rb/Sr ratio (e.g. older mafic or ultramafic volcanics). This initial ratio together with the low Rb/Sr ratio of 0.11 preclude derivation of the Duffer Formation magmas by remelting of older sialic crust. Other major and trace element data (Barley 1980) provide objections to mafic or ultramafic eclogite or amphibolite melting hypotheses (Jahn *et al.* 1981),

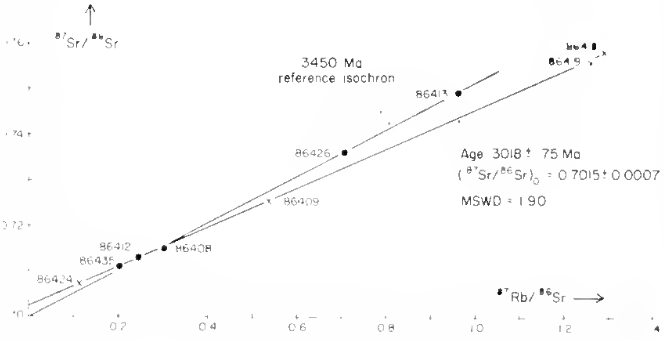

Figure 2.—$^{87}Sr/^{86}Sr$ *vs* $^{87}Rb/^{86}Sr$ diagram for samples from McPhee Creek. ● = least altered sample. x = altered sample.

indicating that a process involving fractionation of a mantle-derived mafic parent magma is best able to explain the origin of this suite of felsic volcanics.

Samples from Spinaway Creek (Table 2 and Fig. 3), define an isochron with an MSWD = 0.88 to give an age of 3 063 ± 114 Ma together with an initial $^{87}Sr/^{86}Sr$ ratio of 0.703 0 ± 0.000 7. It is likely that the "secondary isochrons" from McPhee Creek and Spinaway Creek with ages of 3 018 ± 75 Ma and 3 063 ± 114 Ma respectively, are the result of local isotopic homogenization of Sr.

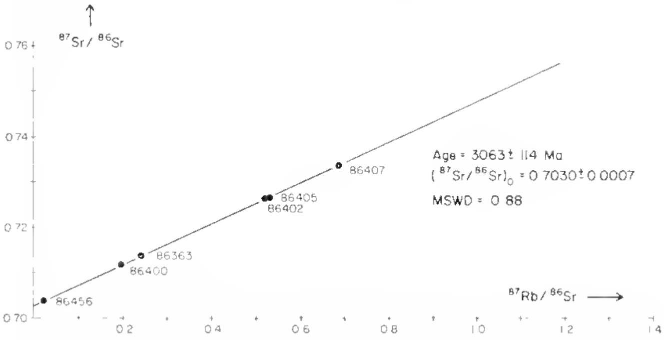

Figure 3.—$^{87}Sr/^{86}Sr$ *vs* $^{87}Rb/^{86}Sr$ diagram for samples from Spinaway Creek.

The Rb-Sr whole-rock systems of many granites and gneisses in the eastern Pilbara also appear to have been disturbed, and commonly indicate ages in the range 2 900 to 3 100 Ma (de Laeter and Blockley 1972, de Laeter *et al.* 1975, Pidgeon 1978b, Cooper *et al.* 1980).

The secondary isochron from McPhee Creek (Fig. 2) includes altered samples from pink sericite-rich metadomains which have anomalously high Rb contents (125 ppm) and Rb/Sr ratios. This observation suggests that the secondary isochrons may have resulted from either:

1. Sr isotopic homogenization during metamorphism and alteration which involved the formation of metadomains or
2. Sr isotopic homogenization (during metamorphism between 3 000 and 3 100 Ma ago) along ^{87}Sr abundance gradients generated by ageing in rocks which had previously been altered (e.g. Cameron *et al.* 1981).

However, because the processes capable of modifying Rb-Sr whole-rock systems are complex and not well understood, the geological significance of these secondary isochrons remains uncertain.

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The harzburgite member of an ultramafic body in granulites, Lake Kondinin, Western Australia

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Abstract

An ultramafic body is enclosed in granulite facies metamorphic rocks, and is composed of lherzolite and harzburgite units. The harzburgite and some associated strongly feldspathic rocks are discussed in this paper. Their petrography is described, and chemical analyses of rocks and their constituent minerals are presented. The harzburgite appears to have been emplaced during the metamorphism. Deformation of orthopyroxene grains in the harzburgite suggest that it was partly crystalline during emplacement. Its chemistry suggests that it consists of two sub-units, one rather more fractionated than the other. The feldspathic rocks form small bodies of unknown form: compared with the harzburgite, they are rich in Al, Ca, Na, and, elements that are not easily accommodated in the lattices of the harzburgite minerals. The feldspathic rocks may represent either a late stage "pegmatitic" phase of the harzburgite, or be the result of an alkali metasomatism induced by later granitoid intrusive activity.

Introduction

This report further explores the theme of the author's earlier paper (Morgan 1982) concerning the emplacement of ultramafic material during high-grade metamorphism, and the retention of relic igneous structures after crystallization during the metamorphism.

Harzburgite, together with very minor bodies of plagioclase-rich rocks, are part of an ultramafic complex emplaced in high-grade Archaean gneisses (Morgan 1982), 3 km north of the Corrigin-Kondinin road, 217 km east-south-east of Perth, Western Australia (Fig. 1). The complex occurs mainly beneath a salt lake. Only very poor exposures can be seen on the western shore of the lake where, during the late 1960's, the Elecrolytic Zinc Company drilled four holes into the ultramafic body. This report results from a study of diamond drill cores very kindly made available to the author by the company. The locations of the drill holes are shown in Figure 1.

In the sequence exposed by drilling (Fig. 2), harzburgite occurs "down-hole" from the felsic gneiss exposed in DDH C2 and C4, and "up-hole" from lherzolite exposed in DDH C4 and C5. The feldspathic rocks form small bodies of unknown form within the harzburgite, and consist of an anorthosite and two magnetitebiotite andesinites. As will be discussed in a later section, the harzburgite is considered to have been emplaced after the lherzolite described by Morgan (1982).

The harzburgite unit

Petrographic study of the cores of DDH C3, C4, and C5 supplemented by rock and mineral analyses, shows that the harzburgite consists of two sub-units, megacrystic harzburgite, and lenticular-textured harzburgite. Close to its contact with the lherzolite (Fig. 2), the magacrystic harzburgite has a textural variant, referred to as radial pyroxene harzburgite. DDH C2 was not examined, due to lack of time and facilities.

Petrography

Minerologically, the harzburgite consists of olivine, orthopyroxene, magnetite, and minor quantities of phlogopite. Averages of modal analyses from each of the sub-units are shown in Table 1. Modal analyses of individual samples are considered meaningless and not tabulated, because of the irregular distribution through the core of orthopyroxene megacrysts and lenticular aggregates.

Serpentinization of both olivine and orthopyroxene is almost complete in DDH C3. The original mineralogy can, however, be easily deduced from the textural and pseudomorphous appearance of the serpentine. In DDH C4 and C5, serpentinization affects between 20% and 80% of the samples examined. In the uppermost 80 m to 90 m of all the cores, serpentinized harzburgite is very strongly silicified and ferruginized.

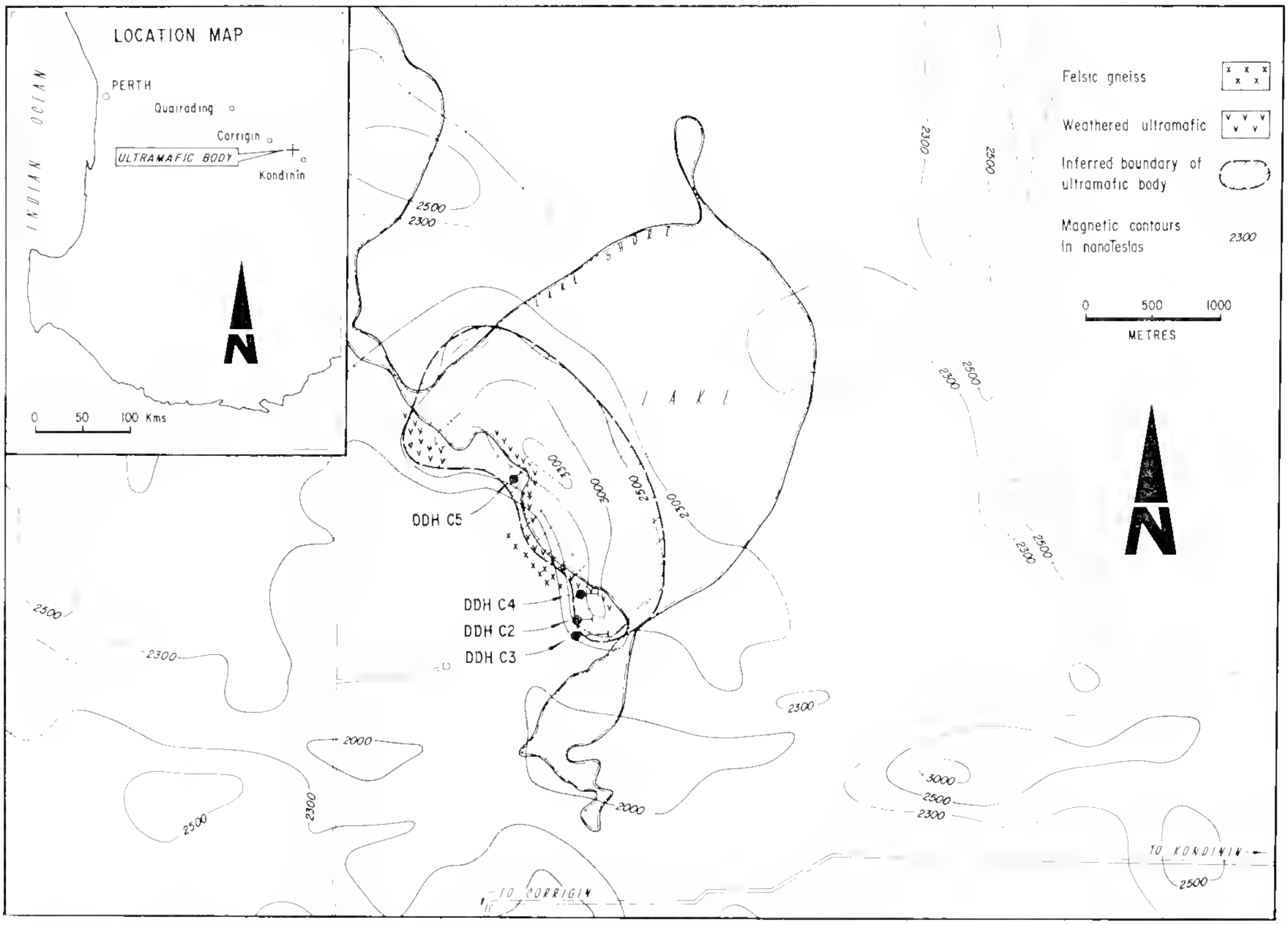

Figure 1.—Simplified aeromagnetic anomaly map of the ultramafic near Lake Kondinin. Reproduced by permission of the Electrolytic Zinc Co. of Australasia. *Inset*: Location map, South Western Australia.

Megacrystic harzburgite.

The extent of the magacrystic harzburgite is shown in Figure 2. In this rock, megacrysts of orthopyroxene, ranging up to 20 mm long, are enclosed in a matrix of polygonal olivine and orthopyroxene grains that have an average diameter of 1 mm. In the southernmost drill hole (C3) the megacrysts are euhedral prismatic, and have a preferred orientation. Although they are almost completely serpentinized, inset relics of orthopyroxene in any one megacryst are in complete optical continuity, indicating that they are unstrained. Relics of olivine in the serpentinized matrix likewise show no evidence of deformation.

However, in DDH C4 and C5, the orthopyroxene megacrysts are commonly strained, with mosaic substructure and, more rarely, kink-banding. Very often they are polygonized to aggregated of strain-free grains on their margins. Particularly in DDH C5—the northernmost hole—the megacrysts tend to be almost completely polygonized, with the constituent grains of the aggregates showing a preferred orientation. In the matrices of these rocks, olivine and orthopyroxene are almost entirely unstrained. Where not obscured by serpentinization, the matrix texture is polygonal, with the grains having curvilinear to straight boundaries meeting in triple points. Here and there, incomplete crystallization equilibrium is suggested by sub-amoeboid grain boundaries.

Magnetite occurs as granular to sub-amoeboid grains, 0.2 to 1 mm in diameter. Phlogopite, where it occurs, forms subhedral, nearly colourless books that tend to have a preferred orientation parallel to that of the orthopyroxene megacrysts.

Table 1

Harzburgite Modal Analyses

	Megacrystic	Radial Pyroxene	Lenticular	Average
Olivine . .	67·7	72·2	69·3	69·7
Orthopyroxene	24·5	21·8	20·5	27·3
Magnetite	5·8	3·9	5·9	5·2

Radial pyroxene harzburgite is a textural variant of megacrystic harzburgite, because they are geochemically similar to each other, whereas the lenticular-textures harzburgite shows significant differences in both composition and texture. The radial pyroxene harzburgite is adjacent to the contact of harzburgite with lherzolite in DDH C4 and C5. It contains sub-radial growths of orthopyroxene measuring up to 15 cm across. Within the growths, sub-radiating, thin orthopyroxene grains are elongated nearly parallel to their crystallographic c-axes, their grain boundaries being finely sutured. Some mosaic sub-structure is seen in places, but otherwise there is little evidence of deformation. The associated olivine is strongly serpentinized; relic grains suggest that their sizes range up to 10 mm, that they have an amoeboid shape, and that they are entirely unstrained.

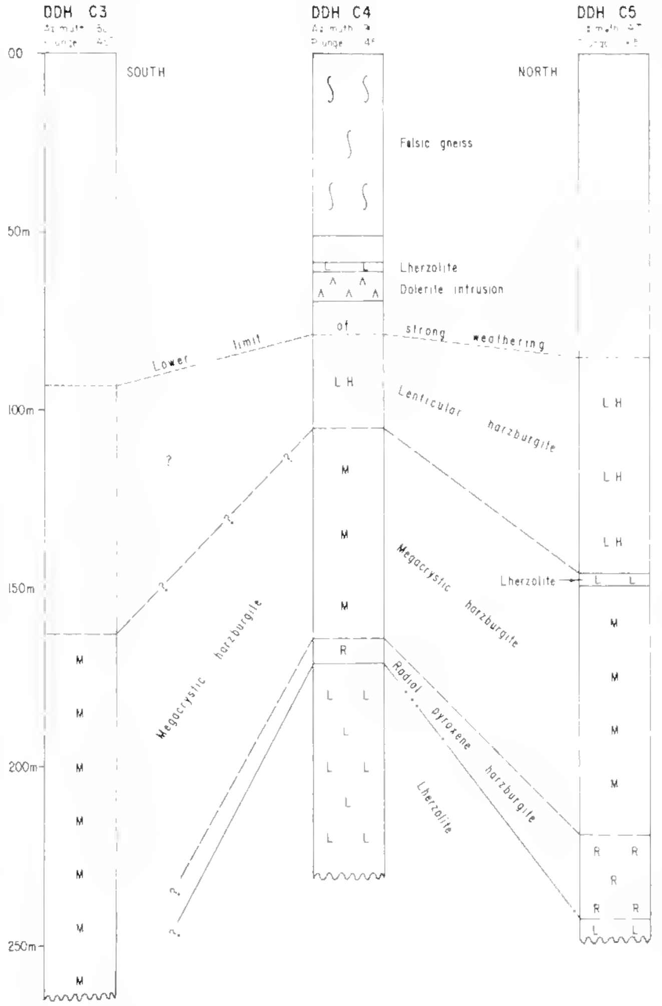

Figure 2.—Schematic diagram, from diamond drill hole data, of the relationships between the megacrystic, lenticular, and radial pyroxene harzburgite.

Lenticular-textured harzburgite.

The core samples display a lenticular-banded appearance. The lenticles—composed of orthopyroxene—measure up to 1.5 cm wide by 4 cm long, and are enclosed in an olivine-rich matrix. In some cores, particularly around 100 m depth in DDH C5, the lenses form tight, isoclinal folds.

In section, the lenses are seen to consist of aggregates of polygonal orthopyroxene grains showing no strain whatsoever. The matrix olivine, where it is not strongly serpentinized, is also polygonal and strain-free. The very sparse phlogopite flakes have a preferred orientation parallel to the lenses.

Chemistry

Major and some minor element analyses of five samples of harzburgite are presented in Table 2. Each analysis was made from a representative sample taken from 1.5 m lengths of core, in an attempt to balance out the irregular distribution of orthopyroxene.

The harzburgite samples consist essentially of SiO_2, iron oxides, and MgO, with only very minor quantities of the other oxides when compared with ultramafics in alpine-type bodies (eg. Loney *et al.* 1971), high temperature peridotites (eg. Green 1964), ultramafic nodules (eg. Carswell and Dawson 1970), komatiitic peridotites (eg. Neshitt and Sun 1976), and the ultramafic portions of layered gabbroic intrusives (eg. Hess 1960, Hall 1932).

There are differences between the lenticular-textured and magacrystic sub-units of the harzburgite. The lenticular-textured harzburgite is poorer in Cr, Ni, Co, V, and Zn. However, the most significant difference is in the Fe/Mg ratios. In the megacrystic sub-unit, these range between 0.55 and 0.69, distinctly higher than the value of 0.45 in the lenticular harzburgite. The differences suggest that the sub-units represent two different—though possibly related—intrusives, one of which (the megacrystic sub-unit) is rather more fractionated than the other.

The least differentiated members of the lherzolite unit's cycles all contain more Al_2O_3 and CaO (Morgan 1982). Their Fe/Mg ratios (0.57-0.70), however, fall within the range of the megacrystic harzburgite.

Mineral chemistry

Electron microprobe analyses of olivine, orthopyroxene, and magnetite are presented in Tables 3, 4, and 5 respectively. All analyses were carried out by the author with the W.A. Institute of Technology's Seimens Etec Microprobe analyser, using an accelerating voltage of 20 kV, a specimen current of 0.25×10^{-7} amps, and a 1 - 2 um beam diameter. X-ray intensities were converted to oxide percentages using the Magic IV programme.

Olivine (Table 3)

The Mg/(Mg + Fe) ratios range between 0.90 and 0.95, i.e., within the range of olivines from alpine-type ultramafics, and distinctly more Mg-rich than those from the lherzolite unit (Morgan 1982), as will be seen from Figure 3, or from the layered intrusives (eg. Green 1964, Cameron 1978). Olivines from the lenticular-textured harzburgite contain more Mg than those from the megacrystic sub-unit.

