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Kelvin Medallist, 1955 : H. W. Bennetts, C.B.E., D.V.Sc.

The Kelvin Medal of the Royal Society of Western Australia Incorporated, was inaugurated in 1924, and is awarded at intervals of four years or more for distinguished work in science connected with Western Australia. The medal for 1955 has been awarded to Dr. H. W. Bennetts, Principal of the Animal Health and Nutrition Laboratory of the Department of Agriculture of Western Australia.

Harold William Bennetts was born in Melbourne on 18th July, 1898, and educated at Wesley College and the University of Melbourne, where he gained the degrees of B.V.Sc. (1919), M.V.Sc. (1920) and D.V.Sc. (1931). After serving in the Field Artillery in World War I, he became Microbiologist in the Commonwealth Department of Health and was in North Queensland during 1921 and 1922. In 1923 he was appointed Lecturer and Demonstrator in Pathology and Bacteriology in the Melbourne Veterinary School and in 1925 became Veterinary Pathologist in the Department of Agriculture in Perth. He has remained an officer of that department, apart from the period 1928-1935, when he was seconded to C.S.I.R. and has been Principal of the Animal Health and Nutrition Laboratory at Nedlands since its establishment in 1947. He has also been a Visiting Lecturer in the Faculty of Agriculture of the University of Western Australia.

Dr. Bennetts was a member of the Council of this Society for most of the period 1929-1944 and was President during 1934-1935. His Presidential Address was entitled "Plants Poisonous to Live Stock in Western Australia." This was a field in which he took a great deal of interest and worked in association with the Government Botanist (Mr. C. A. Gardner). The fruits of their joint work are soon to appear in a richly illustrated work "The Toxic Plants of Western Australia."

Dr. Bennetts first made his name in veterinary research by his solution of a sheep disease (entero-toxaemia), known in the early days as the Beverley sheep disease and latterly as the braxy-like disease, which had worried sheep-owners and baffled veterinary investigators for years. Subsequently he made notable contributions to the understanding and treatment of copper deficiency and the oestrogenic effects of subterranean clover, both major problems to the stock-owners of Western Australia. He also made many valuable contributions to other problems and the results of his researches between 1926 and 1955 are published in over 50 papers in various scientific journals.

Dr. Bennetts is a Fellow of the Australian and New Zealand Association for the Advancement of Science and was President of Section L at the Adelaide Meeting in 1946. He is also a Fellow of the Australian Veterinary Association and an Honorary Member of the Royal Society of Medicine, London. In 1948 he was honoured by the award of a C.B.E.

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1.—Laterite and Materials of Similar Appearance in South-Western Australia

Presidential Address, 1954

By S. E. Terrill, B.Sc., A.R.A.C.I., F.G.S.

Delivered—19th July, 1954

Introduction

The publication in 1952 of two small books, namely, "Problems of Clay and Laterite Genesis" and "Laterite and Lateritic Soils" emphasises the differences of opinion concerning the nature of laterite. It is difficult, at times, when reading these two books, to realise that both are written about what is supposed to be the same thing, namely, Laterite.

Laterite and lateritic gravels are to be found advertised in the daily press "For sale" columns as "gravel, best conglomerate," and whatever various scientific workers may say laterite really is, all are agreed that it is not a conglomerate, that is, a rock made up of waterworn boulders or pebbles set in a matrix usually of sand—mixed with a little clay perhaps—and hardened to a firm, solid rock.

A term in common use is "ironstone" and for general comprehensive use for dark coloured more or less massive, vermicular or concretionary, strongly coherent forms this term is very suitable for field use whilst "ironstone gravel" can be well applied to the loose unconsolidated material. This is not a strictly correct use of the term "gravel" perhaps but is sufficiently descriptive of the dark, reddish brown to black rounded stones in a loamy sand or sandy loam matrix. There are other forms which are light in colour and obviously do not contain much iron for which the term "ironstone" is clearly unsuitable. These forms are generally light brown and have the appearance of consolidated gravel or of a rock which will readily yield gravel but it is still more or less coherent: to these forms, for want of a better name, the term "gravelstone" is applied by the speaker for a field use prior to a more detailed examination in the laboratory.

Such names, while not attractive perhaps, are nevertheless descriptive and do not suffer from any implication of origin. Nor do they serve to cloak—as does the term "laterite" as it is widely used—manifest differences in mineral constitution and of structures and textures.

There is still considerable confusion at the present time in the use of the term "laterite." It is necessary that there should be some sorting out of the different types of rock now commonly included in the term by many who have contact with these, and the development of new names for some of them.

Mineralogical science was to see an immense proliferation of terms during the 19th Century. A different name would be given to a mineral from a new locality because it differed in some physical aspect such as colour or form from a previously described mineral of essentially the same composition. That process has been reversed of late, following upon a better understanding of the essential characters of minerals which has followed upon the X-ray studies of the past 40 years or so. Mineralogical nomenclature is becoming simpler and many names are gradually falling into disuse.

It is interesting to trace the application of the term "laterite" from the time it was first used by Francis Buchanan, M.D., F.R.S. up to the present dilemma, and to try and see along what lines further progress can be made. Despite assertions from time to time by various authors that this or that particular interpretation is generally accepted, there is indeed no universal acceptance of any particular usage even to this day, nor has there been over the past 50 years or so.

Since there is considerable emphasis placed on Buchanan's usage by some, particularly by soil scientists in Australia and elsewhere, it is perhaps desirable to examine Buchanan's journal of his journeyings in Southern India. This excursion was performed under the orders of the then Governor-General of India, the Most Noble the Marquis of Wellesley, and occupied the closing months of the 18th Century and the beginning of the 19th Century. The book, in three volumes, recorded his observations concerning the manner in which the people lived: their customs, the economy, and the nature of the countryside and the rocks occurring therein. In this journal, Buchanan recorded the occurrence of a peculiar rock, new to him, to which he gave the English name of "laterite" or "brickstone" and for science, the latinised version "lateritis."

Some years ago the speaker had the good fortune to add to his personal library a sound copy of this journal, in its three volumes, and it is interesting to read the original entries of the author of the term. More particularly is this so when one considers the nature of opinions and statements attributed to Buchanan by various writers on the subject of laterite terminology.

As an example of the kind of thing that has happened, Johannes Walther formed the opinion that a red colour was the significant criterion for laterite. Following this idea, Hellmers believed that Buchanan considered the red colour to be essential and that the rock was formed as a result of volcanic action. Neither of these concepts has been found by the speaker among the nearly 20 entries concerning laterite, not all of which are referred to in the index.