Table 2

Analyses and Norms of the harzburgites

	Megacrystic Harzburgite			Lenticular-textured Harzburgite	
Drill Hole	C4	C4	C4	C4	C5
Depth	169·3m	156·4m	125·9m	101·7m	115·8m
SiO_2	36·87	38·93	40·58	41·05	36·05
TiO_2	0·04	0·07	0·04	0·06	0·06
Al_2O_3	0·37	0·38	0·32	0·40	0·64
Fe_2O_3	7·98	11·71	8·88	6·77	9·04
Cr_2O_3	0·95	N.D.	1·07	0·83	0·84
FeO	7·49	8·58	7·09	6·51	4·81
MnO	0·22	0·18	0·20	0·19	0·28
MgO	34·12	36·03	32·33	35·95	37·06
NiO	0·29	N.D.	0·29	0·22	0·25
CaO	0·30	0·13	0·18	0·24	0·03
Na_2O	0·04	0·03	0·06	0·05	0·03
K_2O	0·04	0·05	0·03	0·09	0·01
P_2O_5	0·002	N.D.	0·01	0·01	0·01
Loss	10·77	3·60	8·11	6·85	11·00
Total	99·48	99·69	99·19	99·21	100·11
Co	248	N.D.	249	201	217
Cr	6 510	N.D.	7 348	5 678	5 722
Ni	2 300	N.D.	2 250	1 700	2 000
V	23	N.D.	17	8	12
Zn	130	N.D.	135	80	75
Fe/Mg	·554	·685	·601	·451	·450
or	0·22	0·28	0·17	0·56	0·06
ab	0·37	0·26	0·52	0·42	0·26
an	0·70	0·64	0·50	0·58	0·08
C	..	0·02		....	0·45
di—					
Wo	0·33	...	0·14	0·23	....
en	0·27	...	0·11	0·19	....
fs	0·03	...	0·001	0·01	....
hy—					
en	27·76	31·74	45·74	37·24	25·82
fs	2·35	2·23	3·18	2·61	0·42
ol —					
fo	39·90	40·63	24·29	36·53	46·59
fa	3·73	3·14	1·85	2·83	0·86
il	0·08	0·14	0·08	0·12	0·12
mt	11·58	16·97	12·87	9·82	13·12
ct	1·41	.	1·57	1·23	1·23
ap	0·003		0·02	0·02	0·02
Loss	10·77	3·60	8·11	6·85	11·00
Total	99·50	99·65	99·15	99·24	100·03

Analyst: S.G.S. Australia Pty. Ltd., Perth.
N.D.—No Data

The distribution of Mg and Fe between olivines and their co-existing orthopyroxenes is fairly uniform (Fig. 3), the values of $K_D \frac{Fe/Mg\ opx}{Fe/Mg\ ol}$ having an average of 1.05 and a range of 0.9 to 1.2. The values are close to those of Morgan (1982), Frost (1975), Challis (1965), and Green (1964).

Ti, Al, Cr, Ca, Na and K are low or absent, Mn is low, and Ni shows, as one would expect, a preference for olivine over orthopyroxene.

Orthopyroxene (Table 4)

The Mg/(Fe + Mg) ratios range between 0.895 and 0.95. Like the olivines, these values are distinctly higher than those of the lherzolite unit (see Fig. 3), which range between 0.79 and 0.89. Orthopyroxenes from the lenticular-textured sub-unit are more Mg-rich than those of the megacrystic harzburgite.

The harzburgite orthopyroxenes are low in Al, Ca, Cr, and Ti, when compared with those in the lherzolite unit (Morgan, 1982), alpine (eg. Loney *et al.* 1971), nodule (eg. Boyd *et al.* 1976, Dawson *et al.* 1970), and layered intrusion harzburgites (Cameron 1978). This, of course, is a condition imposed by the host rocks, which are themselves poor in these elements.

Magnetite (Table 5)

Total iron was analysed as Fe_2O_3; Fe^{+2} and Fe^{+3} were calculated assuming ideal stoichiometry. The magnetite, like that in the lherzolite unit (Morgan 1982) is chromiferous, with Cr being concentrated in this mineral, very little being in the co-existing orthopyroxene. Al_2O_3 ranges between 0.70% and 2.18%. Al_2O_3 is very low in the harzburgite rock analyses (Table 2), but, like Cr, is concentrated in magnetite rather than in the associated silicate phases. MgO ranges between 0.4% and 4.46%; $Mg/(Mg + Fe^{+2})$ ratios tend to be rather higher in the lenticular-textured harzburgite sample when compared with those of the megacrystic sub-unit.

Table 3

Electron microprobe analysis of olivine.

Analyst: W. R. Morgan

	Megacrystic Harzburgite				Lenticular-textured Harzburgite			
				DDH C4				DDH C5
Depth	169·3 m	156·4 m	146·9 m	143·8 m	101·7 m	99·7 m	94·5 m	115·8 m
SiO_2	42·14	40·49	40·23	40·70	41·85	41·82	41·79	39·80
TiO_2	Nil	0·05	0·02	0·02	Nil	Nil	Nil	0·04
Al_2O_3	Nil	0·13	0·09	Nil	0·20	0·10	0·19	0·19
Cr_2O_3	Nil	0·01	0·03	Nil	0·05	0·06	0·01	0·01
FeO	9·35	10·21	9·37	9·09	6·92	7·36	6·43	4·47
MnO	0·25	0·21	0·19	0·23	0·19	0·20	0·14	0·27
NiO	0·56	0·49	0·32	0·33	0·30	0·52	0·49	0·44
MgO	47·10	49·11	49·37	50·05	50·95	50·06	51·38	53·75
CaO	Nil	0·01	0·01	0·02	0·03	0·01	Nil	Nil
Na_2	Nil	0·01	0·14	Nil	Nil	0·08	0·08	0·08
K_2O	Nil	Nil	Nil	Nil	Nil	Nil	0·01	0·04
Total	99·40	100·73	99·77	100·43	100·48	100·22	100·53	99·09

Numbers of ions on the basis of 4 oxygens

Si	1·034	·990	·989	·992	1·007	1·012	1·004	·968
Al	....	·004	·003		·006	·003	·005	·006
Ti	....	·001	·001	·001	..	...	.	·001
Fe	·192	·209	·193	·185	·139	·149	·129	·091
Cr	....	Tr	·001	...	·001	·002	Tr	Tr
Mn	·005	·004	·004	·005	·004	·004	·003	·006
Ni	·011	·010	·006	·006	·006	·010	·010	·009
Mg	1·723	1·789	1·809	1·818	1·827	1·805	1·840	1·947
Ca	....	Tr	Tr	·001	·001	Tr	.	.
Na	....	Tr	·007	. .	.	·004	·004	·004
K	...		...				Tr	·001
Mg	10·0	10·5	9·6	9·2	7·1	7·6	6·6	4·5
Fe	90·0	89·5	90·4	90·8	92·9	92·4	93·4	95·5
Mg/(Fe + Mg)	·900	·895	·904	·908	·929	·924	·935	·955
Fe/(Fe + Mg)	·100	·105	·096	·092	·071	·076	·066	·045
Fe/Mg	·111	·117	·107	·012	·076	·083	·070	·046

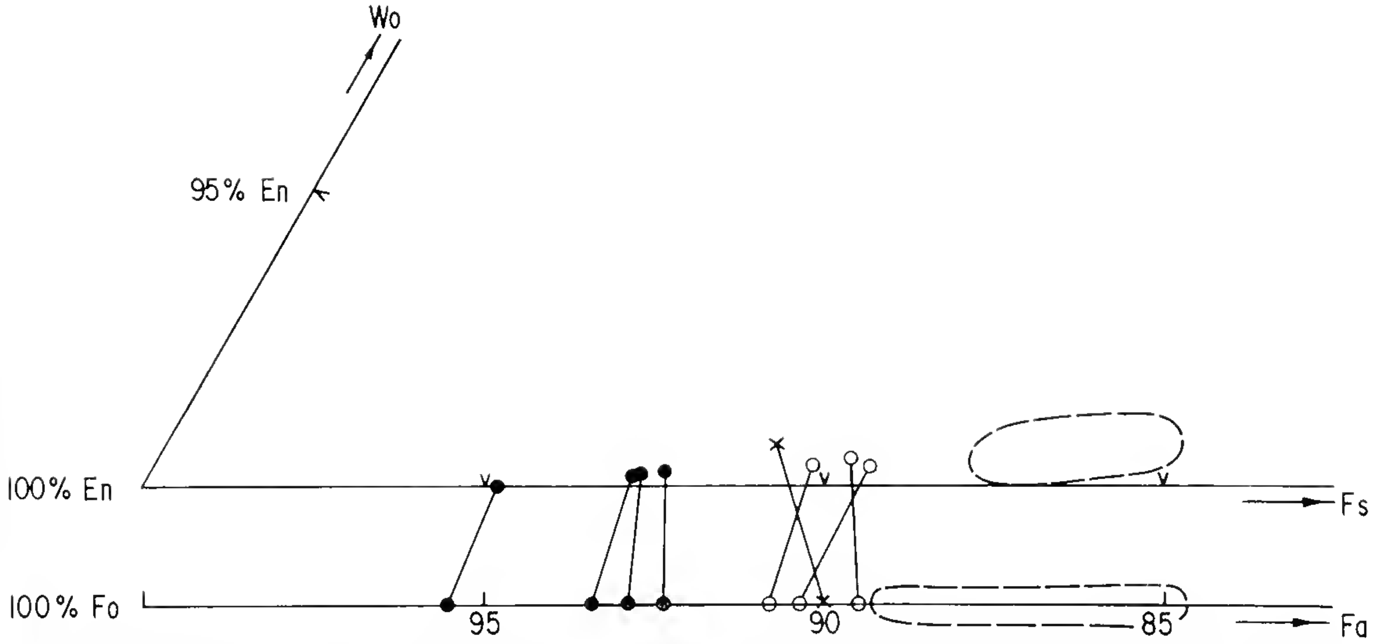

Figure 3.—Plot of co-existing olivines and orthopyroxenes. Filled Circles: lenticular harzburgites; Open Circles: megacrystic harzburgites; x: radial pyroxene harzburgite: Dashed outline areas: olivines and orthopyroxenes in the lherzolite unit (Morgan 1982).

Table 4

Electron microprobe analyses of orthopyroxene.
Analyst: W. R. Morgan

	Megacrystic Harzburgite			Lenticular-textured Harzburgite				
	DDH C4							DDH C5
Depth	169·3 m	156·4 m	146·9 m	143·8 m	101·7 m	99·7 m	94·5 m	115·8 m
SiO_2	58·27	56·69	58·84	57·04	58·23	58·39	59·35	58·38
TiO_2	Nil	0·02	0·01	0·04	0·04	Nil	0·05	0·05
Al_2O_3	0·53	0·11	0·45	0·23	0·19	0·41	0·44	0·66
Cr_2O_3	0·05	0·13	0·08	0·03	0·05	0·05	0·06	0·22
FeO	6·21	7·00	7·05	6·81	4·86	5·21	4·84	3·56
MnO	0·25	0·21	0·23	0·28	0·20	0·22	0·23	0·31
NiO	0·12	0·09	0·05	0·11	0·04	0·10	0·07	0·04
MgO	34·93	34·79	33·58	35·59	35·30	36·07	35·46	36·27
CaO	0·34	0·28	0·14	0·17	0·11	0·13	0·11	0·03
Na_2O	Nil	0·07	0·03	0·01	Nil	Nil	Nil	0·05
K_2O	Nil	0·01	Nil	0·01	Nil	Nil	Nil	0·01
Total	100·70	99·38	100·26	100·32	99·02	100·58	100·63	99·38

Numbers of ions on the basis of 6 oxygens

Depth	169·3 m	156·4 m	146·9 m	143·8 m	101·7 m	99·7 m	94·5 m	115·8 m
Si	1·993	1·997	2·019	1·969	2·009	1·989	2·013	1·997
Al^{iv}	·007	·005		·009		·011		·003
Al^{vi}	·014		·018		·008	·006	·018	·023
Ti		·001	Tr	·001	·001		·001	·001
Fe	·178	·204	·202	·197	·140	·149	·137	·101
Cr	·002	·004	·001	·001	·001	·002	·002	·006
Mn	·007	·006	·007	·008	·006	·006	·007	·009
Ni	·003	·003	·001	·003	·001	·003	·002	·001
Mg	1·780	1·808	1·717	1·831	1·815	1·832	1·793	1·837
Ca	·013	·011	·005	·006	·004	·005	·004	·001
Na		·002	·002	·001				·003
K		Tr		Tr				Tr
Mg	90·3	89·4	89·2	90·0	92·6	92·2	92·7	94·7
Fe	9·0	10·1	10·5	9·7	7·2	7·5	7·1	5·2
Ca	0·7	0·5	0·3	0·3	0·2	0·3	0·2	0·1
Mg/(Mg + Fe)	·909	·899	·895	·903	·928	·925	·929	·948
Fe/(Mg + Fe)	·091	·101	·105	·097	·072	·075	·071	·052
Fe/Mg	·100	·113	·118	·108	·077	·081	·076	·055

Table 5

Electron microprobe analyses of magnetite.
Analyst: W. R. Morgan

	Megacrystic Harzburgite			Lenticular-textured Harzburgite				
	DDH C4							DDH C5
Depth	169·3 m	156·4 m	147·5 m	143·8 m	101·7 m	99·77 m	94·5 m	115·8 m
TiO_2	0·16	0·39	0·02	0·19	0·29	0·10	0·07	0·26
Al_2O_3	2·11	1·74	0·94	0·70	1·15	1·43	0·94	2·18
Cr_2O_3	13·61	7·20	7·77	5·52	12·43	9·01	7·95	8·29
Fe_2O_3	54·69	59·96	59·65	62·62	56·17	58·88	60·47	59·72
FeO	27·62	28·04	30·13	29·07	25·60	27·68	27·04	24·38
MgO	2·80	2·21	0·40	1·29	3·59	2·31	2·61	4·46
Total	101·00	99·94	98·91	99·39	99·23	99·41	99·08	99·29

Numbers of ions on the basis of 32 oxygens

Depth	169·3 m	156·4 m	147·5 m	143·8 m	101·7 m	99·77 m	94·5 m	115·8 m
Al	·730	·616	·341	·252	·404	·507	·335	·758
Cr	3·155	1·708	1·889	1·330	2·929	2·142	1·899	1·932
Fe^{+3}	12·069	13·541	13·806	14·361	12·600	13·323	13·747	13·252
Ti	·035	·088	·004	·046	·063	·023	·016	·058
Mg	1·223	·988	·185	·586	1·594	1·035	1·175	1·960
Fe^{+2}	6·777	7·038	7·751	7·409	6·382	6·962	6·831	6·012

The feldspathic rocks

There are three very minor occurrences of unusual plagioclase-rich rocks within the harzburgite unit. All are intersected by DDH C5. The occurrences are:

216.3 m-215.7 m	Biotite-magnetite-andesine rock.
187.7 m-187.2 m	Biotite-andesine rock.
157.3 m-157.4 m	Spinel-bearing anorthite rock.

Structure and relationships

A few points can be noted:

(1) There is strong alteration of the harzburgite on both sides of the anorthite rock. Such alteration occurs only on the "down-hole" side of the andesine rocks. The alteration takes the form of talcose, serpentinic material that provided very little core recovery.

(2) Internally, the anorthite body is the most simple: a thin zone of anorthite rock is bounded on the "up-hole" side only by a selvage of phlogopite.

(3) The two andesinic rocks are more complex. That at 187 m has a bilateral zonation: a central zone of soft clay-sericite material is bounded either side by successive zones of biotite, biotite-plagioclase, and biotite. The occurrence at 216 m is rather less symmetrical. A central zone of incompletely recovered micaceous rock has zones of magnetite and biotite-magnetite-andesine rock either side of it. The "uphole" margin is composed of magnetite-biotite rock, and the "down-hole" side of a biotite-sericite rock which may represent a hydrothermally altered biotite-plagioclase rock.

(4) The form of the bodies is not known. Prider (1945) reported hypersthene andesine rock forming a segregation within hornblende hypersthenite at the Dangin railway cutting, 80 km north-north-west of Lake Kondinin. However, whether the Lake Kondinin occurrences are segregations or intrusive bodies is difficult to tell from the core samples available.

Petrography

Anorthite rock: 157 m. The upper marginal zone consists of crumpled, nearly colourless flakes of phlogopite that show a rough preferred orientation parallel to the contact with the anorthite rock. Accessory zircon is present.

The plagioclase rock consists almost entirely of polygonal grains of anorthite ranging between 0.1 and 1.5 mm in size. Very minor quantities of weakly pleochroic biotite are present. Irregularly zoned green to brown spinel forms grains about 0.2 mm across the triple junctions of plagioclase grains. Also present are very thin stump prisms of apatite, and grains of a metamict mineral that perhaps represents zircon.

Biotite-andesine rock: 187.2-187.7 m. The micaceous zones are composed of very pale brown, intergrown mica flakes measuring up to 3 mm across. The flakes are strongly contorted and the edges are crumpled and even fragmented.

The two zones of biotite-andesine rock are very similar. Plagioclase forms angular to amoeboid grains ranging between 0.5 and 10 mm across; in a few grains, the twin lamellae are slightly strained. Biotite is pleochroic from pale-brown to mud-brown, and forms sub-tabular to anhedral flakes that are frequently clustered, and which—particularly in the upper zone—show a preferred orientation parallel to the contacts. Accessory apatite and zircon are present.

Biotite-magnetite-andesine rock: 215.7-216.3 m The micaceous margin is very similar to that described above. The andesine rocks contain polygonal plagioclase grains 0.5 to 2 mm in size, along with amoeboid magnetite grains up to 5 mm across, and subhedral, randomly oriented books of biotite about 1 mm long. Accessory prismatic apatite and sub-rounded zircon are present.

The lowermost zone is probably heavily altered andesine rock: the plagioclase is replaced by extremely fine-grained clay minerals which occur as a matrix forming about 70% of the rock, and which encloses subhedral biotite flakes up to 1 mm long, and minor amounts of magnetite. Accessory apatite and zircon are present.

Chemistry (Table 6)

Two samples, at 215.6 m and 187.8 m—are fairly similar to each other, except that the sample at 187.8 m contains 52% SiO_2, and that at 215.5 m has 45% SiO_2; the sample from 215.6 m has 5% Fe_2O_3, a reflection of the presence of magnetite. Otherwise, these rocks have moderate to low FeO and MgO. Compared with the harzburgites, they have high Al_2O_3, CaO, Na_2O, and K_2O—in fact, those elements that are not easily accommodated in the lattices of the harzburgite minerals.

The anorthite rock at 157.3 m is particularly rich in CaO and Al_2O_3 with small amounts of MgO; all the other oxides are very low in amount.

All three samples are undersaturated, and contain nepheline in their norms.

Mineral chemistry (Table 7)

The *plagioclase* at 215.5 m and 187.8 m is andesine; that at 157.3 m is anorthite. All three contain very little K_2O. *Phlogopite*, when compared with the examples in Deer, Howie and Zussman (1962), contain rather more SiO_2, Al_2O_3, total iron oxide and Na_2O, and somewhat lower MgO and K_2O. The *spinellid* at 215.5 m is virtually pure magnetite, containing only minor quantities of Ti, Al, Cr, and Mg. That at 157.3 m is a pleonaste; it contains only minor Fe^{+3} and trace quantities of Ti and Cr.

Table 6

Analyses and norms of the anorthositic Rocks, DDH C5.
Analyst: S.G.S. Australia Pty. Ltd., Perth.

Depth	215·5 m	157·3 m	187·8 m
SiO_2	45·18	43·40	51·85
TiO_2	0·41	0·04	0·46
Al_2O_3	22·20	33·55	23·15
Fe_2O_3	5·04	0 26	0·35
Cr_2O_3	Tr	N.D.	0·02
FeO	3·67	0·45	2·53
MnO	0·05	0·01	0·02
MgO	5·04	1·72	6·54
NiO	0·03	0·01	0·04
CaO	6·18	17·03	5·85
Na_2O	4·99	0·97	5·12
K_2O	1 64	0·53	2·29
P_2O_5	0·35	0·17	0·09
Loss	2·42	1·90	1·98
Total	100·20	100·04	100·29
Ba	780	220	490
Co	46	N.D.	N.D.
Cr	27	N.D.	107
Ni	200	90	320
V	32	N.D.	< 5
Zn	10	N.D.	N.D.
Ne	4·23	2·05	5·57
or	9·68	3·12	13·52
ab	34·39	4·57	33·03
an	28·34	83·36	28·45
c	1·82	0·83	1·83
ol —			
fo	8·79	3·01	11·41
fa	1·59	0·45	2·85
il	0·77	0·08	0·88
mt	7·32	0·37	0·51
ct	...		0·02
ap	0·84	0·40	0·20
Loss	2·42	1·90	1·98
Total	100·20	100·14	100·25

Discussion

The petrogenesis of the harzburgite and the feldspathic rocks must be considered in relation to the lherzolite (Morgan 1982), because all three form parts of the same ultramafic body.

Harzurgite-lherzolite relationship

The harzburgite occurs in the drill cores, stratigraphically, above the cyclic layering in the lherzolite. Hence, it cannot be regarded as an early crystal cumulate that preceded the lherzolite.

Three features, noted from drill hole data, and from outcrop on the western lake shore, strongly suggest that the harzburgite was emplaced after the lherzolite. First, mapping along the shore line showed the presence of three bodies of lherzolite. One is in contact with the gneissic country rock, but is partly enclosed by harzburgite. The others are entirely enclosed by harzburgite. They measure from 20 m by 25 m up to 50 m by 350 m, and are elongated parallel to the contact with the gneiss. They appear to be contact remnants and rafts isolated by the intrusion of the harzburgite.

Second are the occurrences at 58 m to 61 m and 149 m to 151 m both in DDH C5 of lherzolite, enclosed within harzburgite. These, following on from the field observations just described, are thought to be rafts of lherzolite intersected by the drilling.

Table 7

Mineral analyses, feldspar rocks, DDH C5.
Analyst: W. R. Morgan

Plagioclase

Depth	157·3 m	187·8 m	215·5 m
SiO_2	44·39	57·08	58·14
Al_2O_3	35·26	26·33	25·68
Fe_2O_3	0·14	0·20	0·15
MgO	Nil	0·03	0·02
CaO	19·66	8·52	8·59
Na_2O	0·84	6·90	6·58
KO	0·01	0·02	0·06
	100·31	99·11	99·00

Biotite

Depth	157·3 m	187·8 m	215·5 m
SiO_2	40·23	44·75	41·87
TiO_2	0·34	1 91	2·17
Al_2O_3	20·75	14·69	16·71
Cr_2O_3	Nil	0·07	0·01
FeO	4·81	8·92	7·97
MnO	0·02	0·07	0·14
NiO	Nil	0·08	Nil
MgO	23·78	20·14	20·82
CaO	0·03	0·01	Nil
Na_2O	2·18	1·30	1·33
K_2O	7·10	8·20	8·19
	99·24	100·14	99·21

Spinellids

Depth	157·3 m	215·5 m
TiO_2	0·03	0·01
Al_2O_3	63·49	0·12
Cr_2O_3	0·02	0·05
Fe_2O_3	2·21	68·90
FeO	17·87	31·42
MgO	15·45	0·02
	99·07	100·52

Zircon

Depth	187·8 m
SiO_2	30·98
ZrO_2	66·21
TiO_2	0·03
Al_2O_3	1·13
Fe_2O_3	0·30
MnO	0·03
MgO	0·01
CaO	0·15
ThO_2	0·09
P_2O_5	0·07
	99·00

Number of ions

32 oxygens

	157·3 m	187·8 m	215·5 m
Si	8·202	10·330	10·481
Al	7·681	5·618	5·458
Fe^{+3}	·019	·028	·020
Mg		·008	·004
Ca	3·893	1·652	1·660
Na	·302	2·421	2·301
K	·002	·004	·013
Ab	7·2	59·4	57·9
An	92·7	40·5	41·8
Or	·1	0·1	0·3

24 oxygens

	157·3 m	187·8 m	215·5 m
Si	5·403	6·059	5·725
Al^{IV}	2·597	1·941	2·275
Al^{VI}	·688	·407	·419
Ti	·034	·195	·223
Cr		·001	·001
Fe^{+2}	·540	1·739	1·822
Mn	·002	·008	·016
Ni		·008	..
Mg	4·760	4·070	4·243
Ca	·004	·002	
Na	·568	·342	·353
K	1·217	1·419	1·428

32 oxygens

	157·3 m	215·5 m
Al	15·674	·043
Cr	·003	·012
Fe^{+3}	·348	15·987
Ti	·005	·002
Mg	4·822	·009
Fe^{+2}	3·129	8·057

16 oxygens

	187·8 m
Si	3·833
Zr	3·995
Ti	·003
Al	·165
Fe^{+3}	·028
Mn	·003
Mg	·002
Ca	·020
Th	·003
P	·007

Third, the radial pyroxene harzburgite, adjacent to the Harzburgite-lherzolite contact in DDH C4 and C5 is believed to be a contact facies, caused partly by the strain and physical disruption of near solidfied harzburgite magma during emplacement against lherzolite. It is suspected that the subradial structures of unstrained orthopyroxene evolved by recrystallization due, perhaps, to heat derived from solid, but still hot, lherzolite. This would imply that there was no great time gap between the emplacement of the lherzolite and the harzburgite.

Harzburgite-gneiss relationship

The gneissic country rocks occur at the tops of the drill cores in DDH C2 and C4. However, the contact relations exposed by the drilling are inconclusive (Morgan 1982). However, evidence from the very poor lake shore exposures show that the harzburgite intrudes the gneisses. Detailed mapping carried out by geology students from the Western Australian Institute of Technology, under the author's direction, at the north-west shore showed a trail of four bodies of andradite-salite-anorthite rock extending over 200 m within strongly serpentinized harzburgite, aligned parallel to the contact with the gneiss.

Modal and chemical analyses of this material, together with electron microprobe analyses of the constitutent minerals, are given in Table 8. From these data, it is considered that these bodies are xenoliths of calc-silicate metasedimentary rocks.

Harzburgite emplacement

The megacrystic harzburgite

In this unit, the large orthopyroxene grains show the results of considerable deformation—lattice strain, mosaic substructure, to complete polygonization—in the northerly diamond drill core (DDH C5). It could be argued that this unit was emplaced prior to tectonism, with the deformation resulting from the tectonism. However, the megacrysts in DDH C3 (the most southerly drill hole) are euhedral and unstrained, which strongly suggests that they were phenocrysts in a magma that was emplaced after tectonism. Their deformation in the northerly cores thus suggests that the ultramafic magma was crystallizing during intrusion, with the still largely liquid material in the vicinity of DDH C3 pushing northwards against partly to mostly crystallized magma in the vicinity of DDH C4 and, more particularly, DDH C5.

The lenticular-textured harzburgite

The origin of this unit is much more difficult to explain, principally because its relationship to the megacrystic harzburgite is unknown. In composition, it is rather more Mg-rich than the megacrystic harzburgite, being closer to the alpine-type ultramafics. However, the ultramafic body as a whole—including the lherzolite and the megacrystic harzburgite—is certainly not alpine-type.

An explanation that could satisfy both its textural characteristics and its more magnesian character is to regard it as an early-crystallized part of the harzburgite, chilled against the relatively cool gneisses. The zone containing the lenticles, which, in DDHC4, extends 80 m to 105 m depth, would represent deformed, mostly crystallized material dragged by the motion of the more liquid megacrystic harzburgite. The gneissic country rock, at the height of granulite metamorphism, would have had temperatures of around 760° to 900°C (Hewins 1975). A partly crystallized harzburgite magma with, say, 20% to 30% crystals, would have a temperature between 1 400-1 700°C (Ito and Kennedy 1967).

Table 8

Xenolithic calc-silicate rock: modal and chemical analyses of the rock, and chemical analyses of its constituent minerals

Rock

Mode		*Chemical	
Anorthite	53·2	SiO_2	43·3
Salite	27·1	TiO_2	1·25
Andradite	20·2	Al_2O_3	18·5
		Fe_2O_3	5·18
	100·0	FeO	3·05
		MnO	0·26
		MgO	4·25
		CaO	22·9
		Na_2O	0·36
		K_2O	0·02
		LO1	0·49
		Total	99·56

Minerals

	§Andradite	§Salite	§Anorthite
SiO_2	36·18	49·96	44·24
TiO_2	1·04	0·12	0·01
Al_2O_3	6·19	2·76	33·91
Cr_2O_3	0·08	0·01	0·01
Fe_2O_3	21·47†		0·45†
FeO		11·44‡	....
MnO	0·57	0·55	0·04
NiO	0·01	0·01	0·02
MgO	0·29	10·67	0·03
CaO	32·98	23·27	19·70
Na_2O	0·24	0·32	0·76
K_2O	Nil	0·02	0·02
Total	99·06	99·13	99·18
Numbers of ions:	24 oxygens	6 oxygens	32 oxygens
Si	5·960	1·919	8·264
Al^{iv}	0·040	0·081	7·539
Al^{vi}	1·150	0·043	...
Ti	0·139	0·004	0·002
Fe	2·635†	0·368‡	0·064†
Cr	0·098	0·001	0·002
Mn	0·792	0·018	0·007
Ni	0·001	Tr	0·003
Mg	0·710	0·611	0·008
Ca	5·822	0·958	3·961
Na	0·077	0·024	0·277
K	....	0·001	0·005

*Analyst: S.G.S. Australia Pty. Ltd. Perth. §Analyst: W. R. Morgan, W.A.I.T. †Total iron calculated as $Fe_20_3(Fe^{+3})$. ‡Total iron calculated as FeO (Fe^{+2})

However, this argument suffers because there is nothing chemically or texturally equivalent to the lenticular-textured harzburgite adjacent to the lherzolite. It may be therefore, that the lenticular-textured harburgite represents a third intrusive body, younger that the lherzolite, but whose age relationship to the megacrystic harzburgite is not known.

Interpretation of textures

The writer (Morgan 1982) discussed the petrography of the lherzolite unit in terms of metamorphic textures superimposed on relic igneous structures. In the discussions above, he has stressed the igneous emplacement of the harzburgite, using the deformation of megacrysts and other features to support his argument. Nevertheless, apart from the megacrysts, textural features of the harzburgite have a metamorphic appearance. Even in rocks where the megacrysts display strong straining and sub-mosaic structures, the matrix grains are entirely unstrained, and have curvilinear to straight-line boundaries, i.e., the grain shapes range from amoeboid to polygonal.

The causes of the metamorphic texture are probably two-fold. First, the effect of the heat of the intrusion itself annealing matrix crystals strained whilst emplacement of the crystal mush was taking place. Second, the effect of the continuing heat of the regional metamorphism of the country rocks enclosing the body. Morgan (1982) believes that the lherzolite unit was intruded during granulite facies metamorphism of the country rocks, after the completion of tectonic deformation; the writer suggests, earlier in this report, that the harzburgite unit was emplaced only a short time after the lherzolite, i.e., during the metamorphism.

The feldspathic rocks

Age relationships

The feldspathic rocks and veins of granite material were emplaced after the harzburgite. The granitic material intrudes both the lherzolite and the harzburgite. The feldspathic rocks occur only in the harzburgite. Both have hydrated and possibly metasomatized the ultramafic body. The relationship between the granitic veins and the feldspathic rocks is not known. However, for reasons given below, it is possible that the feldaspathic rocks are related to the ultramafic body. The granitic veins are probably related to a much younger period of granitic emplacement (eg. Wilson 1958).

Emplacement

The feldspathic rocks are very minor occurrences in the harzburgite, and their origin is problematical. Prider (1945) referred to andesinites within granulite facies ultramafics at Dangin as "segregations". If that is their occurrence here, they could be interpreted in one of two ways.

First, they could represent a late stage "aplitic pegmatitic" phase of the ultramafic, emplaced on primary cooling joints in the harzburgite. The feldspathic rocks contain elements (Al, Ca, Na, K, Zr), and volatiles that are incompatible with the lattice sites of orthopyroxene and olivine. Their emplacement would have been accompanied by hydration and potash metasomatism of the harzburgite.

A second view is that, petrogenitically, they are entirely unrelated to the harzburgite. Granulite facies rocks in the Western Australian wheat belt are regarded as xenolithic masses fragmented by subsequent granitoid invasion (Wilson 1958, 1959; Prider 1945, Davidson 1968). Potash metasomatism associated with the feldspathic rocks, along with the presence of zircon, suggest that they represent a metasomatism induced by the granitoid invasion which took place about 2 800 m.y. ago (Wilson 1958).

Concluding remarks

The diamond drill cores have given us only a glimpse of what must be a complex ultramafic body. Because of extremely poor exposures in the field, really very little is known of the ultramafic-country rock relationships, or of the relationships of the consitutent members of the unltramafic body. In fact, there may well be other units in the ultramafic, besides harzburgite and lherzolite, not exposed by the drilling. Hence, any conclusions drawn from this, and the author's previous study (Morgan 1982) must be tenuous.

The relationship between the lherzolite and the harzburgite is not clear. The lherzolite, from chemical and modal evidence (Morgan 1982) appears to be a series of cumulate-rocks resulting from the differentiation of a basaltic magma. On the other hand, the slightly younger harzburgite seems to be the result of the *in situ crystallization* of an ultramafic magma. Hence, there can be no intimate petrogenic relationship between them: one is not derived from the other. Yet they are intimately related in time and space, hence they must both have been derived from the same source during the course of a continuing geological event.

One might guess that rising upper mantle temperatures resulted, first, in the generation of tholeiitic magma as a parent of the lherzolite, followed by the melting of much more refractory material, producing the harzburgite. This postulated upper mantle "hot spot" may well be the reason for the granulite facies metamorphism in the area, and could be an event in a long-continued process of sedimentation, igneous activity, tectonism, and metamorphism that was ultimately completed with the emplacement of granitoids about 2 800 m.y. ago.

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Vegetation of Yule Brook Reserve near Perth, Western Australia

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Abstract

The Yule Brook reserve is a small block located 20 km S.E. from Perth (32°S115°W) in a climate of cool wet winters and hot dry summers. A clay flat is crossed by two parallel sand ridges.

The vegetation of the deep leached sand of the ridges is Banksia woodland on the crests with low shrub undergrowth continued on the treeless slopes.

The clay flats which have a shallow cover of sand and are waterlogged in winter and baked hard and dry in summer have a perennial cover of the rush type *Leptocarpus* interrupted by scattered low shrub mounds and saline depressions.

Slightly raised sections which still have some waterlogging in winter are dominated by the shrub *Leptospermum* or the conifer *Actinostrobus* in each case with a varied understorey of sedges and shrubs, semishrubs and herbs.

As a result of the extreme contrasts between the conditions in winter and summer the herbaceous flora is markedly seasonal with numerous geophytes and ephemerals. Of special interest are the many insectivorous plants *Drosera, Byblis, Utricularia* and *Polypompholyx*, and the "Trigger plants" *Stylidium* spp.

Altogether there are at least 370 indigenous species on the block, a large number for a block of less than 50 ha.

Introduction

The Yule Brook Reserve lies 20 km southeast from the centre of Perth (32°S 115°E) in a region of poorly-drained flats on the coastal plain at the foot of the Darling Scarp. One area of these flats, near Kenwick, has long been a favourite haunt of botanists because of the rich variety of unusual plant species found there. The former Government Botanist, the late Mr. C. A. Gardner for example, collected extensively in the region and Lloyd (1942), in his classic monograph on carnivorous plants, refers to it.

In 1949 the University of Western Australia purchased 34.6 ha of the "swamp region" for research and teaching purposes by members of its Botany Department. Known officially as the "Yule Brook Botany Reserve, Kenwick", but more commonly referred to by local botanists as "Cannington Swamp", the Reserve is listed in the Western Australian Government Gazette (9th November, 1979) because of its special nature. Consequently, no development of the Reserve is permitted without the approval of the Metropolitan Regional Planning Authority in addition to that of the local authority, the Gosnells City Council. The site is important as a remnant of natural swamp vegetation which is rapidly diminishing with urbanisation of the region.

The major portion of the Yule Brook Reserve was described and mapped and contoured in 1950 by the late Dr. N. H. Speck as part of a M.Sc. thesis (Speck 1952). Although his maps and descriptions of the plant communities are frequently used by staff and students of the Botany Department his work remains largely unpublished.

Since the original mapping, roads have been built (in 1961 and later) on two sides of the block, formerly only accessible from an early pipeline track (Bickley Road) along the south-western boundary. Drainage along the road verges, damage in the course of road building, and firebreaks put down and maintained since 1964 have somewhat reduced the communities mapped by Speck. Fires have been frequent and their impact is described in a second paper (Baird in prep.).

This general account of the vegetation is based primarily on Speck's work with some later observations. It is hoped that the paper will provide a background against which future changes can be assessed. A species list has been revised to incorporate some additions and many recent changes in nomenclature.

General Features of the Reserve

The Reserve site is distinctive within the general area of the swampy flats in that the flats are crossed diagonally by two parallel north-south sand ridges, the larger eastern one rising to 5-6 m above the flat while the smaller western one, which does not reach the north-west boundary, is less than 2 m. Both ridges rise steeply on the western side with a long, gradual slope to the east.

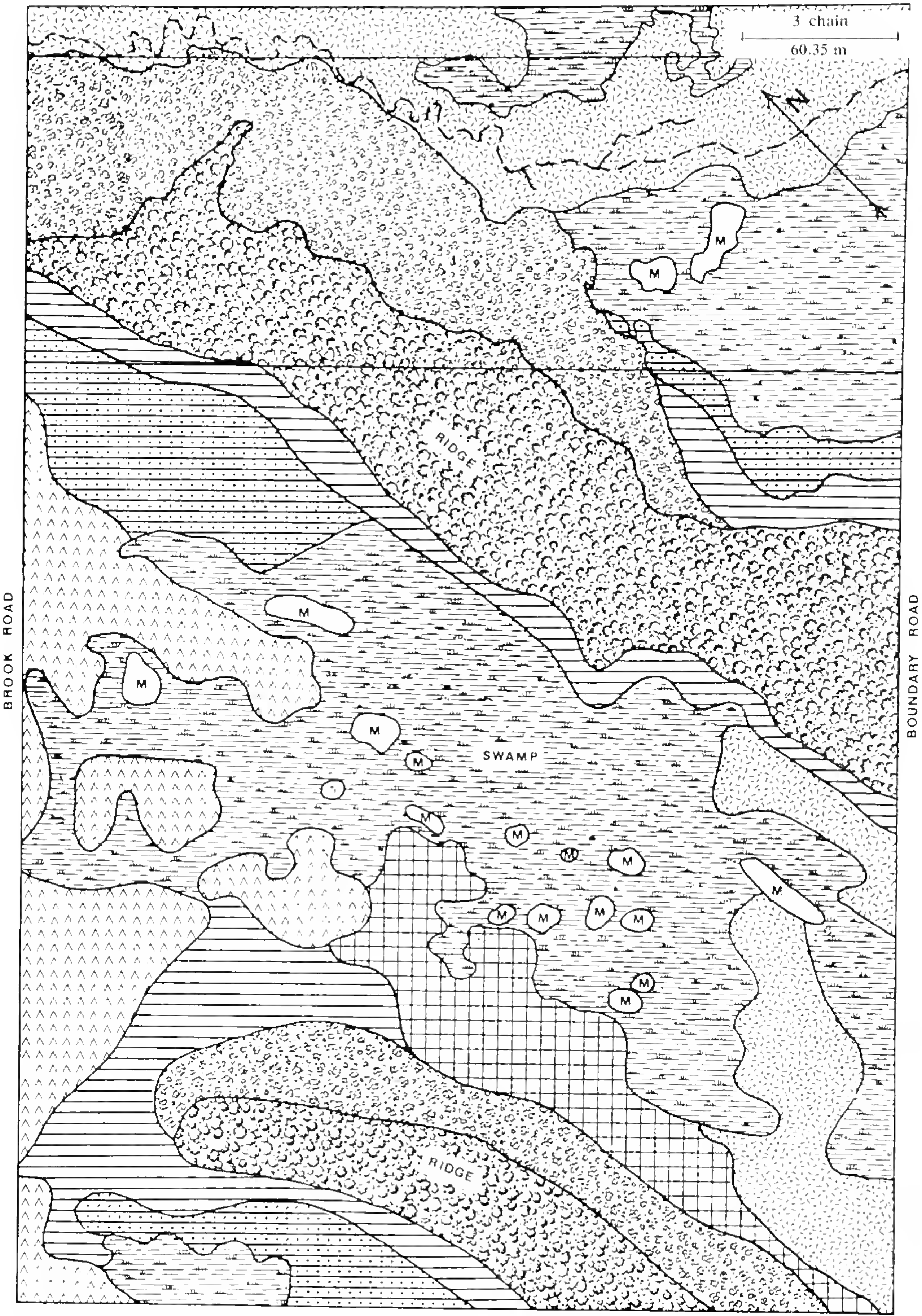

FIG 1 VEGETATION OF THE RESERVE (as mapped by N.H. SPECK 1950)

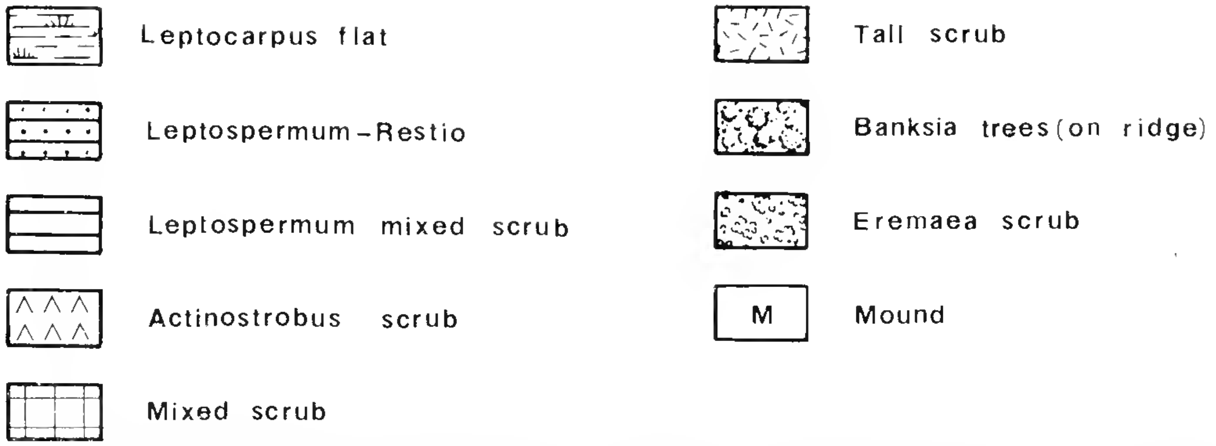

Figure 1.—Map of plant communities. This shows the communities recognised and mapped by N. H. Speck. The outlines were copied from his M.Sc. thesis 1952 with an extension at the north eastern end.