Buchanan's first entry concerning this material was that of 9th December, 1800, when he was in the vicinity of Kunamkulam south-east of Calicut. "Cunnung colung curry Angady," as he called the place, in a "Nazareny or Christian" village which he visited. He recorded:

"An old church . . . . . is now unroofed; but the walls, although built of indurated clay only, continue very fresh and strong. The altar is arched over with the same materials . . . . ."

The first entry concerning the field occurrence was made three days later, when in the vicinity of Angadipuram, a few miles north of Kunamkulam.

"After crossing the river, I came to a country like that near the *Nazareny* town in the Cochin Raja's dominions, and consisting of narrow vallies surrounded by low bare hills. The soil, in many places of these hills, is very intractable, and consists of a kind of indurated clay, which, on exposure to the air, become as hard as a brick, and serves indeed all the purposes of stone."

For the 20th and 21st December, 1800, Buchanan made the following entries concerning the iron ore which was smelted for the manufacture of steel.

"In all the hills of the country the ore is found forming beds, veins, or detached masses, in the *stratum* of indurated clay that is to be afterwards described, and of which the greater part of the hills of Malabar consists. This ore is composed of clay, quartz in the form of sand and of the common black iron sand. This mixture forms small, angular nodules compacted together and very friable. It is dug out with a pickaxe and broken into powder with the same instrument. It is then washed in a wooden trough . . . . placed in the current of a rivulet; . . . . The powdered ore is placed at the upper end . . . and . . . a man continually stirs it about with his hand. The metallic sand remains . . . . the quartz is carried to the lower end and the clay is suspended in the water and washed entirely away."

Thus Buchanan recorded the primitive character of part of the steel industry of that time and place. Note that it is the iron ore, which occurs in the so-called indurated clay "forming beds, veins or detached masses" that is smelted for the iron content, not the laterite itself. In another part of India, Pendleton recently saw slag heaps which he believed to have signs of the smelting of laterite for iron. While this laterite may be what might be described more properly as lateritic iron ore, it is possible that it was the iron ore in the laterite that was smelted.

After describing the furnaces and the smelting process Buchanan went on to state, and here I quote in full an oft-quoted entry:

"What I have called indurated clay is not the mineral so-called by Mr. Kirwan, who has not described this of which I am now writing. It seems to be the *Argilla lapidea* of Wallerius I, 395, and is one of the most valuable materials for building. It is diffused in immense masses, without any appearance of stratification and is placed over the granite that forms the basis of *Malayala*. It is full of cavities and pores and contains a very large quantity of iron in the form of red and yellow ochres. In the mass while excluded from the air, it is so soft, that any iron instrument readily cuts it and is dug up in square masses with a pickaxe and immediately cut into the shape wanted with a trowel, or large knife. It very soon after becomes as hard as a brick and resists the air and water much better than any bricks that I have seen in India. I have never observed any animal or vegetable *exuvia* contained in it, but I have heard that such have been found immersed in its substance. As it is usually cut into the form of bricks for building, in several of the native dialects it is called the brickstone (Itica cullu). Where, however, by the washing away of the soil, part of it has been exposed to the air, it has hardened into a rock, its colour becomes black . . . The most proper English name would be *Laterite*, from *Lateritis*, the appellation that may be given to it in science."

It is interesting to find that the reference to "Mr. Kirwan" is almost certainly to R. Kirwan, who published several books on agricultural chemistry and allied subjects and in particular, in 1894, a book in which he described, among things, indurated clay, citing as the typical example the clays at Stourbridge, England, now considered to be kaolinic in character.

The reference to *Wallerius I, 395* is, with very little doubt, a reference to page 395 of Volume 1 of the 1778 Vienna Edition of Wallerius' "Systema Mineralogicum," a reference work on systematic mineralogy written in a form of Latin, then the universal language of learned men in all parts of Europe. I am indebted to Miss Ethel Curran for assistance in the translation of the relevant passages. Wallerius gave the Swedish, French and German names, all meaning hardened, lithified or indurated clay. It may perhaps be significant that the German name is given as "steinthon" and not "steinlehm," suggesting a hardened china clay or a clay with little colouring impurity.

All the forms described by Wallerius—who, incidently was Professor Royal of Chemistry, Metallurgy and Pharmacy in the University of Uppsala in the middle and late 18th Century—have the appearance of clay, mostly unstratified, are stoney-hard and entirely lack the unctuous feel of most clay: they cannot be softened with water: they are softer than steel but become so hard when burnt that they will strike sparks from steel.

The group in which Wallerius placed the *argilla lapidea* is one which also included soapstones, serpentines and potstones or altered talcose greenstones. It would seem that Buchanan considered the laterite to have some of the properties of the group, but here again, we cannot recognise all the properties as applying to any one form of laterite. These rocks are all of them light coloured, structureless for the most part, amorphous, soft enough for use as a substitute for chalk, can be scraped with a knife, do not throw sparks when struck with steel. When exposed to the air they become harder rather than undergo disintegration, but they do disintegrate in time, becoming more earthy in appearance like the yellowish or greyish clay seen in fissures of potstones or impure talcose greenstones. When dry they absorb water but are not softened by it. When calcined they become so hard as to strike sparks with steel and burn to light yellow or grey colours. Fused with various salts they yield light or ash coloured strong masses or glasses. Mixed with clay the powders harden somewhat but with lime and gypsum they do not fuse unless siliceous material is added. These rocks do not effervesce with mineral acids but some does go into solution, more with hydrochloric acid than with nitric acid and with this more than sulphuric acid, as is shown by the amount of precipitate obtained with alkali carbonates. However, the amount that goes into solution seems to be proportional to the depth of colour of the stone. One of the several types of *argilla lapidea* is tawny to dark in colour.

I have given the properties of this rock at length, partly in order to indicate the scanty nature of the information there existed then concerning some rocks. Relatively simple tests and keen observation had to be relied upon, for this was in the days before microscopes of any kind were in common use, and 50 years or so before the petrological microscope came into being. It is well-nigh impossible to distinguish the nature of laterite, so far as its constituent minerals are concerned, from descriptions such as this.

Coupled with Buchanan's description, the references indicate that, although it "contains a very large quantity of iron in the form of red and yellow ochres" these constituents, hydrous oxides of iron, cannot be regarded as the principal constituents of laterite. It can even be argued that the essential constituent was some mineral other than ochre, for it would seem that Buchanan regarded the laterite as a mineral, that is, a substance which is homogeneous.