Drainage east of the main ridge is into a small tributary of Yule Brook, but over the main flat is very sluggish so that water lies on the surface for much of the winter. A poorly-defined drainage line meanders to the west.

There is evidence from a series of straight parallel lines on aerial photographs that a portion of the flat adjacent to the eastern ridge had once been cleared and cultivated—the spacing suggests viticulture, although this is unconfirmed. It has been known in its present uncultivated state since early in this century.

The soils are strongly-leached, whitish-grey siliceous sands overlying an undulating heavy yellowish clay. On the flats the sand varies between 10-45 cm, whereas on the ridges it may be several metres deep. In parts of the flats, calcareous particles occur in the subsoil, and some low lying parts are markedly saline. In sections at the foot of the ridges a greater organic content in the wet soil produces a humus podsol and at some lower levels of the ridges an accumulation of brown iron leachate known locally as 'coffee rock' occurs at the interface between sand and clay. Details of soil profiles are given in Appendix 1.

The climate is that of the Perth metropolitan region, i.e. one of cool, wet winters and long, hot, dry summers. Of the average annual rainfall of 883 mm, 70% falls in the four winter months May-August, and only 5% in the four summer months December-March. Conditions are made more extreme on the flats by waterlogging in winter and exposure to hot drying winds in summer.

The Plant Communities

There is a clear distinction between the wooded crests and shrub covered slopes of the well drained sand ridges and the predominantly rush covered flats, which are waterlogged in winter and have a rich ephemeral flora, most conspicuous as the water recedes in spring and early summer. Intermediate levels are complex and less readily classified. Figure 2 shows general views of the reserve.

Speck in 1949-50 mapped about two thirds of the area on a chain* square grid. His map is reproduced in Fig. 1. The map has been extended to include the remainder by sketching in approximately the most obvious boundaries using aerial photographs.

For the purposes of mapping, Speck was able to identify and delimit communities as listed below:—

on the flats

Leptocarpus aristatus meadow

Leptospermum ellipticum—*Restio tremulus* low scrub

Leptospermum ellipticum mixed scrub

Actinostrobus mixed tall scrub

on the ridges

Banksia low scrub woodland

Eremaea low scrub

The following description uses these community names even though they may not be consistent with later terminology (e.g. Specht 1970). The photographs have been selected to show samples of the communities shown on Speck's map (Fig. 1) which should be referred to.

The Leptocarpus aristatus meadow

The species is clearly dominant and in its best development forms a dense uniform sward up to 35 cm high with a distinctive pinkish brown colour given by the persistent flowering heads. It occurs on the flats between and beyond the ridges. The section on the western first flat on the map is small but it is cut off from the major part of this sward (Fig. 2A) by the long established Bickley Road. On the third flat to the south east of the higher eastern ridge the *Leptocarpus* occurs mostly as isolated tufts on bare white sand (Fig. 6B).

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* 1 chain = 22 yards = 20.2048 metres; the chain was a standard surveyor's measure.

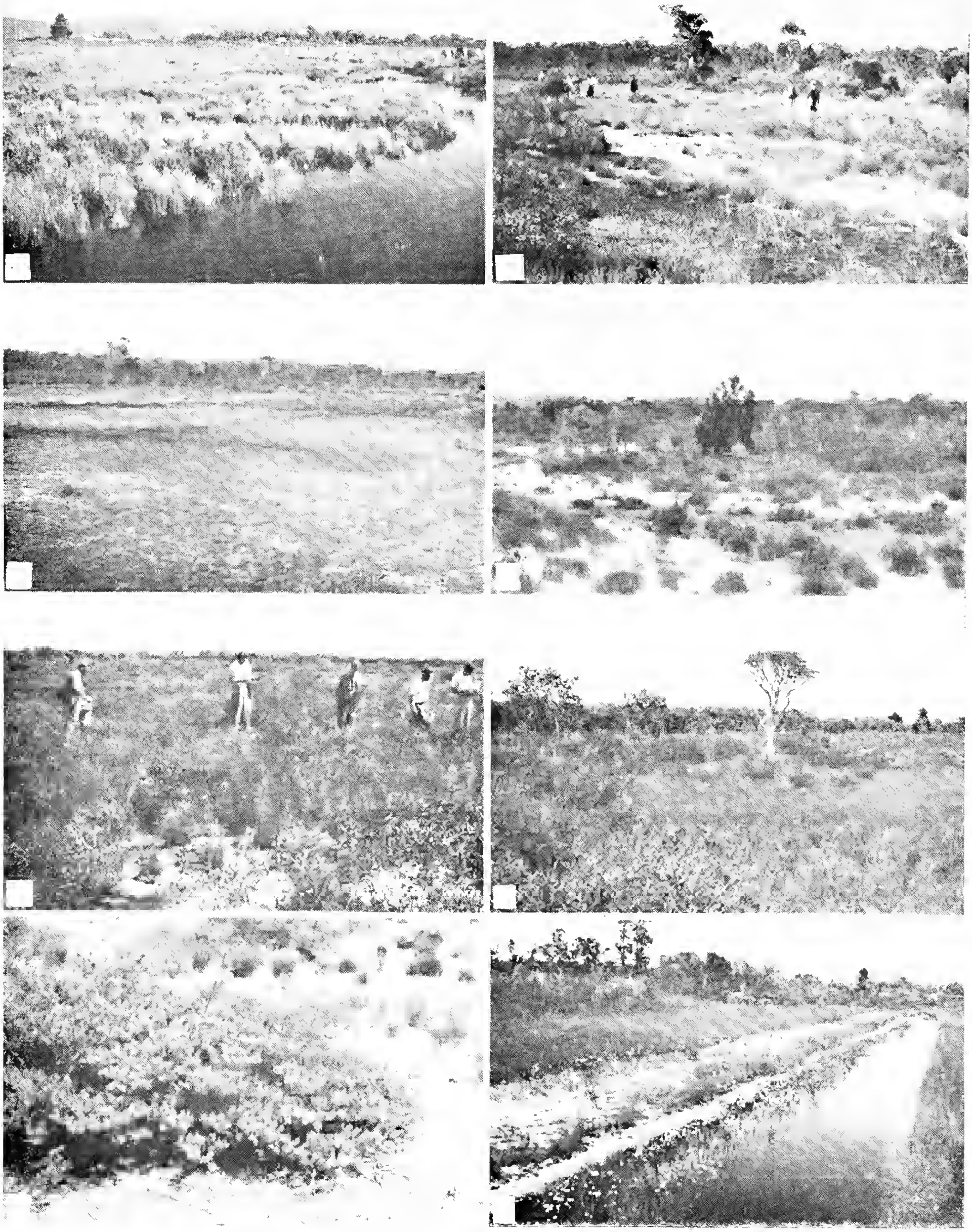

Figure 2.—Vegetation of the flats. A. *Leptocarpus* sward looking east to Darling scarp in background. August 1957. B. View across main flat to ridge. June 1970. Flat had been burnt in 1967. C. Part of the flat with numerous small bushes of *Banksia telmatiaea* and *Calothamnus villosus*. September 1955. D. A spreading bush of *Calothamnus villosus*. E. Flat at foot of ridge, depression with black mud and ephemerals in foreground, low mounds left and right, a tall paperbark *Melaleuca* (*M. preissiana*) on edge of ridge. September 1956. F. A broad spreading mound with central *Actinostrobus*, saline depression with *Halosarcia halocnemoides* right foreground. October 1959. G. Close to the tall *Melaleuca preissiana* in figure B. *Leptocarpus* flat and shrub covered slope to woodland, *Banksia littoralis* left skyline. September 1955. H. Looking along the flat where a scraped firebreak was put down in 1964 providing deeper water and a raised sandy rim; *Utricularia inaequalis* in water *Tribonanthes* on sand *Drosera gigantea* right hand corner. October 1965.

The most extensive area of flat lies between the two ridges (Fig. 2B). The sward of *Leptocarpus* is interrupted by an occasional isolated shrub of *Hakea varia, Melaleuca bracteosa (M. fasciculiflora)* or *Calothamnus villosus* (Fig. 2D). In places nearer the ridge, shrubs, including *Banksia telmatiaea (B. sphaerocarpa)* are more abundant (Fig. 2C). In some depressed parts *Leptocarpus canus* (Fig. 4E) replaces *Leptocarpus aristatus*.

Scattered unevenly through the flats are mounds (Fig. 2 E and F) which are initiated by the accumulation of drifting sand against low spreading *Melaleuca bracteosa bushes*. The mounds vary from a single shrub with a few small associates to extensive mounds with an assortment of other shrubs surrounding the *Melaleuca* and sometimes including a tall *Actinostrobus* (Fig. 2F).

Saline depressions with *Halosarcia (Arthrocnemum) halocnemoides* (Fig. 2F) throughout the flats. Small depressions may have only a single plant, larger ones a group of the samphires, in some cases with a fringe of *Selenothamnus (Plagianthus) squamatus* a species slightly less salt tolerant than *Halosarcia*.

A small colony of *Wilsonia backhousei*, occurs in a wet saline depression on the south eastern extension of the reserve.

The soil of the *Leptocarpus* flats consists of heavy domed clay covered by white sand of varying depth. (Fig. 3 and Profile appendix I.) This is a habitat of extremes. Water lies on the surface of the flats through much of the winter and gradually evaporates through spring and early summer. In summer the flats are hot and dry and windswept, consequently the herbaceous flora is markedly seasonal.

From soon after the first rains some species can be found growing and flowering, e.g. *Drosera bulbosa* in May. *Ultricularia menziesii*, a tiny rosette perennial with a single long-tubed scarlet flower, *Drosera heterophylla* and the sweet scented orchid *Thelymitra antennifera* are blooming through winter on the open flats. Where water is deeper *Polypompholyx multifidia* (Fig. 4A) and the smaller and less common *P. tenellus* and *Utricularia violacea* are in flower between August and October and slightly later the purple *Utricularia hookeri*. This species is most abundant at the western foot of the ridges where seepage from the sandy slope provides longer lasting water. It is associated here with the branched sundew *Drosera gigantea* (Fig. 4B). A graded firebreak (Fig. 2H) cut through this zone in 1964 provided a new habitat for the *Utricularia*.

The peak flowering period for herbaceous geophytes occurs through August-September with *Tribonanthes variabilis* (Fig. 4C), *Burchardia multiflora*, and many orchids (e.g. *Diuris* spp.) and sundews (*Drosera* spp.) conspicious. Also flowering in spring are the "ephemeral geophytes" such as *Utricularia menziesii, Drosera palaecea, Stylidium pulchellum* and the lycopod *Phylloglossum drummondii*. The fringes of the mounds provide a particularly favourable habitat for many of the herbaceous species.

Figure 3.—A spadeful of soil from the main flat showing the clear boundary between the sand and the underlying domed clay. May 1967. The flat had been burnt January 1967.

Most of the common annuals flower later than the perennials, usually in October-November. Members of the Asteraceae e.g. *Brachycome pusilla* (Fig. 4E) *Angianthus spp.,* (Fig. 4D, F) and many small ephemerals flower over a short period and die away as the surface soil dries out. Among the most abundant of these species is the inconspicuous *Centolepis aristatus*, but species of *Hydrocotyle, Calandrinia, Aphelia* and tiny annual species of *Stylidium* are also common. The black surface of saline depressions is often densely covered with *Angiathus strictus* (Fig. 4F).

Over the summer the flats are bare of herbaceous plants, and where the *Leptocarpus* cover is sparse (or absent) the sand is moved by small "willy willies", airwhirls which tend to remove loose sand from the bare areas and pile it up against the mounds.

It is probable that these flats, although remaining basically stable show a good deal of instability in surface detail. Slight changes in drainage or

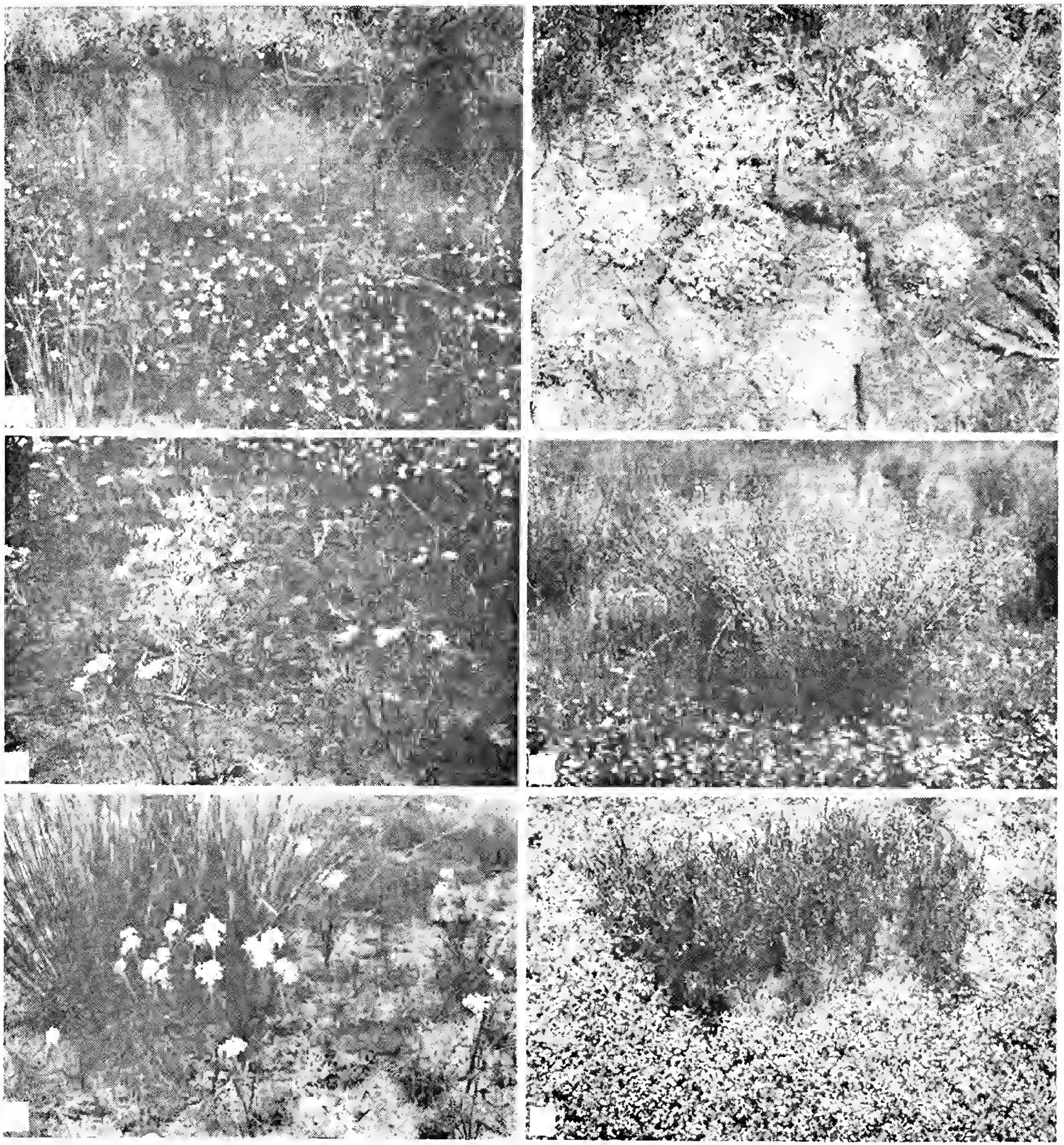

Figure 4.—Herbs of the flats. A. *Polypompholyx multifida* in flower in water, September 1965, B. *Drosera gigantea* in flower. C. *Tribonanthes variabilis* in front of a clump of *Gahnia trifida*. D. *Angianthus humifusus*. December 1st 1964. E. *Brachycome pusilla* in front of clumps of *Leptocarpus canus*. October 29th 1975. F. Dense cover of *Angianthus strictus* in a saline depression with *Halosarcia halocnemoides*. October 29th 1975.

differences in annual rainfall in different years may vary the distribution and abundance of annual species. For example in the particularly dry year of 1959 no *Utricularia hookeri* was found in flower although it was present in its usual profusion in the following year. Loneragan (1973) has demonstrated marked fluctuations in numbers and distribution pattern of the geophyte *Tribonanthes variabilis*.