After travelling northwards along the western coast of the peninsula as far as Karwar, with deviations inland at several places, Buchanan turned away from the ocean and ascended the Ghats to the plains of southern Bombay Presidency and western Mysore State. He then travelled southwards more or less parallel to the scarp of the Ghats and then turned in a north-easterly direction, along the valley of the Tunga River, through Shimoga. All along this route he reported the presence of laterite until he reached a point a little west of Shimoga.

Near Gati, Buchanan recorded:

" . . . a hill producing iron ore, which is wrought to some extent. It is found in veins intermixed with *Laterite*, like the ore of *Angada-puram* (Angrypar) in *Malabar*. The ore is of the same nature with what is usually smelted in the peninsula; that is to say, it is a black sand ore . . ."

In all, there are nearly 20 entries concerning laterite or brickstone, most of them being merely a record of the occurrence of laterite at the locality referred to. In one of his last entries concerning laterite Buchanan merely refers to it as brickstone. In a later book concerning Bihar he refers to it merely as brickstone also, so that it would appear that Buchanan did not have such a fancy for his brain-child as we have at the present day.

The first half of the 19th Century saw the gradual adoption of the term "laterite" by travellers, mostly geologists, more particularly in India and the near-by countries. Rocks having the same general characteristics as Buchanan's laterite were found scattered far and wide through India and Burma, and most of those who recorded the occurrence of laterite seemed to have considered it some form of ironstone, that is, an impure hydrous iron oxide rock. This is very understandable, for much of it had developed over highly ferruginous crystalline rocks and consequently this laterite contained more iron oxide minerals than the laterite formed over granites and similar rocks, as was that seen by Buchanan. It must be remembered always, that this was in the days before the development of the techniques now used for the study of rocks. Complete chemical analyses, or merely analyses for ten or a dozen constituents were not available. The petrological microscope had not been developed, and sure methods of mineral identification had not yet come to light, even for the study of comparatively simple crystalline rocks. Even today we have no sure method of determining the content of some rocks with respect of the more indefinite materials developed by weathering, such as for instance, amorphous hydrated aluminium and iron oxides, secondary silica and the like: approximations are all that can be obtained at best, even employing a whole battery of techniques such as chemical analysis, the petrological microscope, differential or simple thermal analysis, X-ray diffraction, and so on. In those days reliance had to be placed on comparatively simple tests of a discriminatory nature only, as I have just outlined.

Knowledge concerning the nature of the laterite seen by Buchanan came slowly. Southern Malabar was examined by Philip Lake whose findings were published in 1890. This geologist could distinguish three distinct types of laterite. Firstly, the "plateau laterite" which caps the hill tops as a kind of "summit bed" so to speak, which Lake considered to have been formed *in situ* by the decomposition of the gneiss. A second type was what Lake termed "terrace laterite," to be found on the slopes below the "plateau laterite." The third type "valley laterite" occurred at still lower levels. It is the "summit bed" that Buchanan appears to have referred to most.

The latter half of the 19th Century saw the slow development of the present day techniques of examining and describing rocks. Chemical analysis was applied more and more, to ascertain the constituent elements of rocks and their relative proportions. Following Sorby's work of the 1850's the petrological microscope was developed and used to ascertain in what way those elements were combined, that is, the mineral expression of the chemical composition. Not only this but the mutual relationships of the different minerals were also studied. Rock textures were found to have a definite meaning in many instances, and a large body of knowledge gradually accumulated.

Naturally, sooner or later, someone was bound to apply these new techniques to the study of laterite. To Max Bauer, of the University of Marburg, who had been examining European bauxites late in the 19th Century, goes the credit of first publishing work of this nature dealing with tropical laterite. He microscopically examined specimens of laterite and associated crystalline rocks from Mahé, one of the Seychelle Islands, in conjunction with chemical analyses by Busz. The chemical analyses showed the highly aluminous nature of the laterite, which Bauer attributed to the presence in quantity of the hydrated aluminium oxide gibbsite, to be seen in the thin sections. Further, he showed the close relationship there existed between the laterite and the underlying crystalline rocks, not only chemically as to constituent elements, but also with regard to micro-structure. Particularly was this so in the instance of the laterite found over the diorite, for he found that this laterite retained in itself the structure of the diorite: the laths of feldspar seen in the diorite were represented by colourless rectangular areas of gibbsite and the ferromagnesian mineral by limonite-bearing areas. The lime and magnesia of the diorite had disappeared from the laterite, as also the silica. The laterite over the granite had quartz grains of similar size and shape to those of the granite and Bauer could recognise the granitic structure retained in the laterite. Standing alone, the evidence concerning the laterite over the granite could be heavily discounted, for the holocrystalline allotriomorphic equigranular structure of granite is not particularly distinctive when retained in weathered products, in contradistinction to the structure of some basic igneous rocks, especially the ophitic texture of dolerites and closely related rocks, for these structures are often readily recognisable even when the rocks are completely altered by weathering.

However, the evidence was such that the conclusion was inevitable: the laterite of Mahé was formed *in situ* by the weathering of the granite and of the diorite, and, furthermore, those weathering processes had removed the combined silica, the lime and the magnesia, leaving the iron and aluminimum as hydrated oxides, and the quartz.

About this time, geologists of the Geological Survey of India had been paying some attention to the problem of the formation of laterite. The results of Max Bauer's work was considered to have settled the question as to the real nature of primary laterite, that is, laterite which has been produced directly by weathering processes acting upon parent materials, before any redistribution of the constituents has occured consequent upon the continued action of weathering processes involving the movement of ground water through the laterite mass.

The results of chemical analytical work by the Warth brothers were published soon after the turn of the century. Their work showed that the term laterite had been applied by geologists in India to a wide range of materials, so far as chemical—and therefore mineral—composition was concerned. On the one hand, highly aluminous varieties existed, rich in the hydrated aluminium oxide mineral gibbsite and containing little limonite; on the other hand, highly ferruginous rocks, almost free of alumina, were also termed laterite, rocks consisting mainly of limonite, principally goethite; and there were all manner of varieties between these two extremes.

These last, rich in limonite, to which Buchanan would have applied the term "brown hematites," were considered best designated "iron ore," so, towards the close of the first decade of this century some authors considered the term "laterite" to be of more value as a rock name if it were restricted to mean those more highly aluminous rock types which lie in composition between iron ore on the one hand and the aluminium ore bauxite on the other.

Thus, when a chemical analysis of such a material showed an alumina figure above 52 per cent. and less than 5 per cent. iron and a very low silica figure it was considered to be bauxite. On the other hand, if the ferric oxide figure rose to something over 40 per cent. or so it was considered to be iron ore. In between lay laterite.