At the intermediate levels between the waterlogged flats and the sandy ridges the vegetation is perhaps at its richest and most varied, but it is also more difficult to classify. Speck recognised three communities:

Leptospermum ellipticum—Restio tremulus low scrub

Leptospermum ellipticum mixed scrub

Actinostrobus tall scrub

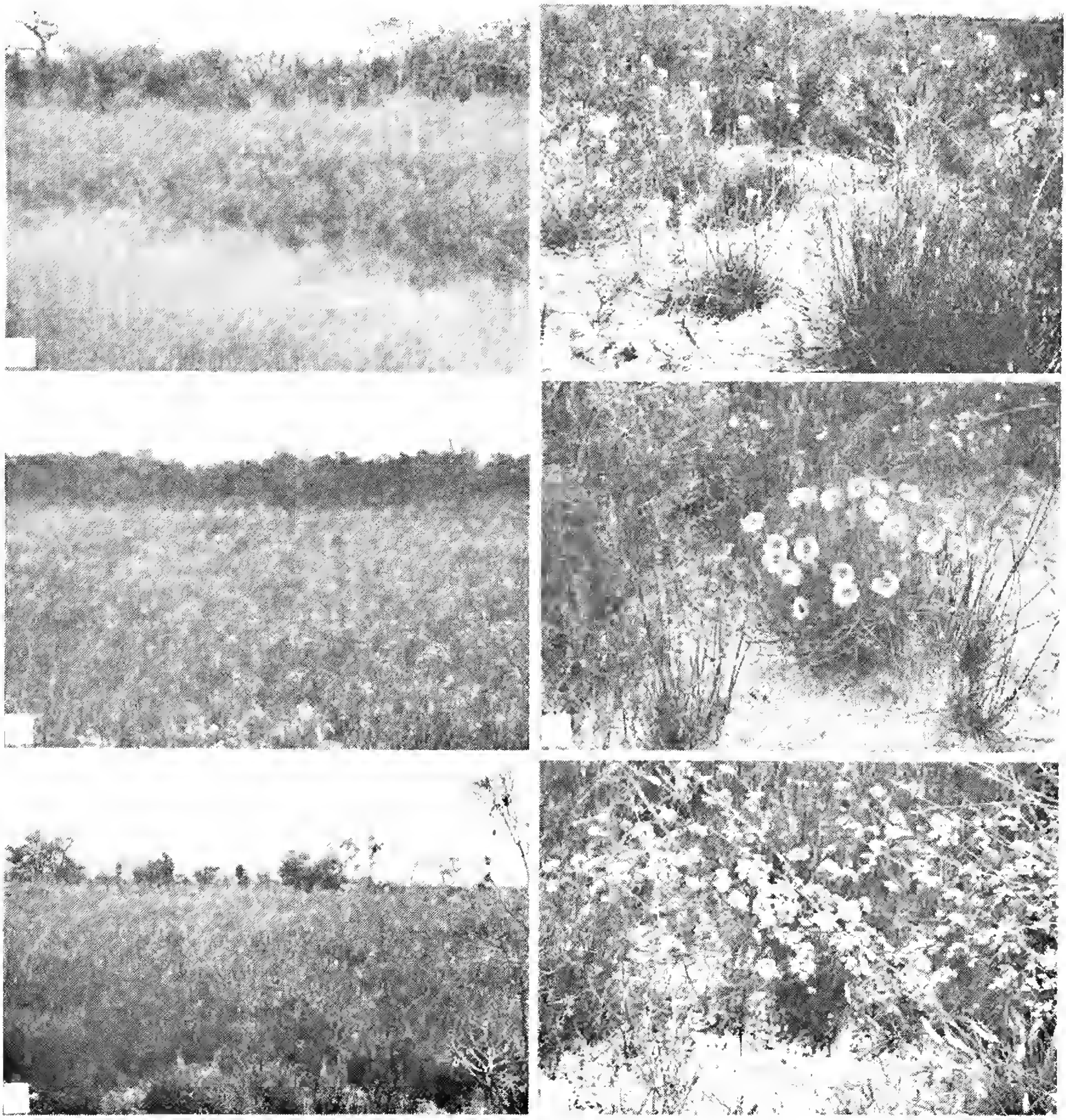

Figure 5.—*Leptospermum* communities. A. Narrow zone of *Leptospermum ellipticum* on the steep western slope of the eastern ridge, *Leptocarpus* sward in foreground, *Adenanthos* shrubs behind *Leptospermum*, *Nuytsia* projecting on left skyline. October 31st 1968. B Broad zone of *Restio* and *Leptospermum* (in flower) eastern slope, *Banksia* woodland in background. October 31st 1968. C. Very gradual slope up to northern end of low western ridge. Dense low scrub of *Restio*, *Leptospermum*, *Banksia telmatiaea*, *Nuytsia floribunda* and slender *Eucalyptus calophylla* on the skyline. *Leptocarpus* in foreground. October 1965. D. *Conospermum huegelii* in flower on firebreak, dense mixed scrub behind. September 18th 1977. E. *Byblis gigantea* in flower. November 5th 1970. F *Lechenaultia expansa* in flower, *Johnsonia* sp. left corner. October 31st 1968.

Leptospermum ellipticum—Restio tremulus low scrub

This is a clearly defined community with usually a sharp boundary where adjacent to the *Leptocarpus* meadow (Fig. 5A) made even more conspicuous when the *Leptospermum* is in flower. The two species *Leptospermum* and *Restio* are codominant although in old stands the *Leptospermum* may grow above and conceal the *Restio* (Fig. 5A).

Where the ridge rises steeply on the western slopes there is a narrow zone of *Leptospermum-Restio* with an upper rim of *Leptospermum* without *Restio* (Fig. 5A); where, as towards the northern end of both ridges, there is a fairly extensive shelf just above the main level of the flat but still waterlogged in winter a wide *Leptospermum-Restio* (Fig. 5B) community is particularly rich, with a great variety of other swamp tolerant species. Common shrub species included are *Banksia telmatiaea*, *Hakea ceratophylla*, *H. sulcata*, *Calothamnus villosus*, the semishrubs *Conospermum huegelii* (Fig. 5D), *Conostylis filifolius*, *Leschenaultia expansa* (Fig. 5F), *Petrophile longifolia* and many different sedges and rushes, for example, *Cyathochaeta avenacea*, *Schoenus* spp., and *Anarthria gracilis*.

The seasonal herbaceous flora is again rich and varied with the insectivorous *Byblis gigantea* (Fig. 5E) and *Drosera neesii* common, with *Anigozanthos viridis*, *Stylidium* spp. and many of the herbs of the *Leptocarpus* flats previously listed.

Compared to the soils of the flats, the soil here contains a greater quantity of organic matter and is more a humus podsol with a tendency to coffee rock formation (see profile B west of first ridge and profile 2 west of main ridge, Appendix 1.).

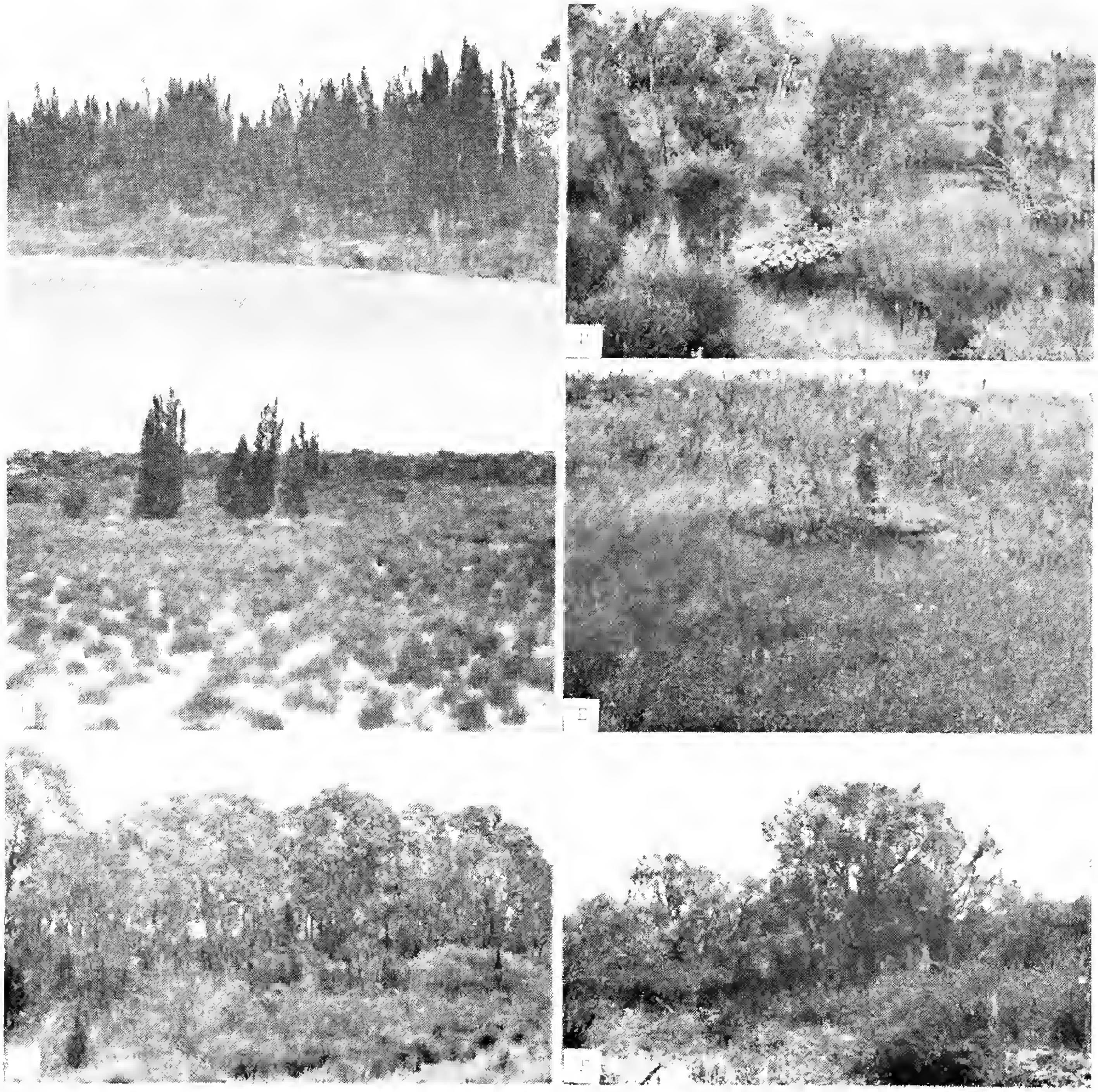

Figure 6.—*Actinostrobus* and other tall shrubs. A. A long unburnt stand of *Actinostrobus pyramidalis* outside the Reserve November 1971. B. Tall *Actinostrobus* on the edge of the rise from the 3rd flat, *Leptocarpus* in foreground. October 1968. C. Young *Actinostrobus* growing under a stand of marri adjacent to the *Actinostrobus* of A. D. A mixed wet area. *Actinostrobus* centre, *Leptocarpus canus* foreground, *Viminaria* background right, *Melaleuca* background left. 23rd August 1956. E. Corner of the western flat, *Leptocarpus aristatus* foreground, prostrate *Calothamnus* with erect young *Actinostrobus*, *Viminaria* background. 9th December 1969. F. *Melaleuca rhaphiophylla* in flower on edge or creek, eastern boundary of reserve. 31st October 1968.

Leptospermum ellipticum mixed scrub

As the ground slopes up onto the ridge the *Leptospermum* increases in height, *Restio* gradually disappears, and new species appear with many of those from the lower zone. In Speck's description, "there is no sharp floristic boundary between the two *Leptospermum* zones, the change is one of structure; on the better drained and rising ground the *Leptospermum* increases to almost twice its height in the lower one and this is also true for other species." The mixed *Leptospermum* scrub grades from the lower *Leptospermum-Restio* and it is only where the changes in slope are sudden that a definite boundary can be recognised. Nevertheless, there is on both sides of the ridges this zone of dense scrub of variable composition but containing species which do not occur further up the ridges. The more abundant shrubs here include *Banksia telmatiaea, Beaufortia squarrosa, Daviesia incrassata, Euchilopsis linearis* and *Hypocalymma angustifolium*, and in some parts, *Astartea fascicularis* or *Regelia ciliata*. Of these species *Banksia telmatiaea* (Fig. 7C) has a greater vertical range than most, extending from the *Leptocarpus* flats to beyond the uppermost *Leptospermum*. A few specimens of *Melaleuca preissiana* (old man paperbark, Fig., 2G) and *Banksia littoralis* (swamp banksia) also occur at this level and, although this is not its best habitat, several small trees of *Eucalyptus calophylla* (marri) (Figs. 2H, 6C). In the long unburnt southeastern slope of the main ridge this scrub developed into a dense thicket 1.5-2.0 m tall with *Banksia telmatiaea, Beaufortia squarrosa, Daviesia incrassata* and *Hakea varia* as the principle components.

The soil, as for the lower zone, is a humus podsol but as this zone is higher up the ridge than the *Leptospermum-Restio*, the sand is deeper above the water level. The coffee rock layer is better developed here than in any other soil of the reserve (profile C, Appendix 1).

Mixed low scrub

Towards the south eastern section at the foot of the low ridge the Leptospermum dominated community of the northwestern end is replaced by a mixed assemblage of low shrubs in which the mound building *Melaleuca bracteosa* is conspicuous with *Hakea varia, Banksia telmatiaea, Verticordia spp.* and other shrubs and herbs some indicating lime in the soil eg. *Grevillea thelemanniana* and *Acanthocarpus. Acacia lasiantha* is abundant, particularly after fires. All these plants belong to species present in adjacent communities, but form a somewhat distinct grouping. Speck outlined the area on the map as mixed low scrub.

Actinostrobus pyramidalis tall scrub

Because of the characteristic conifer habit and dark foliage *Actinostrobus* communities (Fig. 6) are easily recognised and can be mapped on the basis of the presence of the species. At its best it forms almost a miniature conifer forest with slender crowded small trees. One such stand (Fig. 6A) occurs adjacent to the reserve and, in contact with this, young plants were growing under marri (Fig. 6C). Tall plants on the edge of the eastern flat are shown in Figure 6B.

Most stands on the reserve have scattered *Actinostrobus* associated with some of the shrubs of the *Leptospermum* zones *Hypocalymma angustifolium* is particularly common, other species are *Melaleuca lateritia, Beaufortia squarrosa, Leptospermum ellipticum, Kunzea micrantha, Verticordia* spp., *Andersonia aristata, Conostylus* spp., *Restio* spp. and a wealth of seasonal herbaceous species. *Stackhousia huegelii, Philydrella pygmaea, Brachycome pusilla* (Fig 4E) and others. *Isoetes* is sometimes found growing in black mud in water filled depressions often but not invariably near *Actinostrobus* or *Viminaria*. Although *Actinostrobus* stands are at approximately the same contour level as the *Leptospermum-Restio* the soil contains less humus, and the underlying clay has a high pH and usually contains calcarous nodules.

A new road and parallel firebreak cut through the *Actinostrobus* stands on the north west side of the block have considerably reduced the area shown in Speck's map, and repeated fires have prevented the development of tall stands. Near the north-eastern corner of the reserve a few trees have escaped fire and reached an age of some 160 years as shown by ring counts (Loneragan pers. com.).

Viminaria juncea, a tall broom-like legume dominates big areas of swampy flats in the district which have clay at the surface. It has spongy pneumatophores which project up through the water covered clay from horizontal roots. On the Reserve where most of the clay is covered by sand there are no extensive suitable habitats and the occurrences are too scattered to justify separate mapping. Speck simply mentions it as occurring in some of the *Leptospermum-Restio* and *Actinostrobus* areas. It is shown in figures 6D and 6E.

Fringing thickets of tall shrubs

Dense thickets of tall shrubs, mainly species of *Melaleuca, M. rhaphiophylla* (paperbark) (Fig. 6F); *M. uncinata, M. viminea, M. cuticularis*, border the small creek (more a swamp at its southern end) on the eastern boundary of the reserve. Another group of paperbarks occurs along a drainage line in the south western extension across Bickley Road and there is a deeper paperbark swamp near the corner of Bickley and Boundary Roads in an adjacent property.

Banksia woodland

On the crest of the ridge is a low woodland (Fig. 7A, B) of *Banksia attenuata* and *Banksia menziesii* with a few trees of *Casuarina fraseriana* and still fewer of *Banksia ilicifolia*. The slope up to the dense banksias in the background is shown in Figure 7C. The undergrowth is a low shrub layer with a high percentage of harsh perennial monocotyleons. The community is representative of the vegetation of the poor leached sands of much of the coastal plain. Here as with most South-West Australian vegetation dominance of a type of small-leaved sclerophyllous shrub is the pattern rather than dominance of any one species. Common dicotyledons are *Hibbertia* spp., *Hovea trisperma, Bossiaea eriocarpa, Acacia pulchella, Jacksonia flori-*

bunda, *Leucopogon* spp., *Astroloma* spp., *Dampiera linearis* and many others. Common Monocotyledons are *Xanthorrhoea priessii*, *Conostylis* spp., *Patersonia occidentalis*, *Amphipogon turbinatus*. The tall grey foliaged shrub, *Adenanthos cygnorum* (Fig. 7D) in places forms a conspicuous zone fringing the Banksias. Scattered *Nuytsia floribunda* (Christmas tree) trees occur beyond the boundaries of the Banksias on the slopes of both ridges (Figs 5A & C). The small stand of Banksia on the low western ridge was cleared illegally about 1954 and has not regenerated.

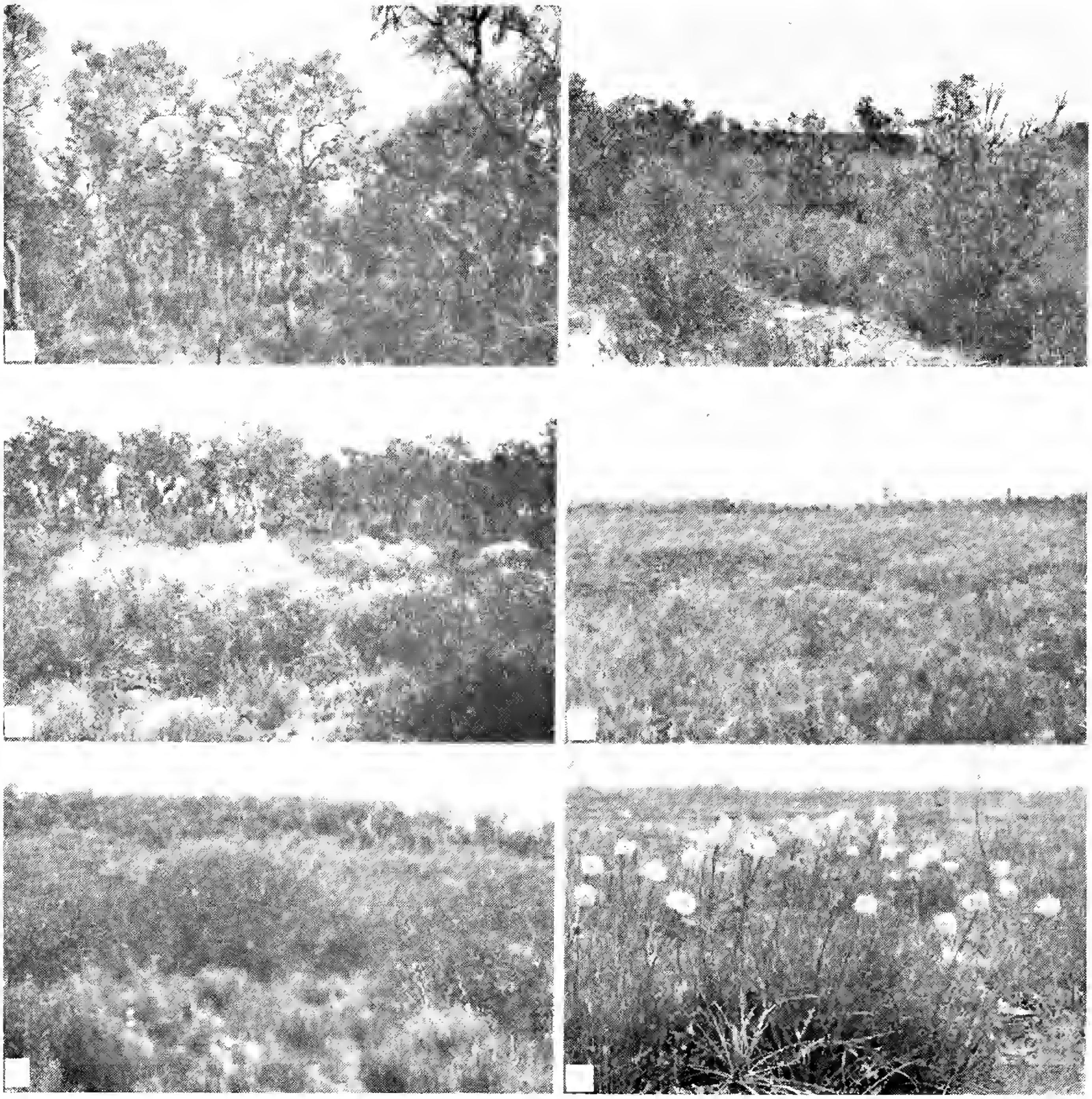

Figure 7.—Vegetation of the ridge. A. Banksia woodland on crest of ridge, *B. attenuata* centre and left edge, *B. menziesii* left of centre, *Casuarina fraseriana* overhanging right corner, low shrub undergrowth. September 19th 1977. B. *Conospermum stoechadis* in flower on eastern slope. September 19th 1977. C. Part of slope up to dense woodland, *Adenanthos* in front of Banksias, rounded bushes of *Banksia telmatiaea* on edge of slope behind *Leptocarpus*. October 29th 1975. D. Shrub cover on upper slope of ridge, *Adenanthos cygnorum* (tall shrub), *Eremaea pauciflora* low rounded shrub centre on edge of firebreak, *Xanthorrhoea* left. October 26th 1965. E. View along eastern slope of ridge with dense low shrub cover. December 9th 1969. F. *Dasypogon bromeliifolius* in flower on eastern slope of low western ridge. October 1959.