This view was by no means universally accepted, as is shown by the letters to the Editor of the *Geological Magazine* in 1910.

Even to this day we find those who advocate strongly the restriction of the term laterite to materials such as those just described: it is the concept widely held by geologists and mining engineers and is implicit in most of the papers read at a symposium dealing with the "Problems of Clay and Laterite Genesis" at the Annual Meeting of the American Institute of Mining and Metallurgical Engineers at St. Louis, Missouri, early in 1951. The one who used the term in a manner differing from this concept was a soil worker, G. D. Sherman.

Among soil workers there is a division of opinion. There are those who follow Pendleton's concept that laterite is "an illuvial horizon, largely of iron oxides, with a slag-like cellular or pistolitic structure, and of such a degree of hardness that it may be quarried out and used for building construction." Apart from the insertion of the concept of origin embodied in the term "illuvial" there is little if any difference between Pendleton's application of the term and that of the geologists of the Indian Geological Survey before the turn of the century and before anything like a thorough knowledge of these materials was obtained by the application of the techniques of rock examination now in use.

The inclusion of a concept of origin in a definition of a rock is considered, by the present speaker and many others, to be fundamentally erroneous: it requires one to secure satisfactory evidence of origin where often it is not possible to do so and to decide which of several modes of origin fit the known data. Further, one can never be sure that one has all the possible information which can enable one to make a valid decision as to origin, one which cannot be negated by subsequent work. In most instances the origin of a rock is a philosophical concept only, and is derived from observable and measurable data. It cannot be sufficiently emphasized that only observable and measurable features should be taken into account when naming a rock. It is possible, in some instances, for the same minerals to be assembled in the same proportions by a variety of methods. This applies generally and not only to laterite and similar products of weathering; it applies to granite, for example. Not infrequently there is some structure present which suggests a particular origin for a rock under discussion but this is not always so, by any means. Furthermore, it is possible for different workers to consider the same rock to have different origins, as indeed is the case with laterite; it would be particularly unfortunate if each worker used a different name for the same rock, just because each considered it to have a different origin.

Fox, in 1936, sought to clarify the position by examining some of the laterite to be found in Malabar and Canara provinces along the south western coast of the Indian peninsula. Unfortunately, it would appear that a thorough examination of all the different types of laterite occurrences was not undertaken, especially of that occurring on the summits of the hills, to which Buchanan referred so often and which Lake called "plateau laterite" some ninety years later. Whereas the exposure at Tellicherry examined by Fox can be interpreted simply as a mass of very impure iron oxide, the other occurrence, of which analyses are given of the profile exposed in the quarries at Cheruvannur, can be regarded as a profile in which there was a certain amount of enrichment by hydrated oxides of both iron and aluminium in the upper portions. From the illustration, this occurrence is down the slope a little distance below the hill-top and may correspond to Lake's "terrace laterite."

Those portions of western Mysore, where Buchanan reported laterite as being abundant, appear to have been entirely overlooked in discussions as to the true nature of laterite.

Amongst the laterite near Shimoga, at Kemmangundi, not far from the route followed by Buchanan, there is some laterite reported by A. M. Sen to have composition as set out in Table I.

Table I

Laterite from Kemmangundi

Al_2O_3	62.50	42.90	41.72
Fe_2O_3	5.10	25.40	30.27
SiO_2	0.36	10.40	2.97
H_2O	31.90	20.70	22.64
CaO			0.56
MgO			0.03
TiO_2			tr.

Parent rock:—Diorite or Hornblende diabase

For the best part of a century the term *laterite* was applied to a wide range of rocks ranging in composition from an impure iron ore containing a large amount of limonite, to a somewhat ferruginous bauxite. The question arises whether the term is best applied in the restricted sense that Pendleton so vigorously advocates, namely an "illuvial horizon" in which the cementing material is largely iron oxide, for which the term *ferricrete*, proposed by Lamplugh in 1897 is very suitable, or whether it should be applied in the sense that it should lie in composition between iron ore, on the one hand and bauxite, the ore of aluminium, on the other.

The difficulties of ascertaining always whether an occurrence is indeed illuvial, or what its origin really is, are manifest. It is not sufficient to assume that it is always of the same origin: indeed, there is much to suggest the contrary.

To the speaker, the restricted sense, developed by geologists early this century, appeals as being the more useful. It is a concept which depends solely upon characteristics of mineral composition and of field occurrence as broad sheets, characteristics which can be determined approximately by carefully planned chemical analysis and by field observations of the extent of an occurrence. It is considered that no concept of origin should be involved in the name given to any rock, be it granite, basalt, sandstone or even laterite. This is not to say that the origin may not be indicated by a suitable adjectival qualifier preceding the name.

The term *latosol*, recently introduced by C. E. Kellogg, offers a solution to one of the problems of the nomenclature of these materials. While he cannot find himself at one with Kellogg in the use of the term *laterite* to include sesquioxide-rich materials in which hydrated aluminium oxides are low or virtually absent, the present speaker considers the introduction of such closely defined terms to be long overdue in pedological science and has little doubt but that further similarly closely defined terms will be introduced in the course of time, to cover adequately the different varieties of these very interesting materials.

For the present purposes, the speaker will use the term laterite to include those consolidated, non-friable materials consisting essentially of hydrated oxides of both iron and aluminium, lying in composition between ironstone or iron ore on the one hand and the aluminium ore bauxite on the other. Where quartz, or any other mineral, becomes at all prominent in the constitution of the rock, say over ten per cent, the term is suitably modified adjectivally.

One must apply very carefully the various definitions depending upon ratios of alumina to silica, either of the rock as a whole or of the "clay fraction" only—this being selected by some because it is considered that this fraction would contain little or no free silica, such as quartz, but would be truly representative of the argillaceous material and therefore of the material produced by chemical alteration during weathering. It must always be borne in mind that these are merely short-cuts used to minimise the work involved in securing knowledge, sufficient for the work in hand, of the chemical constitution and therefore of the mineral constitution of the rocks or soils under investigation.

South-Western Australia

Let us now turn to this south-western corner of the Australian continent.

The features to be observed within 200 miles of Perth conform to the general pattern of the whole of the area and will be referred to principally.

First it is desirable briefly to outline the physiography and geology of the area.