Eremaea low scrub

The shrub community of the slopes is continuous with the undergrowth of the woodland but in the open is denser with a higher proportion of larger species. *Eremaea pauciflora,* a compact spreading microphyllus shrub, is particularly conspicuous in late spring with its massed orange flowers. On the first ridge it is sufficiently abundant to justify Speck's giving its name to the community but there are many associated shrub species. The monocotyledons, *Dasypogon bromeliifolius* (Fig. 7F), *Lyginia barbata, Schoenus curvifolius, Anigozanthos humilis, Loxocarya fasciculata,* and *Calectasia cyanea* are also abundant. Since the clearing of the Banksias this low scrub continues right across the ridge.

On the extensive eastern slope of the main ridge (Fig. 7E) the shrub community is richer and more diversified and *Eremaea* though abundant is only one of several conspicuous shrubs. *Casuarina humilis* forms bulky cover in places and there is a stand of *Conospermum* sp. (Fig. 7B), very conspicuous when in flower, at a mid level on the slope. *Jacksonia floribunda* is common throughout, its flowering shoots projecting above the general level. However, the main character is the large number of species of low shrubs and semi-shrubs, and fibrous or shrubby monocotyledons. At least eighty species in these categories have been recorded on the ridges and there are also seasonal herbaceous plants.

At the northern part the slope goes down to a small creek meandering along the eastern boundary. At the southern end it goes through the series of *Leptospermum* scrubs to the third *Leptocarpus* flat (Fig. 6B).

There is a gradual change in species composition down the slopes with some not very clear zoning—for instance *Jacksonia furcellata* grows on the lower slopes of both ridges *Jacksonia floribunda* right across the upper levels. *Xanthorrhoea* is more abundant at lower levels. On the lower parts of the low ridge. *Eremaea* is replaced by another myrtaceous shrub of similar habit, *Melaleuca seriata,* before the more definite *Leptospermum zone* is reached.

Flowering on the ridges extends from soon after the first winter rains into late summer but as on the flats with a marked spring maximum. Undershrub species which have their buds formed the previous season eg. *Acacia stenoptera* and several epacrids are the first to bloom followed by *Hovea, Daviesia, Hibbertia, Bossiaea* and others some with flowering extending over several months (eg. *Hibbertia hypercoides*). *Eremaea, Jacksonia* and *Adenanthos* are slightly later. The tree species of Banksia supply flowers throughout the year *B. menziesii* and *B. Littoralis* autumn-winter; B. attenuata spring-summer. Flowering of seasonal herbaceous species is also spread but with each species lasting a shorter time as illustrated in the orchids. As on the flats annuals are in general later than geophytes.

Tall scrub

A strip along the southeastern side between the ridges was mapped by Speck as tall scrub but with some doubts as to its status. This is a disturbed area crossed by old tracks, with uneven ground and numerous weeds. The tall species remaining are *Kunzea vestita,* several species of *Melaleuca,* some *Actinostrobus, Adenanthos* and abundant *Acacia saligna,* a species which often increases on disturbed ground as seen also along the road-verges to the northwest of the Reserve. The profile is very uneven but some bushes reach a height of 3-4 metres.

Flora

The Flora of the sand ridges is as found in Banksia woodlands on poor leached sand in other parts of the coastal plain. It consists of representatives of the characteristics south-west families and genera, for example Proteaceae (8 spp.) Paplionaceae (10) Myrtaceae (8) Epacridaceae (8) Dilleniaceae (3) Liliaceae (6) Xanthorrhoeaceae (16) Haemodoraceae (7), orchids and a few grasses and annual composites.

The flora of the varied levels of the wet flats is much more diverse and unusual containing a large number of species of specialised wet habitats, many of exceptional botanical interest. *Actinostrobus* is an endemic W.A. conifer restricted to certain types of swamp which although widely scattered are becoming reduced by clearing. *Phylloglossum* is a highly specialised Lycopod. There are no true ferns.

Insectivorous plants are particularly well represented with five species of rooted bladderworts: three of *Utricularia* and two of *Polypompholyx; Byblis gigantea,* (rainbow plant); six species of *Drosera* (sundews) on the flats and others on the ridges. Another genus of special interest is *Stylidium* the "trigger plants" with their sensitive column involved in insect pollination. There are at least 20 species including those on the ridges.

Small geophytes and annuals belonging to many different genera and families from Centrolepidaceae to Asteraceae (Compositae) and Apiaceae (Umbelliferae) as seen in the species list are found on the flats.

As usual in swampy ground there are many sedge and rush types Cyperaceae (9-10 spp.) Restionaceae (10) and a few Juncaceae.

Among shrubs on the wet flats Myrtaceae (± 20) are numerous with ten species of *Melaleuca* and six of *Verticordia.* Proteaceae are represtend by Hakea (4), Grevillea (1), Petrophile (2) and Conospermum (1) and there are several semi herbaceous Goodeniacaeae.

The total indigenous flora of the reserve numbers at least 370 species in 52 families of which Dicotyledons number 39 families, 113 genera and 226 species, and Monocotyledons 13 families with 62 genera and 142 species; 1 Conifer, 1 Cycad, 3 Pteridophytes.

Aliens

Introduced plants have not been included in the species list. Many common metropolitan weeds have occurred on parts of the site since long before it was a botanical reserve, e.g. *Romulea rosea, Briza maxima* and other grasses and medics, *Ursinea anthemoides* (on the ridge) and other annuals. *Parentucellia viscosa* and *Dittrichia graveolans* are well established on the western ridge. Recently more aggressive weeds have been invading from the road verges: e.g. *Watsonia pyramidata, Gladiolus caryophyllaceus* and other bulbous species mainly of South African origin. The perennial veld grass *Ehrharta calycina* is a more recent invader. Monitoring the spread of weeds could be a project for the future.

Bryophytes have not been listed. This would be better done for a much wider area. The habitat of the reserve with most of the surface loose sand is unfavourable for liverworts which however do form a surface cover in parts of the regional flats where the surface is a clay loam. On the reserve there are moss cushions in the shelter of bushes on some of the old established mounds and small isolated occurences of liverworts.

Discussion

This paper gives a general idea of the topography of the reserve, types of vegetation and species present. The vegetation has been described under community types. In a situation such as this where habitat differences are marked as between well drained sandy ridges and waterlogged flats there is a distinct assemblage of species tolerant of each condition, and as the change in physical gradient is steep the ecotone is narrow. Furthermore where there are clear dominants as in the *Leptocarpus* and *Leptospermum* and *Actinostrobus* zones it is possible to draw boundaries based on the boundaries of these species, although the continuum concept may apply if all species are considered. On the long gradual slopes with many species but none clearly dominant there are slight gradients in species distribution but the same type of low shrub vegetation with many species so that the whole slope can be classed as one community.

Although the flats are clearly dominated by the *Leptocarpus* sward there is on the flats a mosaic pattern of minor species which results from small habitat differences; e.g. slight difference in level, exposure of clay at the surface, amount of humus, presence of underlying calcareous nodules, and slight differences in salinity apart from the well defined saline depressions with *Halosarcia*.

Noteworthy in all of the wetlands and to a lesser extent on the sand ridges is the larger number of herbaceous geophytes including some tiny "ephemeral geophytes". In the valuable study by Pate and Dixon (1981) of the bulbous, cormous and tuberous plants of W.A. no fewer than 50 of the species occurring in the Southwest occur on the small Yule Brook Reserve. Some have been studied in detail; morphology and growth of underground organs and changes in chemical resources through the seasons, thus increasing understanding of the methods of survival and reproduction in the difficult environment.

In addition to the herbaceous geophytes there are the many wiry rhizomatous plants which do not die down in summer but have the geophyte character of protected underground growing apices.

Changes in the vegetation and habitat since 1950 are difficult to assess as no quantitative records have been kept until recently. Part of the *Actinostrobus* stands was totally removed by the road put down in 1961 and firebreaks have cut into all communities near the boundaries and at the foot of the ridges. The effect of drains along the roads does not appear to extend far into the block. Until a few wet seasons follow the long drought (1975, 6, 7) it is difficult to say whether changed drainage or drought is responsible for the flats being drier and more saline than previously remembered. It remains to be seen whether this is continuing or reversible.

An invasion by aggressive weeds from road verges is an obvious change, and with increased traffic, including earth carrying trucks, the chances of fresh introductions are increasing.

The influence of fire will be discussed in a second paper.

The site has a long history of involvement in botanical studies: taxonomic collections and descriptions over many years by government botanists and others and specialised studies such as *Actinostrobus* Saxton 1913, Baird 1937) insectivorous plants (Lloyd 1942). *Phylloglossum* (Hackney 1950), and recently *Viminaria, Cyathochaeta, Hakea sulcata* (Lamont 1972, 1974, 1976), *Tribonathes* (Loneragan 1973), Pate and Dixon 1981, Goble-Garrett, Bell and Loneragan 1981). Many detailed studies are in progress and the reserve should provide research opportunities for many years. The fact that it is close to the city makes it particularly useful for student work and it is hoped that any deterioration of the site will continue to be slow as it appears to have been to date.

Acknowledgements.—The contribution of the late N. H. Sreck is acknowledged in the use of his name as co-author. My notes have been made intermittently over many years in association with other members of the Botany Department of the University and student classes. My thanks are due to the several members of staff who know the reserve and have read the manuscript and offered suggestions; also to those of the staff of the Western Australian Herbarium who have checked the species list. To all of these I am deeply grateful. I have to thank Mr W. M. McArthur for a set of soil profiles. Thanks also to Mr Miller of the Geography department for preparing the map for publication and to Mr Martin Lucks of Botany for mounting and photographing the figures for publication.

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Appendix I

Soil Profiles of Yule Brook Reserve

Note:—Profiles 1-4 were taken by W. M. McArthur in 1981 on the central swamp flat, adjacent slightly raised areas and on the main sand ridge, all towards the north western side of the block.
Profiles A-F are from N. H. Speck's thesis and were taken in 1950 in a series from the swamp flat at Bickley road to the top and eastern slope of the low sand ridge.

1. *Leptocarpus Zone*

Flat landscape with evidence of salt (NaCl) on the surface and a Solonetz profile (or a strong texture-contrast profile).

0-5 cm	Grey-brown coarse sand.
5-40 cm	Very light grey coarse sand.
40-60 cm	Dull olive brown sandy clay with faint greenish-grey moles. The clay is markedly domed with organic staining on the surface of the domes. Some ferruginous concretions (0.5 cm diam).
60 cm	Ferruginous hard pan.

2. *Leptospermum Zone* Flat landscape

Soil profile is a *humus podzol* with following description:—

0-5 cm	Dark grey-brown coarse sand.
5-30 cm	Light grey coarse sand.
30-60 cm	Very light grey-brown coarse sand.
60 cm	Black indurated organic pan.

3. *Banksia Community on Main Sand Ridge*

The soil is composed of almost white coarse silicious sand which shows no profile differentiation other than organic staining in the surface. The sand may be 6 m deep overlying a clay substrate. There is a surface layer of decomposing organic matter. The profile on the treeless lower slopes of the ridge is similar but is not so deep.

4. *Actinostrobus Zone*

Flat or slightly hummocky landscape, slightly elevated above the *Leptocarpus* Zone—and with a Solonetzic Profile.

0-5 cm	Grey coarse sand.
5-70 cm	Very light grey sand.
70-100 cm	Yellow brown to greenish mottled sandy clay.
100-120 cm	Olive brown sandy clay with soft lime and some limestone nodules pH 8.0.

Profile A. *Leptocarpus aristatus* community on first flat.

Horizon	Depth (cm)	General Description
A0	—	Very little litter.
A1	2-8	Light grey with little organic material pH 7.0.
A2	8-12	Very light grey sand—showing signs of leaching.
	12-35	Very leached white sand.
B	35	Dull yellow sandy clay.
	60-75	Black, gritty nodules appear in the clay.
	75-100	Clay becomes purer and deep yellow.
	100-150	Very sticky bright yellow and blue mottled clay.
	165	Calcareous particles pH 9.0.

Profile B. *Leptospermum-Restio community* at base of first rise.

Horizon	Depth (cm)	General Description
A0		Considerable litter.
A1	0-15	Very dark grey sand, black when wet and considerable organic matter pH 5.
	15-60	Leached light grey sand
B1	60	Sand begins to darken and develops rapidly into a brownish hardpan.
	75-90	Dark brown coffee rock—but is very clayey. Shows definite columnar jointing during the summer.
	90-165	Clay of a light brown colour and with a few black nodules (as similar horizon in Profile A).
	170	Hard white layer of calcareous material pH 8.

Profile C. *Leptospermum-Banksia sphaerocarpa* Community.

Horizon	Depth (cm)	General Description
A0		Abundant litter.
A1	0-12	Very dark grey sand, black if wet; contains abundant organic matter pH 5.0.
	12-20	Light grey sand showing signs of leaching.
	20-90	Leached grey-white sand.
	90+	Very thick hard dark brown coffee rock pH 4.5.

Profile D. Banksia Low Scrub Woodland Community; on first ridge.

Horizon	Depth (cm)	General Description
A0		Very little litter.
A1	0-8	Grey sand with little organic matter pH 5.3.
	8-20	Light grey sand—becoming leached.
	20-152	Very leached white sand.
	152-177	Definately darkened layer of brown sand, which suggests slight tendency to form coffee rock.
	177-200	Yellow-brown clay streaked with blue at depth pH 5.2.

Profile E. *Eremaea Low* Scrub: first ridge.

Horizon	Depth (cm)	General Description
A0		Little litter.
A1	0-8	Mid-dark grey sand. pH 5.4.
	8-30	Light grey sand—showing transition to leached sand.
	30-165	Leached light grey to white sand.
	165-170	A dark brown layer of poorly formed coffee rock.
	170-180+	Brown-yellow clay. pH 5.3.

Profile F. *Actinostrobus* Community: along weak drainage line.

Horizon	Depth (cm)	General Description
A0		No litter.
A1	0-2.5	Very dark sedimentary layer—this is very low lying—represents a part of the very poorly defined drainage channel. pH 6.5.
	2.5-10	Grey sand, rapidly showing signs of leaching.
	10-35	White leached sand.
	35-60	Yellow-brown clay. pH 7.0.

Appendix II

Species List—Yule Brook Reserve

Note—Names in brackets are the names by which the species was formerly known.

PTERIDOPHYTA:

LYCOPODIACEAE:

Phylloglossum drummondii Kunze

SELAGINELLACEAE:

Selaginella gracillima (Kunze) Alston

ISOETACEAE:

Isoetes drummondii R.Br.

GYMNOSPERMAE:

ZAMIACEAEA:

Macrozamia riedlei (Gaud.) Gardn.

CUPRESSACEAE:

Actinostrobus pyramidalis Miq.

ANGIOSPERMAE—MONOCOTYLEDONEAE:

CENTROLEPIDACEAE:

Aphelia cyperoides R.Br.
A. drummondii (Hieron.) Benth.
Centrolepis aristata (R.Br.) Roem et Schultes
C. glabra (F. Muell.) Hieron.
C. humilliana (F. Muell.) Benth.
C. polygyna (R.Br.) Hieron.
Desvauxia drummondiana Nees (*C. drummondii* (Nees) Hieron).

CYPERACEAE:

Cyathochaeta avanacea (R.Br.) Benth.
Cyperus tenellus L.f.
Gahnia trifida Labill.
Isolepis marginata (Thunb) A.Dietr. (*Scirpus antarcticus* L.)
Lepidosperma angustatum R.Br.
L. resinosum (Nees) Benth.
Mesomelaena stygia (R.Br.) Nees
M. tetragona (R.Br.) Benth.
Schoenus andrewsii W.V. Fitzg.
S. asperocarpus F. Muell.
S. benthami F. Muell.
S. brevifolius R.Br.
S. curvifolius (R.Br.) Benth.
S. jamesonianus W.V. Fitzg.
S. nanus (Nees) Benth.
S. pedicellatus (R.Br.) Benth.
S. rigens (S.T.) Blake.
S. trachycarpus F. Muell.
Tetrariapsis octandra (Nees) Kuekenthal

HAEMODORACEAE:

Anigozanthos bicolor Endl.
A. humilis Lindl.
A. manglesii D. Don
A. viridis Endl.
Conostylis aculeata R.Br. ssp *preissii* (Endl.) J. W. Green
C. aurea Lindl.
C. candicans Endl.
C. filifolia F. Muell.
C. juncea Endl. (*C. involucrata* Endl.)
C. setigera R.Br.
Haemadorum brevisepalum Lindl.
H. paniculatum Lindl.
H. simplex Lindl.
H. spicatum Rr.Br.
Phlebocarya ciliata R.Br.
Tribonanthes brachypetala Lindl.
T. uniflora Lindl.
T. variabilis Lindl.

HYPOXIDACEAE:

Hypoxis occidentalis

IRIDACEAE:

Orthrosanthus laxus (Endl.) Benth.
Patersonia juncea Lindl.
P. occidentalis R.Br.
P. umbrosa Endl.

JUNCACEAE:

Juncus bufonius L.
J. capitatus Weig.
J. pallidus R.Br.

JUNCAGINACEAE:

Triglochin calcitrapa Hook.
T. centrocarpa Hook.
T. minutissima F. Muell.
T. mucronata R.Br.
T. procera R.Br.
T. stowardii N. E. Brown

LILIACEAE:

Agrostocrinum scabrum (R.Br.) Baill.
Arnocrinum preissii Lehm.
Arthropodium preissii Endl.
Borya scirpoidea Lindl.
Burchardia multiflora Lindl.
B. umbellata R.Br.
Burchardia sp.
Chamaescilla corymbosa (R.Br.) F. Muell.
Johnsonia lupulina R.Br.
J. pubescens Lindl.
Laxmannia ramosa Lindl.
L. sessiflora Dcne.
L. squarrosa Lindl.
Sowerbaea laxiflora Lindl.
Thysanotus dichotomus (Labill.) R.Br.
T. multiflorus R.Br.
T. patersonii R.Br.
T. scaber Endl.
T. sparteus Lindl.
T. thyrsoideus Baker
T. triandrus (Labill.) R.Br.
Wurmbea dioica (R.Br.) F. Muell.

ORCHIDACEAE:

Caladenia deformis R.Br.
C. discoidea Lindl.
C. flava R.Br.
C. gemmata Lindl.
C. hirta Lindl.
C. huegelii Reichb. f.
C. macrostylis W.V. Fitzg.
C. marginata W.V. Fitzg.
C. patersonii R.Br.
C. sericea Lindl.
Diuris laxiflora Lindl.
D. longifolia R.Br.
D. purdiei Diels
Elythranthera brunonis (Endl.) A. S. George
Leporella fimbriata (Lindl.) A. S. George
Lyperanthus nigricans R.Br.
Microtis atrata Lindl.
Paraceleana nigrita (Lindl.) Blaxell
Prasophylum cyphochilum Benth.
P. hians Reichb. f.
P. drummondii Reich. f.
P. macrostachyum R.Br.
P. ovale Lindl.
P. parvifolium Lindl.
Pterostylis nana R.Br.
P. vittata Lindl.
Thelymitra antennifera (Lindl.) Hook. f.
T. flexuosa Endl.

PHILYDRACEAE:

Philydrella pygmaea (F. Muell.) Car. (*Pritzelia pygmaea* (R.Br.) F. Muell.)

POACEAE:

Amphipogon turbinatus R.Br.
Danthonia occidentalis J. Vickery
Neurachne alopecuroidea R.Br.
Polypogon tenellus R.Br.
Sporobolus virginicus (L.) Kunth.
Stipa compressa R.Br.
S. hemipogon Benth.
S. variabilis Hughes

RESTIONACEAE:

Anarthria gracilis R.Br.
A. laevis R.Br.
Hypolaena exsulca R.Br.
Lepidobolus preissianus Nees
Leptocarpus aristatus R.Br.
L. canus Nees
L. coangustatus Nees
Lepyrodia macra Nees
Loxocarya fasciculata (R.Br.) Benth.
L. flexuosa (R.Br.) Benth.
L. pubescens (R.Br.) Benth.
Lyginia barbata (*L. tenax* (Labill.) Gardn.)
L. aff. barbata
Restio nitens Nees
R. sphacelatus R.Br.
R. tremulus R.Br.

XANTHORRHOEACEAE:

Acanthocarpus preissii Lehm.
Calectasia cyanea R.Br.
Dasypogon bromeliifolius R.Br.
Lomandra caespitosa (Benth.) Ewart
L. endlicheri (F. Muell.) Ewart
L. hermaphrodita (C. Andrews) C. A. Gardner
L. micrantha (Endl.) Ewart
L. preisii (Endl.) Ewart
Xanthorrhoea gracilis
X. preissii Endl.

ANGIOSPERMAE—DICOTYLEDONAE:

AIZOACEAE:

Macarthuria australis Hueg.

AMARANTHACEAE:

Ptilotus drummondii (Moq.) F. Muell.

APIACEAE: (UMBRELLIFERAE)

Actinotus leucocephalus Benth.
Eryngium pinnatifidum Bunge
Homalosciadium homalocarpum (F. M. Muell.) H. J. Eichler
Hydrocotyl callicarpa Bunge
Schoenolaena tenuior Bunge
Trachymene pilosa Sm.
Xanthosia huegelii (Benth.) Steud.

ASTERACEAE: (COMPOSITAE)

Angianthus pygmaeus (A. Grey) Benth.
A. strictus (Steetz.)Benth.
A. tenellus (F. Muell.) Benth.
Brachycome pusilla Steetz
Chrysocoryne drummondii A. Gray
Cotula coronopifolia L.
C...pratense
Craspedia uniflora G. Forster
Helichrysum bracteatum (Vent.) Andr.
Helipterum cotula (Benth.) DC.
Isoetopsis graminifolia Turcz.
Lagenifera huegelii Benth.
Olearia sp.
Podolepis gracilis R.Grah.
P. nutans Steetz
Podotheca angustifolia (Labill.) Less.
P. chrysantha (Steetz) Benth.
P. gnaphalodes Grah.
Quinetia urvillei Cass.
Siloxerus filifolius (Benth.) Ostenf. (*Angianthus filifolius (Benth.)* C.A. Gardn.)
S. humifusus Labill. (*A. humifusus* (Labill.) Benth.)
Trichocline sp.
Waitzia paniculata (Steetz) F. Muell. ex Benth.

BYBLIDACEAE:

Byblis gigantea Lindl.

CALLITRICHACEAE:

Callitriche stagnalis Scop.

CASUARINACEAE:

Casuarina fraseriana Miq.
C. humilis Otto et Dietr.

CHENOPODIACEAE:

Halosarcia halocnemoides (Nees) P. G. Wilson, comb. nov. (*Arthrocnemum halocnemoides* Nees)

CLOANTHACEAE: (VERBENACEAE)

Pityrodia uncinata (Turcz.) Benth.

CONVOLVULACEAE:

Cuscuta epithymum L.
Wilsonia backhousii Hook.

CRASSULACEAE:

Crassula colorata (Nees)Ostf.
C. recurva (Hook. f.) Ostf.

DILLENIACEAE:

Hibbertia aurea Steud.
H. huegelii (Endl.) F. Muell.
H. hypericoides (DC.) Benth.
H. racemosa (Endl.) Gilg.
H. stellaris Endl.

DROSERACEAE:

Drosera bulbosa Hook.
D. erythrorhiza Lindl.
D. gigantea Lindl.
D. glanduligera Lehm.
D. heterophylla Lindl.
D. leucoblasta Benth.
D. macrantha Endl.
D. menziesii R.Br.
D. neesii Lehm.
D. occidentalis A. Morrison
D. palacea DC.
D. pallida Lindl.
D. stolonifera Endl.
D. zonaria Planch.

EPACRIDACEAE:

Andersonia aristata Lindl.
A. gracilis DC.
A. sprengelioides R.Br.
Astroloma pallidum R.Br.
A. stomarrhena Sond.
Conostephium pendulum Benth.
Leucopogon conostephioides DC.
L. oxycedrus Sond.
L. polymorphus Sond.
L. propinquus R.Br.
L. pulchellus Sond.
L. racemulosus DC.
L. squarrosus Benth.
Lysinema ciliatum R.Br.
Needhamiella pumilio (R.Br.) L. Watson

EUPHORBIACEAE:

Monotaxis grandiflora Endl.
Phyllanthus calycinus Labill.
Poranthera microphylla Brongn.

FABACEAE: (PAPILIONACEAE)

Bossiaea eriocarpa Benth.
Burtonia conferta DC.
Daviesia incrassata Sm.
Dillwynia cinerascens R.Br.
Euchilopsis linearis (Benth.) F. Muell.
Eutaxia virgata Benth.
Gompholobium tomentosum Labill.
Hovea trisperma Benth.
Isotropis cuneifolia (Sm.) Benth. ex B. D. Jackson
Jacksonia floribunda Endl.
J. furcellata (Bonpl.) DC.
J. lehmannii Meisn.
J. sternbergiana Hueg.
Kennedya prostrata R.Br.
Oxylobium capitatum Benth.
Sphaerolobium medium R.Br.
Viminaria juncea (Schrad & Wendl.) Hoffmans.

GENTIANACEAE:

Villarsia albiflora F. Muell.

GOODENIACEAE:

Anthotium humile R.Br.
Dampiera linearis R.Br.
Goodenia caerulea R.Br.
G. filiformis R.Br.
Lechenaultia expansa R.Br.
Scaevola canescens Benth.
S. longifolia De Vries
S. paludosa R Br.
Velleia trinervis Labill.

HALORAGACEAE:

Gonocarpus pithyoides Nees (*Haloragis pithyoides* (Nees) Benth.)

LAMIACEAE:

Hemiandra pungens R.Br.

LAURACEAE:

Cassytha flava Nees
C. micrantha Meisn.

LENTIBULARIACEAE:

Polypompholyx multifida (R.Br.) F. Muell.
P. tenella (R.Br.) Lehm.
Utricularia inaequalis A.DC. (*U. hookeri* Lehm.)
U. menziesii R.Br.
U. violacea R.Br.

LOBELIACEAE:

Isotoma hypocrateriformis (R.Br.) Druce
I. pusilla Benth.
Lobelia alata Thunb.
L. gibbosa Labill.
L. tenuior R.Br.
Monopsis simplex (L.) E. Wimm.

LOGANIACEAE:

Mitrasacme paradoxa R.Br.

LORANTHACEAE:

Nuytsia floribunda (Labill.) R.Br.

MALVACEAE:

Selenothamnus squamatus (Nees) Melville (*Plagianthus squamatus* (Nees) Benth.)

MIMOSACEAE:

Acacia huegelii Benth.
A. pulchella R.Br.
A. saligna Wendl. (*A. cyanophylla* Lindl.)
A. stenoptera Benth.
A. lasiocarpa Benth.

MYRTACEAE:
Astartea fascicularis (Labill.) DC
Baeckea camphorosmae Endl.
Beaufortia squarrosa Schau.
Calothamnus lateralis Lindl.
C. aff. villosus R.Br.
Calytrix aurea Lindl.
C. flavescens A. Cunn.
C. fraseri A. Cunn.
Aremaea pauciflora (Endl.) Druce
Eucalyptus calophylla R.Br.
E. rudis Endl.
Hypocalymma angustifolium Endl.
H. robustum Endl.
Kunzea micrantha Schau.
K. vestita Schau. (*K. ericifolia Reichb.*)
Leptospermum ellipticum Endl.
Melaleuca bracteosa Turcz. (*M. fasciculiflora* Benth.)
M. hamulosa Turcz.
M. lateriflora Benth.
M. lateritia A. Dietr.
M. preissiana Schau. (*M. parviflora* Lindl.)
M. rhapiophylla Schau.
M. scabra R.Br.
M. seriata Lindl.
M. uncinata R.Br.
M. viminea Lindl.
Regelia ciliata Schau.
Scholtzia involucrata (Endl.) Druce
Verticordia acerosa Lindl.
V. densiflora Lindl.
V. drummondii Schau.
V. huegelii Endl.
V. lindleyi Schau.
V. plumosa (Desf.) Domin.

POLYGALACEAE:
Comesperma virgatum Labill.

PORTULACEAE:
Calandrinia corrigioloides (F. Muell.) Benth.
C. granulifera Benth. (*C. pygmaea* F. Muell.)

PRIMULACEAE:
Samolus junceus R.Br.

PROTEACEAE:
Adenanthos cygnorum Diels
Banksia attenuata R.Br.
B. grandis Willd.
B. ilicifolia R.Br.
B. littoralis R.Br.
B. menziesii R.Br.
B. telmatiaea A. S. George
Conospermum huegelii R.Br.
C. stoechadis Endl.
C. triplinervium R.Br.
Dryandra nivea (Labill.) R.Br.
Grevillea thelemanniana Hueg.
Hakea candolleana Meisn.
H. ceratophylla (Sm.) R.Br.
H. prostrata R.Br.
H. sulcata R.Br.
H. varia R.Br.
Persoonia angustiflora Benth.
P. saccata R.Br.
Petrophile linearis R.Br.
P. longifolia R.Br.
P. macrostachya R.Br.
P. media R.Br.
P. seminuda Lindl.
Stirlingia latifolia (R.Br.) Steud.
S. simplex Lindl.
Synaphea petiolarie R.Br.
S. spinulosa (Burm. an.) *Merrill* (*S. polymorpha* R.Br.)

RUBIACEAE:
Opercularia vaginata Labill.

RUTACEAE:
Boronia viminea Lindl.
Eriostemon spicatus A. Rich.

SANTALACEAE:
Leptomeria empetriformis Miq.

SAPINDACEAE:
Dodonaea ceratocarpa Endl.

STACKHOUSIACEAE:
Stackhousia brunonis Benth.
S. huegelii Endl.

STYLIDIACEAE:
Levenhookia preissii (Sond.) F. Muell.
Stylidium amoenum R.Br.
S. brunonianum Benth.
S. bulbifera Benth.
S. calcaratum R.Br.
S. canaliculatum Lindl.
S. carnosum Benth.
S. dichotomum DC.
S. diuroides Lindl.
S. divaricatum Sond.
S. ecorne (F. Muell ex Erickson & Willis) comb & status nov.
S. guttatum R.Br.
S. inundatum R.Br.
E. obtusatum Sond.
S. perpusillum Hook. f.
S. petiolare Sond.
S. piliferum R.Br.
S. pulchellum Sond.
S. repens R.Br.
S. roseo-alatum Erickson & Willis
S. schoenoides DC.
S. striatum Lindl.
S. utricularioides Benth.

THYMELAEACEAE:
Pimelea imbricata R.Br. var. gracillima Meisn.
P. sulphurea Meisn.

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The Silvereye (*Zosterops lateralis*: Aves: Zosteropidae): a review

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Abstract

Silvereyes have been pests of fruit crops since the last century but research to combat the problem has been minimal. They have a catholic diet with most documented items being arthropods from stomach contents. Nectar is an important food item in Western Australia because an abundant supply limits damage to crops of grapes. Migration in the eastern states is well known but only after the banding of more than 100 000 individuals. The banding of 36 000 in Western Australia has shown little evidence of systematic movements. The study of agonistic behaviour has suggested that aggressive behaviour is disadvantageous at feeding stations. Dominant individuals, however, survive better through winter and are more likely to breed. The study of a colour-banded population in New Zealand in 1939-40 provided information on breediing and territorial and vocal behaviour. Adult Silvereyes moult completely post-nuptially and partly pre-nuptially. Juveniles hatched early moult similarly but late-hatched juveniles' first moult is arrested and then the pre-nuptial moult is a complete moult. Variation in plumage colouration was first used to suggest the eastern migration and has been used with varying degrees of success to predict the sex of an individual. Body weight is lowest in the morning and 7% heavier in the late afternoon. Weight has been shown to be negatively correlated with daily air temperature and southern birds are heavier than northern ones. Maximum weight is attained during winter.

Introduction

Although Silvereyes are well known to amateur and professional ornithologists, many who have worked with them find them frustrating subjects to study because they are small, well camouflaged and secretive and, therefore, difficult to observe. In addition, the extent of our present knowledge is not great enough to allow an interpretation of some aspects of their biology that have been under investigation for some time. For instance, many amateur bird-banders in Western Australia are frustrated by the low recapture and recovery rate of their banded Silvereyes and by the fact that banded individuals do not seem to visit between banding stations that are as close as two km any more than between those that are 20 km apart. The resolution of such problems will undoubtedly take place as more data accumulates. In the meantime, it is valuable and encouraging to realise that many years of patient and dedicated work has provided substantial information about this animal. The purpose of this paper is to demonstrate that our knowledge of the Silvereye is greater than many may realise as well as to provide a basis for further research.

I have divided the information into seven sections: pest status, diet, movements, social behaviour, moult, colour variation and body weight.

Pest Status

Silvereyes have been well known to fruit growers in Western Australia ever since the days of the early settlements. Dalkeith Farm, described as a fruit garden extending along the Swan River and worked by James Gallop from 1877, was an important property to the new colony because of the produce it supplied to the north-west ports and Albany, as well as to Perth and Fremantle. By 1886 Silvereyes had become troublesome amongst the fruit and two Aborigines were employed to shoot the birds, more than 8 500 being shot in one year (Oldham and Williams 1980). Later, Aborigines were employed to frighten the birds away from the crops by beating kerosene tins with sticks (Hallack 1891, Oldham and Williams 1980). At least 20 000 Silvereyes were shot on this property and in another orchard near Bunbury 1 200 were shot in one day (Serventy and Whittell 1976, p. 403). Milligan (1904) claimed that 20 000 Silvereyes were often shot in a single orchard in a season.

Silvereyes were thought to be such a serious pest that in 1897 the Bureau of Agriculture proposed a bonus for their destruction of one shilling per 100 birds. The bonus was dependant upon a similar sum being paid by the Local Agricultural Societies (Anon. 1897).

In 1902 a deputation from the Bunbury district met with the Minister for Lands advising him of the considerable damage the Silvereye was causing to fruit in their area and that a recent meeting at Bunbury had resolved to ask the Minister to send an officer "to inquire into the habitat of the bird." They, too, wanted the Government to provide money for a bounty payment (Anon. 1902).

In 1904 a bonus of two shillings per 100 was proposed in a letter to the Minister for Lands by a frustrated fruit grower (Anon. 1904). He claimed that Silvereyes, as well as damaging fruit, destroy beneficial insects such as ladybirds which would otherwise have saved his citrus crop from a bad infestation of scale insects. Amongst his suggested methods for exterminating the species was that the Department's ornithologists should look to the possibility of parasitising the Silvereye. Milligan (1904) replied in defence of Silvereyes maintaining their usefulness in controlling insects that would otherwise be a problem. He proposed that a study be initiated to analyse the gut contents of Silvereyes to determine exactly what insects they do eat, as well as suggesting several methods to reduce the damage caused by Silvereyes to fruit. Newman (1924) supported the role of Silvereyes in maintaining the "balance of nature" by destroying unwanted insects. He claimed that the bulk of food found in the Silvereyes' stomachs was insects, particularly scales and aphids. He did not say if this latter claim was the result of the study proposed by Milligan (1904).

Apart from the limited use of a promising acoustic device developed by Knight and Robinson (1978a and 1978b), methods for controlling Silvereyes in fruit crops have advanced little from that of shooting to picking the crop early.

Diet

It is now well documented that Silvereyes are insectivorous as first reported by Cleland (1911 and 1912) and later summarised (Cleland *et al.* 1918). Matthiessen (1973) and Matthiessen and Springett (1973) found that Silvereyes ate arthropods of eight orders when they were feeding in and near potato crops in the Manjimup-Pemberton area of southwest Western Australia. The most common food was Lepidopteran larvae (mainly potato moth, *Phthorimaea operculella*), Coleopteran larvae and Hemiptera. In years when a particular food item was most abundant in the potato crops, that food item was found to be most common in the Silvereyes sampled. This shows that Silvereyes adjust their foraging behaviour to take the most abundant food item. In addition to this, Springett and Matthiessen (1975) showed that Silvereyes preferred to eat the larger fourth instar of the potato moth when larvae densities were low but, when larvae densities increased, the smaller third instar became increasingly attractive. This occurred despite equal abundance of both instars and indicates that Silvereyes respond to prey on a cost/reward basis. When prey numbers are low the birds prefer the larger items because the energy cost of capturing the smaller prey is too great with respect to the energy reward. When the prey is abundant no such preference is shown because the smaller items are common enough for their capture to require less energy expenditure.

In a New Zealand apple orchard, Moeed (1979) found that the food of Silvereyes in winter consisted of 14 orders of arthropods as well as earthworms, fruit and seeds. Lea and Gray (1936) and Rose (1973) also listed arthropods that they found in stomachs of Silvereyes.

It is generally known that Silvereyes have a wide range in diet, but little has been published on their diet other than arthropods. In South Africa the Yellow White-eye (*Zosterops senegalensis*) has been seen eating very strong red peppers that "pack a powerful punch" when added to a Chadian curry (Elliott 1977). Silvereyes regularly eat soft fruits, particularly grapes, in southern Australia and in late summer can be a nuisance in vegetable gardens eating such things as capsicums and tomatoes. In March, 1980, near Margaret River, Western Australia, two birds that I had banded were found in a bucket of milk where they had drowned, presumably whilst trying to drink the milk. Nectar is a favourite food of Silvereyes although confirming data is difficult to collect for such small birds.

Cage experiments have shown that they prefer sugar water more than various fruits (Rooke unpub.) and Ford (1979) reported observations of foraging Silvereyes that gave a ratio of nectar to insect feeding of 20:80. There is strong circumstantial evidence that Silvereyes have a preference for nectar over fruit. In southwest Western Australia, when the marri (*Eucalyptus calophylla*) produces large amounts of nectar during the fruit ripening season, Silvereyes are not seen in orchards and vineyards. Conversely, when the nectar crop is poor, Silvereyes cause great damage to the fruit (Robinson 1960, Rooke in prep.). Additional circumstantial evidence is that Silvereyes carry heavy loads of eucalypt pollen during times when marri flowers and the birds are absent from vineyards (Rooke unpub.). Observation of feeding as well as analysis of stomach content of Silvereyes in southwest Western Australia are showing the variety of food items taken. As well as 11 orders of arthropods, fruit or berries are taken from 18 species of plants, and nectar is taken from eight species (Rooke unpub.).

Hopper and Burbidge (unpub.) observed 57 plant species from which Silvereyes have been seen to eat nectar, berries, insects or seeds. Forty-nine of these are records of nectar feeding.

Table 1 summarizes the orders of arthropods that Silvereyes are known to eat.

Movements

My banding of Silvereyes around the Margaret River area of southwest Western Australia is indicating that the local population does not move far. Out of 11 000 birds banded so far only one has been recovered at a distance—at Manjimup 100 km ESE. All other recoveries have been within 50 km (Fig. 1).