Physiographically one of the most outstanding features is the Darling Scarp, which forms the western edge of the Great Western Plateau. Here, along a line sub-parallel to the coast, and about 20 miles or so inland, the land surface drops from altitudes of 800 to 900 feet above sea level to the coastal plains standing less than 100ft. above sea level for the most part, rising to higher altitudes only in the belt of coastal limestone hills, which rarely rise to an altitude greater than 200ft.

The Great Western Plateau can be regarded as having several elements.

One, the Darling Peneplain, is a general level of flat-topped hills and ridges or divides between fairly broad valley systems, the tops of the ridges standing at some 900 to 1,000ft. above sea-level.

Rising above this peneplain are a number of higher, comparatively isolated hills such as Needling Hills and Mount Bakewell, remnants of an older land surface, the roots of earlier divides between broad valley systems which collectively form the Darling Peneplain.

Cutting down into this Old Plateau or Darling Peneplain is a system of valleys with gentle slopes and broad salt river flats, standing at an altitude of some 600 ft. or so above the present sea-level. These broad valleys with their salt flats are remnants of an old drainage system which appears to have flowed in a general direction from North to South. The various branches of the Mortlock River and the extensive salt river flats to be seen between Kellerberrin and Merredin afford good examples of this system. In this region, the valley systems are very broad and only small remnants of the old Darling Peneplain remain. The lower reaches of these river systems are characterised by the much narrower, steep-sided valleys of young rivers.

These various elements are not seen clearly near Perth but are best seen if one goes up onto the higher places east of the Avon River or southwards beyond the Beaufort River.

The rocks of the western portion of the Great Western Plateau consist mainly of granitic gneisses and granites, granulites, metasedimentary schists—some of which are sillimanite- and andalusite-bearing-quartzites and slates. Cutting these are dykes of dolerite and epidiorite. To the east of the North Branch of the Mortlock River and of the Avon River at York and along the Albany Highway from 120 miles or so from Perth onwards and extending eastwards, the wheat belt has occurrences of moderately well lithified conglomerate, argillaceous grits and sandstones—some of which show horizontal bedding—and very sandy clays. These sediments lie upon the undulating eroded surface of the crystalline rocks, and are comparatively young, judging by their lithification, which is comparable with rocks of the Plantagenet beds and are believed to be of terrestrial origin. Gritty sediments underly much of the high level sand-plain country of the north-eastern and eastern wheat belt, the sandy soils of the elevated sand-plains being residual soils derived from these gritty sediments.

To the west of the Darling Scarp the comparatively low-lying coastal plains consist of a narrow belt of sandy limestone and sand hills, in part of aeolian origin, with a broad belt of lenticular beds of very sandy clays and argillaceous sands. These yield loamy sands and sands at the surface. In places there are patches of fresh-water limestone. These sediments rest upon a thick series of calcareous shales with inter-bedded coarse grits and shales below, these grits being the aquifers of the artesian basin around Perth. Laterite does not occur west of the vicinity of the Darling Scarp.

The Darling Peneplain is characterised by the presence of a group of ferruginous and aluminous rocks and gravels which form a sheet or cuirass upon the old rocks beneath. As exposed at the surface these materials are of two kinds. The fairly hard stone is popularly referred to as *ironstone* or *conglomerate* while the *gravel* consists of an unconsolidated mixture of ferruginous nodules with some quartz sand and clay. The more firmly lithified materials are commonly medium- to dark-brown, sometimes quite light-brown. In most places they consist of nodules set in a matrix of fine grained material, the so-called "concretionary" laterite, much of which is better referred to as *laterite with concretions*. In places the laterite consists almost entirely of more or less spherical pellets around about 5 to 10 mm. across, firmly joined at their points of contact: this form appears to be confined to channels through the less porous rock, these channels having developed along joints inclined at any angle. They constitute zones of free passage to lower levels for rain-water falling on the surface above or higher up the slope. This is a purely concretionary laterite commonly styled "pisolitic laterite" on account of the size and shape of its constituent nodules resembling those of peas. Another less common form is the so-called vesicular type which consists of massive material through which irregularly shaped anastomosing channels pass: this type not uncommonly has a splotchy appearance in light and dark browns, though fair uniformity of a dark brown is quite common. Rarely, one finds a massive form of laterite, free from nodules except near the surface: in places it may be quite porous, but on the whole is fairly massive and dense. Whatever the type of laterite, some form of nodular structure is generally present somewhere in any exposure of laterite and this nodular structure has come to be regarded, by some, as the distinguishing characteristic of laterite, so much so, that when they see a light or dark brown or reddish brown nodular material occurring as an extensive layer they immediately identify it as laterite. It is intended to return to a consideration of this nodular structure later and to show that the vesicular, nodular and pisolitic types are derived from the dense, massive variety by the continued action of waters passing through the laterite to lower levels. Before doing so, however, it is first desirable to give some attention to certain features of the laterite and of the materials closely associated with it.

Firstly, concerning the composition. A number of analyses of laterite occurring in and near the Darling Range have been published and a few of these will suffice to indicate the general nature of this rock (see Table II).

Table II

Laterites from the Darling Range

		Wongan Hills	Gooseberry Hill	Parkerville	Ridge Hill
SiO_2	....	5·96	6·41	15·83	10·30
Al_2O_3	....	44·66	36·74	31·68	22·53
Fe_2O_3	....	19·08	39·80	24·95	48·56
FeO	....	....	....	2·52	....
MnO	....	....	0·06	...	0·05
MgO	....	tr.	0·15	0·62	....
CaO	....	tr.	0·10	0·01	....
Na_2O	....	....	....	0·14	....
K_2O	....	....	. ..	nil	....
$H_2O—$	....	0·58	1·20	2·69	} 15·82
H_2O+	....	26·44	13·73	19·55*	
TiO_2	....	3·10	1·98	2·07	3·24
SO_3	....	0·18	....	....	....
P_2O_5	....	tr.	tr.	0·09	....
Cr_2O_3	....	....	0·03	....	....
V_2O_5	....	....	0·23	....	....
		100·00	100·43	100·15	100·50
Combined SiO_2	....	....	1·97	10·17	4·94
Analyst	....	E.S.S.	E.S.S.	S.E.T. D.B.	R.T.P.
Date	....	1901	1912	1947	1946

* By ignition loss

These analyses show the laterite to consist mainly of hydrated oxides of iron and of aluminium, together with some hydrous silicate of aluminium, some free silica and a little oxide of titanium. The most probable mineral expression of this chemical composition is a rock consisting mainly of gibbsite and limonite with some kaolin or halloysite and quartz and a little doelterite or leucoxene or possibly traces of residual ilmenite.

Much of the limonite is probably goethite, but the presence of some lepidocrocite and maghemite is suggested by the magnetic properties of nodules derived from laterite. Some nodules collected at Kalamunda, for example were quite strongly magnetic as collected but rapidly lost their magnetic response when heated to 800°C in a neutral atmosphere. This suggests the presence in the nodules of the magnetic anhydrous iron oxide mineral maghemite, which in turn is derived from lepidocrocite by dehydration. A number of years ago, Professor R. T. Prider drew attention to the polar magnetic properties of laterite at Wattle Flat.

It will be noted that the soda and potash, the lime and magnesia, to be found in abundance in the underlying rocks, are almost completely absent from the laterite. The Darling Range laterite manifestly conforms to the concept of laterite in the restricted sense of a material somewhere between a bauxite on the one hand and iron ore on the other; most of the occurrences, so far examined chemically, are somewhat impure from the admixture of quartz and clay.

There are certain features of the field occurrence to which I would direct your attention.

Firstly, beneath the laterite there is commonly a zone of partially or completely bleached clay. Simpson, in 1912, referred to the laterite as an efflorescence which drew ferric oxide and alumina from the rocks below, resulting in a layer from which most and often practically the whole of the ferric oxide has disappeared, leaving this stratum of white or pale-coloured clay.

In 1915 Walther visited this State and described the occurrence of laterite here. Figure 1 is a diagrammatic profile after that author. It shows the massive cuirass or crust of laterite overlying a mottled horizon which in turn overlies a bleached horizon which in its turn passes into the rock beneath.

This sequence has come to be regarded as the normal sequence of horizons of laterite-bearing profiles when truncated. It is postulated that above the hard laterite crust there existed incoherent, leached, sandy soils which have been eroded away from those areas in which laterite or lateritic gravels are exposed.

In evidence of this, pale yellowish grey loamy sandy soils exist which have a brown, obviously ferruginous horizon some eighteen inches to three feet or so beneath. In places, local erosion has removed the overlying loamy sands and exposed the gravelly horizon and this gravelly horizon has much the same appearance as the gravel associated with the solid rock laterite elsewhere. These gravelly horizons are regarded by many as the same as the more massive occurrences of laterite. It is proposed to show that they differ materially and so cannot be regarded as the same as the aluminium oxide-bearing laterite of the Darling Range, for instance.

Walther's diagram may be taken to represent closely the features to be observed in an occurrence of laterite at Parkerville. At that place, where some quarrying has been done in the past to secure material for roads and where a Roads Board Hall and tennis courts are now situated, there is exposed a section of massive laterite developed *in situ* from a quartz dolerite dyke.

minerals of the parent rock are now a mixture of dark brown limonite with a small proportion of ironstained, presumably colourless mineral, possibly a mixture of gibbsite and clay minerals. A little quartz is scattered through the section.

When the chemical composition of the laterite close to the boulder is compared with that of the quartz dolerite from which it was formed, it may be observed that the ratio of ferric oxide to alumina of the laterite is what it should be if there has been no movement of the iron with respect to the alumina. If most

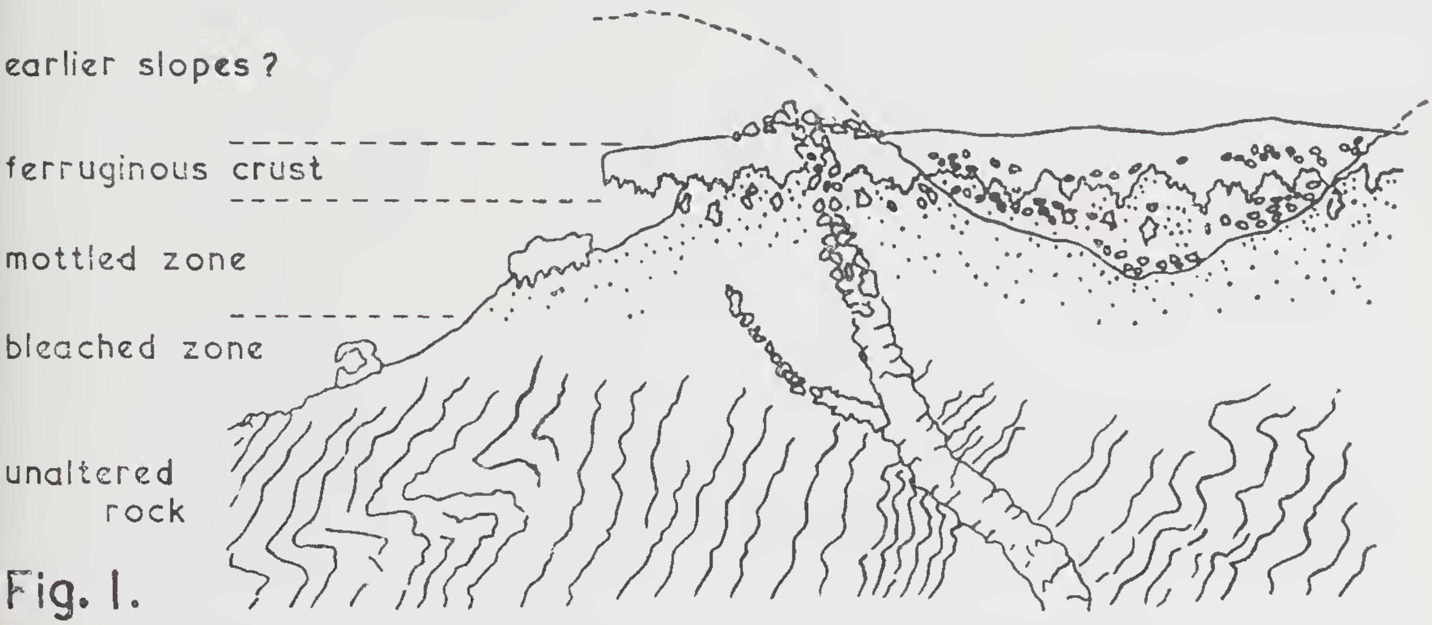

Fig. 1.

This section has much to offer in enlightment as to the nature of laterite in the Darling Range and the sequence of events in connection with it.

First, there is a layer of laterite, much thicker in proportion than the layer figured in Walther's diagram: the topmost 18 inches or so is gravelly, but below this the laterite is massive. Immediately below the laterite there is a mottled red and pale greenish blue clay and lower still a pure white koalinic clay.

The laterite has the typical composition of rocks of this group, using the term in the retricted sense of a rock lying in composition between an iron ore on the one hand and an aluminium ore on the other. The analysis of the rock has been published in the Society's *Journal* recently.