Banding work at Middlesex near Manjimup, by Dick and Molly Brown has shown a few distant movements (one 267 km N, one 114 km NNE, two 100 km WNW) but other recoveries have been within 35 km (Dick and Molly Brown 1978-79;

Table 1

Orders of arthropods that Silvereyes are known to eat.

Order	Reference 1	2	3	4	5	6	7
Collembola					x	x	x
Blattodea						x	x
Orthoptera							x
Psocoptera						x	
Phthiraptera							x
Hemiptera	x	x	x	x	x	x	x
Thysanoptera	x					x	x
Neuroptera	x				x		
Coleoptera	x	x		x	x	x	x
Diptera	x			x	x	x	x
Lepidoptera	x	x	x	x	x	x	x
Hymenoptera	x	x		x	x	x	x
Pseudoscorpionidea						x	
Araneida	x	x	x		x	x	x
Opiliones						x	
Acarina	x					x	
Amphipoda						x	

1—Cleland *et. al.* (1918); 2—Lea and Gray (1936); 3—Rose (1973); 4—Matthiessen (1973); 5—Matthiessen and Springett (1973); 6—Moeed (1979); 7—Rooke (unpubl. data).

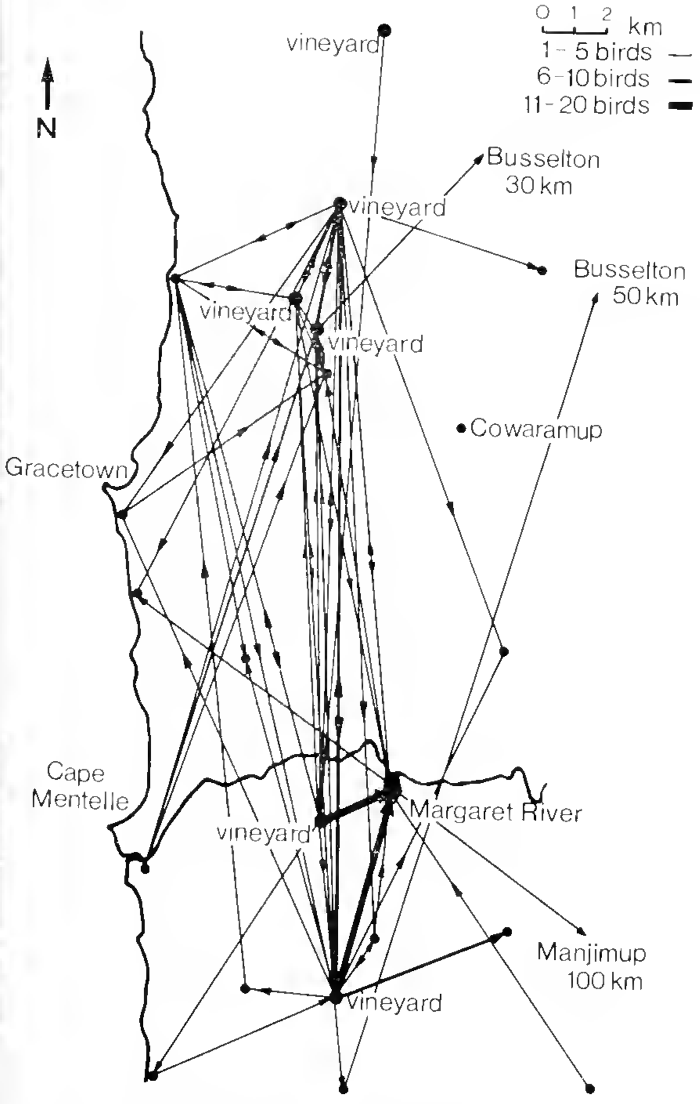

Figure 1.—Movements of Silvereyes near Margaret River, Western Australia. (Rooke unpubl. data)

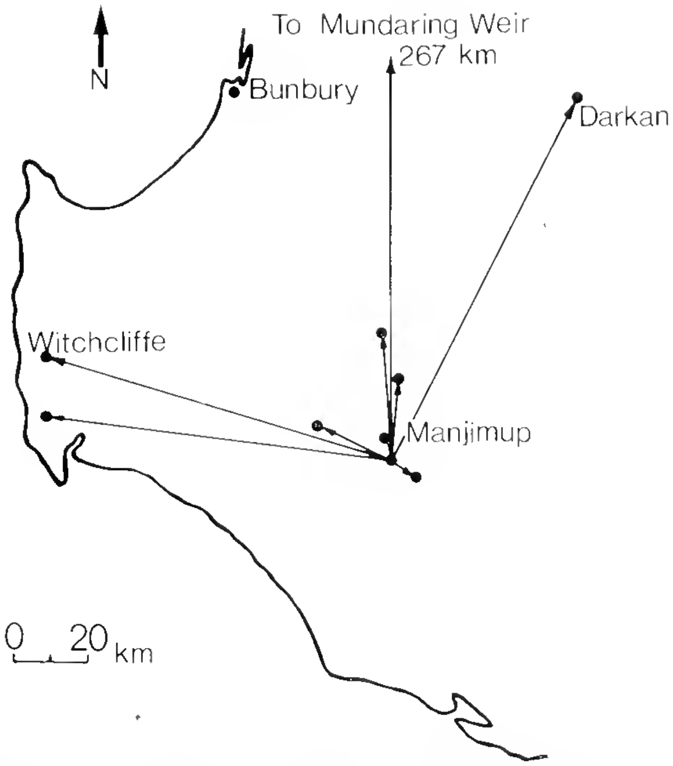

Figure 2.—Movements of Silvereyes from Middlesex, Western Australia. (from Brown 1978-9, 1979-80)

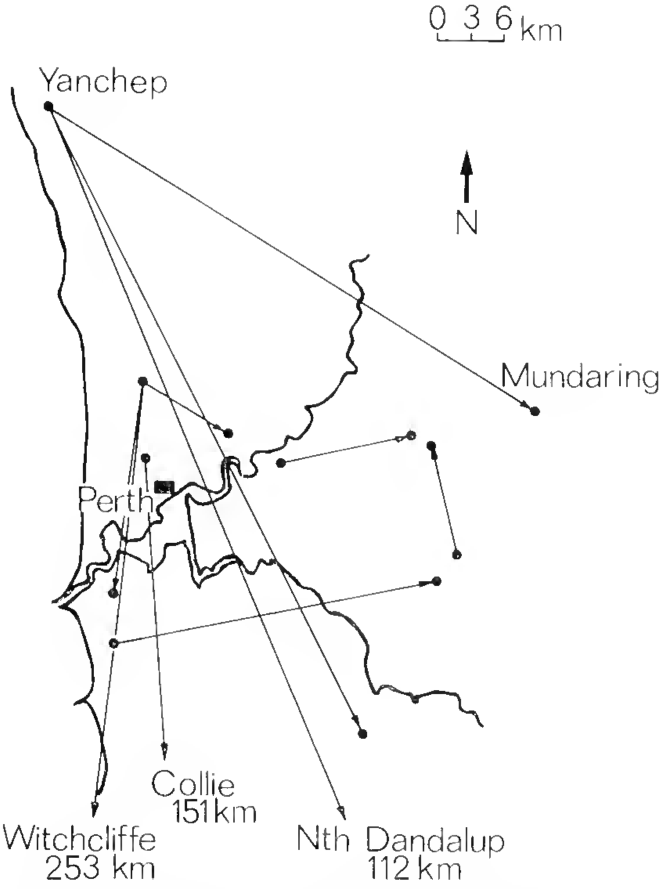

Figure 3.—Movements of Silvereyes from areas near Perth, Western Australia. (P. de Rebeira, unpubl. data)

1979-80) (Fig. 2). The Browns have banded approximately 10 000 Silvereyes but their efforts have failed to show any systematic movement.

Over the past 10 years, a number of people in and near Perth have banded approximately 15 000 Silvereyes. They have demonstrated several long movements of 100 to 300 km, all of which have been recovered south from where they were banded (Fig. 3). It may be that the birds which move south are a particular category of bird (e.g. juvenile) or perhaps recoveries have been made in the regions south rather than north of Perth because there are more settlements south and therefore more people to find banded Silvereyes. In addition to this, small flocks of Silvereyes have been observed moving southward along the coast in late summer. However, there is no evidence to suggest a return, northward movement (P. de Rebeira, pers. comm.).

Western Silvereyes may be more sedentary than some of their eastern counterparts, although such a conclusion may be rather hasty when viewed with the experience of the banding work in the eastern states. In 10 years, more than 100 000 birds were banded in the eastern states and the recoveries showing the long-distance movements amounted to only 75 (45 moving 50-300 km and 30 moving more than 300 km) (Lane 1972). This is a mere 0.00075% of the total birds banded and is a good example of the enormous effort required to substantiate such a phenomenon. Figure 4, from Hitchcock (1966, p. 11) shows some of these movements.

The idea of migration in eastern Australia was first suggested by Keast (1958) after he had noted the systematic arrival and departure of Tasmanian-type birds, as well as having caged Tasmanian-type birds to demonstrate that their plumage colouration was not changeable as proposed by others. Keast also noticed that the migration was partial because a considerable number of Silvereyes remained in Tasmania all winter.

Observations of Tasmanian-type Silvereyes in New South Wales during winter were also reported by Lane (1962a) and Swanson (1968) and in SE Queensland by Robertson (1971). The migration idea started to receive support by the movement of banded birds between Tasmania and the eastern coast of New South Wales (Lane 1962b, Liddy 1966). Substantial movement occurs at night, northward in autumn and early winter and southward in late spring/early summer (Lane and Battam 1971), although movement continues during the day at lower altitudes (Lane and Battam 1971, Vincent 1978). (Other progressive reports of the Co-operative Silvereye Project are listed in Lane (1972). Some individuals of the eastern Silvereye population, however, are sedentary (Bradley 1963, Liddy 1966, Swanson 1968, Lane 1972) and Lane (1972) suggested two discrete breeding populations one migratory and the other sedentary. The data do not support such a simple explanation for the Tasmanian-type Silvereyes, because some individuals migrate in some years but not in others (Mees 1974). In addition, it is not the juvenile class only that migrates because old birds constitute a large proportion of the migrants *(op. cit.)*.

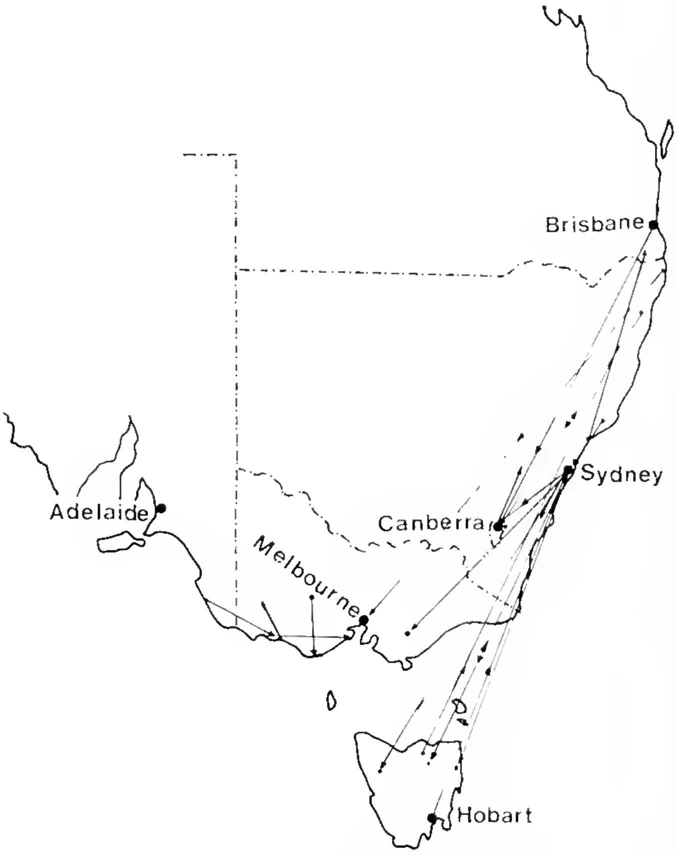

Figure 4.—Movements of Silvereyes in south-eastern Australia. (from Hitchcock 1966)

Fleming (1943) suggested that the Silvereyes in New Zealand do not migrate but that large winter flocks form from the aggregation of the breeding population of the district, and the flocks then disperse over a wider area. This conclusion is supported by the banding work reported by Marples (1944).

Localised movements may be made by particular age classes because Keast (1958) showed that only juvenile Silvereyes moved into vineyards near Sydney whilst the adults remained in the breeding areas. It remains to be shown that this phenomenon is more widespread.

Social behaviour

The social behaviour of Silvereyes has been studied in some detail in various locations by Kikkawa. At Dunedin, New Zealand, Kikkawa (1961) studied aggressive behaviour at a feeding station and in an aviary. He identified five types of aggressive behaviour which serve to establish and maintain the social hierarchy of a group but which, at a concentrated source of food such as the feeding station, seem to be disadvantageous both to the dominant and subordinant birds. Although there were numerous feeding stations in the Dunedin area which were likely to influence the natural population (Kikkawa 1960), Kikkawa (1961) argued that aggressive behaviour would be advantageous to the majority of birds in a less crowded situation.

The aviary birds behaved very aggressively when first caged or when new birds were introduced, but after two weeks of undisturbed occupancy, aggressive behaviour was reduced.

The study of the social hierarchy of winter flocks of Silvereyes was continued at Armidale, New South Wales (Kikkawa 1968). The birds showed the same agnostic displays as those in New Zealand and the southern migratory birds tended to dominate the locals as did males to females. The dominance hierarchy in caged birds did not appear to depend on the weights of the individuals. Territorial behaviour was induced by separating pairs into small cages and then when the small cages were connected, to allow free access to all birds, the original group social hierarchy was evident. This behaviour suggested that the social hierarchy of the winter flock may be important in determining the success of establishing a territory at the beginning of the breeding season.

A more detailed study of the agonistic behaviour of caged Silvereyes was undertaken by Williams *et al.* (1972). They used a numerical technique to analyse the postures of individual birds and, by so doing, were able to identify four of the five behavioural classes originally postulated by Kikkawa (1968), viz: the aggressive bird, the intermediate bird, the submissive bird and the inactive or subordinate bird. Their method failed to identify the dominant bird class. Their results suggested that agonistic behaviour of the flock is initiated largely by a single bird and perhaps influenced by humidity. The social hierarchy appeared to exist at two different levels; one stable hierarchy between groups of birds and another secondary level within each group that is weaker and changeable.

Kikkawa (1977) briefly summarised his earlier work on Silvereyes as a background to describing his work with Silvereyes on Heron Island, Queensland. Between 1965 and 1969 he colour-banded individuals at the beginning of each winter and recorded aggressive behaviour between them. With these data, and by censusing the birds at the end of winter, he found that dominant individuals survived better than submissive ones.

Additional work by Kikkawa and his postgraduate students (Kikkawa *et al.* 1975; Kikkawa 1977) showed that the population on Heron Island does not fluctuate markedly from year to year and, even when the population is severely reduced by cyclones, mortality of the remainder of the population is consequently reduced because of lowered competition for food. The population recovers to its previous density in the next breeding season.

Kikkawa and his students *(op. cit)* studied the breeding success of individuals of various behavioural categories and found that, in years of high density, significantly more pairs high in dominance nested and many first year birds, particularly submissive ones, failed to breed. Independent young were likely to be similar to their parents in dominance status.

The most recent report about the work on Heron Island Silvereyes (Kikkawa 1980) analysed in greater detail the survival through winter between 1965 and 1969 of individuals of different dominance classes. The results showed that socially dominant individuals were more likely to survive their first winter and that juveniles born earlier in the breeding season were more likely to be dominant. Body weight at the start of winter was not significant in affecting a bird's survival through winter. Dominant birds were considered to be more likely to survive because of their superior right of access to food.

Kikkawa's work emphasizes the important difference between dominance and aggressiveness. Dominant individuals (i.e. those that win agonistic encounters) are not always very aggressive and do not spend much energy fighting. On the other hand, aggressive individuals spend much time and energy fighting but but do not always win encounters.

The first published study of colour-banded Silvereyes was carried out in New Zealand by Fleming (1943). He worked mainly on his own property of 0.5 ha during 1939 and 1940. The breeding season was from mid-October until late February or early March with some pairs having three broods in one season. Some individuals and pairs used the same territory and nesting-tree in successive seasons although territorial behaviour did not exist during winter when the birds formed flocks that moved more widely. Fleming provided data about mating, nest-building, egg-laying, hatching, fledging, reproductive success and juvenile mortality. He studied some details of vocal behaviour and touched on the complexities of territoriality.

Moult

Swanson (1971) studied Silvereyes in her backyard in a Sydney, New South Wales, suburb and provided important details about the moult of free-flying birds. The main post-nuptial moult occurs from January to April and is a complete moult in adult birds and juveniles that are hatched early in the breeding season. Juveniles hatched later in the breeding season may commence moulting in their first autumn but this is arrested by the onset of winter and is completed before breeding in the following spring. The pre-nuptial moult of adult birds is mainly a replacement of head feathers. Swanson substantiated the earlier work of Keast (1956), the latter supporting his findings with details of the histology of the thyroid and experiments that demonstrated that changing day-length is the probable environmental factor affecting the timing of the moult. Marples (1945) found that Silvereyes in New Zealand also moult in spring and autumn.

Colour variation

Individual variation in the colour of plumage of Silvereyes has received some attention since Keast (1958) first used such a distinction to infer that Tasmania Silvereyes migrated to the mainland. Robertson (1972) analysed the colour of undertail, throat and flank of Silvereyes in Queensland, and found that the undertail colour decreases in intensity from northern to southern birds. Kikkawa (1963) found that the flank colour of Silvereyes in New Zealand could be used to determine sex, males having a darker or more reddish flank. He suggested that Australian Silvereyes could be sexed on the basis of the colour of the flank but this was not supported by McKean (1965) or Mees (1969). Serventy and Whittell (1976) note that, for Western Australian Silvereyes, the male has brighter yellow on the throat than the female. My observations in the Margaret River area suggest that it may be possible to make such a distinction only if a known pair is being considered because the variation in intensity of the throat colour between males and between females is considerable.

Body Weight

The weights of New Zealand Silvereyes have been analysed on a seasonal and diurnal basis by Marples (1945). He found a diurnal weight fluctuation of 7% with the weight lowest in the early morning and heaviest in the late afternoon. The mean daily weight showed an inverse correslation with the mean daily air temperature. The New Zealand Silvereyes were heaviest in winter which is similar to the data obtained by Dick and Molly Brown (pers. comm.) near Manjimup, Western Australia. McKean (1965) suggested that southern Silvereyes may be heavier than more northern ones, but realised that the issue is complicated by the accumulation and/or expenditure of fat reserves by individuals that have migrated or may be about to migrate. Walker (1964) weighed Silvereyes at Turramurra, New South Wales and, identifying the origin of individuals on the basis of throat and flank colour, found that average weight increased from northern to southern birds.

Conclusion

A great deal of interesting and useful information has been accumulated about numerous aspects of the life of the Silvereye in the Australian and New Zealand regions. Whilst much of this work has been thorough and painstaking, it is clear that there are many unanswered questions.

We know little of the dynamics of the bird's natural food supply and its relationship to movements and consequent damage to crops. Aspects of the bird's physiology may demonstrate why it is such a pest in fruit crops. We know little of the reproductive potential, juvenile recruitment and actual population size, nor of how human agricultural practices affect the population. Studies are needed to determine the age structure of populations in various localities and habitats, to determine whether different classes of birds are involved in different activities. We do not know whether the adult breeding class ever interferes with human activities or whether it remains in natural, undisturbed areas. Answers to these types of questions would allow not only a better understanding of the population dynamics of the species but also a rational assessment of the conflict that this bird presents between agricultural productivity and conservation of natural resources.

We need to known much more about the basic biology of the Silvereye and, because the large number that have been banded suggests that the poulation is large, a concentrated effort by many workers together is likely to be successful in elucidating the broader issues.

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