In the laterite there is evidence of the typical spheroidal weathering of basic crystalline rocks of igneous origin. Also there is immersed in its substance a small boulder of quartz dolerite and near its base, a very large boulder which projects down into the mottled clay horizon and around which is a downward extension of the laterite from the layer above. These boulders have the appearance of being cores of spheroidally weathered blocks of dolerite, the original joint faces of which are still discernable.

Not only are the weathering cracks of the parent rock preserved but in parts the microstructure is preserved also. In thin section the original feldspar laths are now represented by elongated rectangular patches of gibbsite, while the areas occupied by the ferromagnesian

of the ferrous iron of the dolerite—all but the amount shown to be present in the laterite—is considered as having been converted to ferric oxide, then the ratio of ferric oxide to alumina remains virtually undisturbed.

The combination of these three features of preservation, firstly, the preservation of the structure produced by spheroidal weathering, secondly the preservation of evidence of poikilitic structure and thirdly the retention, undisturbed of the iron to alumina ratio, is considered to be sufficient evidence that this laterite has been formed *in situ*, not by deposition from solutions which have brought in the constituents from some place else, be it from some hypothetical horizon directly above, or from higher up the slopes of the hill, but that the laterite has been formed by the removal, in solution in circulating ground waters, of practically the whole of the soda and potash, the lime and magnesia and a large proportion of the combined silica.

The nodular structure in the top portion of the laterite and the gravelly soil above it, are considered to have developed by the continuing action of weathering, probably under different climatic conditions.

There is no reason to believe that the laterite formed from the granite originated in any way differing from the manner in which the laterite was formed from the quartz dolerite, for the junction of the laterite formed from the quartz dolerite with that of the laterite alongside it, formed from the granite, can be traced.

Nor is the laterite at Parkerville the only occurrence where the structure of the parent rock is preserved.

In an old cutting north of the present railway line at Mt. Helena there is a vertical section showing laterite derived from a basic dyke rock preserving perfectly the structure of the original rock, and in which the spheroidal weathering cracks of the original basic dyke can be detected. Further, one can run a knife down the junction between the laterite from the basic dyke rock and that formed from the granitic country rock

Another occurrence of laterite which preserves the structure of the parent basic dyke rock has been found on the Beaufort Downs property: this farm is on the road from the Martup Hills on the Albany Highway to Woodanilling further east. This occurrence is nearly 150 miles away, to the south of those first mentioned.

Emphasis on basic dykes as being rocks which yield laterite in which the structure is well preserved is unfortunate but inescapable. The basic dyke rock possesses a structure which, when preserved in its weathering products, is very readily recognisable and clearly demonstrable to others, while granitic rocks do not possess such a clearly defined structure. It is true that one can consider certain features to be seen in thin sections of some massive laterite specimens to be relicts of the structure of the parent granite, but the evidence is not so clear and is open to doubt.

Once the validity is admitted of the conclusion that the laterite is primarily formed in place from the basic dyke rock by the ground waters removing the alkalis and alkali earths and much of the combined silica, and not by the deposition of the laterite constituents from solutions brought to the place from elsewhere, certain other deductions must necessarily follow. The mottled clay and the pure white, bleached kaolin strata below are quite devoid of any evidence of the structure of the parent rock and further, the regeneration of such a structure from them does not seem possible. Consequently, they cannot be considered to be intermediate stages in the formation of laterite from the parent basic dyke rock.

It is concluded therefore, that the clays were formed neither before the formation of the laterite, nor at the same time, but subsequently thereto, as weathering of the parent rock continued and still continues beneath the protective mantle of laterite.

There is some reason for the belief also that underneath the laterite mantle the conditions are even yet those which led to the formation of a bleached clay, for, at the present day, the granite appears to be still weathering to a bleached, quartzose kaolin underneath the laterite crust. Only where they are exposed directly to the weathering agents or beneath a thin pervious soil layer do the granites or greenstones show evidence of weathering to red or brown iron-bearing clays or loamy soils.

The laterite was formed at some early stage in the development of the present land surface.

Firstly, an undulating surface, in places hilly along divides between broad valley systems, was produced by the erosion of granites, gneisses, metasediments and other crystalline rocks.

More or less argillaceous grits, coarse and fine sandstones—in places showing horizontal bedding—with local conglomerate, were laid down upon the eroded surface, in great measure filling the valleys. The thickness of these sediments is not known but appears to have been considerable for they reach high up the sides of the highest hills where they occur.

Following the deposition of the gritty sediments erosion developed very broad valley systems virtually plains, with isolated hills standing higher, the remnants of the divides between the valleys which constituted the broad plain country. This plain country is the Darling Peneplain.

Following the development of the Darling Peneplain lateritisation occurred during a definite climatic phase. A change in climate followed with the consequent change of final product of weathering of the feldspars and ferromagnesian minerals. Instead of the aluminium-bearing minerals having the whole of their combined silica removed, leaving the hydrated aluminium oxide gibbsite, they had only some two thirds removed, leaving hydrous aluminium silicates, chiefly kaolin.

Local conditions have caused variations in the nature and intensity of colouring of the horizons beneath the laterite, because of varying proportions and state of oxidation of the iron left along with the kaolin.

After the period of laterite development which could well have occurred on a low-lying plain as Woolnough has postulated, elevation has caused a rejuvenation of erosion in the then existing drainage pattern. This gave rise to broad valleys in which extensive, very sandy, mostly unstratified terrestrial sediments were deposited. These sandy sediments blocked the drainage system and have given rise to the widespread elevated sand-plains of our wheat belt and South West.

Following this terrestrial sedimentation, rejuvenation of erosion has occurred in at least two stages. At first the streams cut down to a level about 200-300 feet below the laterite-covered plateau. A major uplift of at least 600 feet then followed and the rejuvenation of erosion has caused the lower reaches of the rivers to cut downwards, while at the same time, the upper reaches continued to extend and are still extending their valleys laterally, so that in many places there is only a line of laterite-covered, flat-topped hills to mark the divides between broad valley systems the lower parts of which consist of flat, marshy or salt river flat country standing about 600 ft. above sea level, Woolnough's 600 feet level. Indeed, in many places the whole of the laterite and underlying clays have now been removed exposing bare granite and gneissic hills, the so-called "Rocks," which are the very roots of the divides between these post-peneplanation mature valleys or of the monadnocks which stood above the peneplain.

Certain features of the landscape and associated soils call for attention at this stage.

First, attention is drawn to figure 2a which shows diagrammatically a section of a side of a valley in granitic country. On the left there is the flat-topped ridge or divide between adjacent valleys. It is laterite covered, the laterite being a residual eluvial horizon which has been further altered as to structure and composition by the continuance of weathering action. The soil cover is thin or absent: in places loose boulders of laterite occur. Such soil as there may be is full of ironstone nodules and is mainly grey sand with a little clay and organic matter. As one progresses down the slope, light brownish or greyish sandy loams derived successively from the mottled or coloured clay horizon and the pallid or bleached clay horizon appear. The valley may not penetrate the pallid, often bleached horizon, but, should it do so, red and brown sandy loams have developed, formed by the weathering of the granitic rocks exposed to the climatic conditions and physiographic circumstances of the very recent past and present.

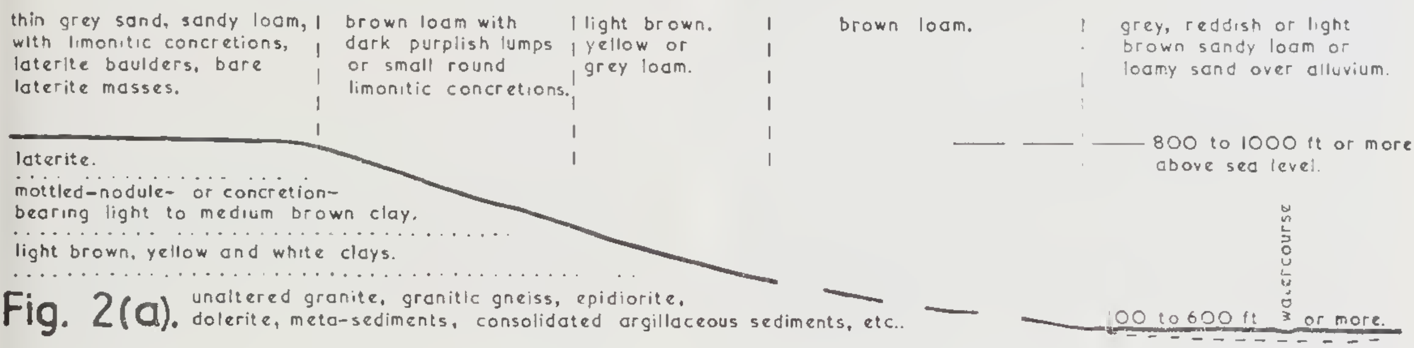

Fig. 2(a).

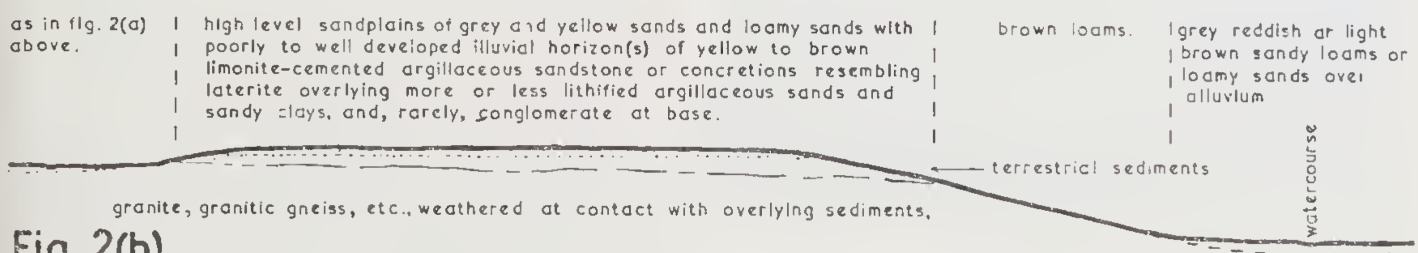

Fig. 2(b).

Where the argillaceous grits and sandstones and very sandy clays form sandplains, the diagram becomes slightly different, as shown in figure 2b.

On the left is a slope such as shown in figure 2a. In the middle is a very sandy flat-topped ridge of gritty sediments which have shared in the mottling and bleaching which followed lateritisation: the residual soils derived from the grits are the very pale yellowish grey slightly loamy sands, which constitute our high level sand plains. On the right the valley slopes down to the zone where residual reddish brown sandy loams occur, similar to those of the valley bottom of figure 2a.

Before closing, it is desirable that some reference be made to the further weathering of laterite and the formation of gravelly soils from the post-laterite yellow sandstones where the gravel and gravel-stone, at first sight, resembles nodular or concretionary laterite.

Figure 3 shows the low wall of a small gravel pit in sandstone country that occurs some 120 miles or so from Perth along the Albany Highway. It shows a yellow argillaceous sandstone which has developed vertical cracks down which iron-bearing solutions have penetrated. These solutions have impregnated the walls of the cracks with reddish hydrous iron oxide. Near the top of the sandstone, a little below the sandy gravel, the columns of sandstone have cracked horizontally with consequent penetration of iron-bearing solutions which have followed the easier courses along the cracks. The isolated fragments thus become impregnated by hydrous iron oxide from all sides and the outer portions are constantly being removed. Such fragments also crack across and become several fragments, all being separated by the rootlets and by loamy sand washed in between them by moving water on its way down to the zone of permanent saturation. Thus are formed "disintegration" type residual nodules.

In places the sandstone does not wholly disintegrate into separate nodules, but on the contrary, irregular more or less vertical "solution channels" develop, leaving an almost nodular mass between with channels filled with loose, grey sand. This "nodular" mass is easily broken to loose sandy gravel.

A similar process of disintegration occurs in laterite, yielding loose ironstone nodules in a very sandy matrix.

Other forms of nodular or concretionary structure have been developed in both the laterite and in the argillaceous grits and sandstone.

In places a spotty type of mottling develops a little below the surface, where isolated spots become enriched with limonite to such an extent that eventually they may consist largely of limonite. Such pellets yield a "residual" type of nodule which may be anything from a very dense almost black and pure limonite to a lump of dark purplish red to brownish black, friable material with a thin, dense, comparatively hard smooth surfacc, very similar to the "disintegration" type of nodule and apparently indistinguishable from them. In sandy loam soils

FIG. 3.

derived from sandstones such nodules may be very numerous forming a principal constituent of a lower horizon in the soil profile. These nodules have a similar origin to that of similar nodules formed in laterite, being deposited in the matrix from solutions and often are very similar in appearance. This has led many to consider an horizon rich in such nodules a laterite horizon: it is considered, however, that such nodules should be styled "laterite" only if they consist largely of hydrated aluminium oxide minerals rather than the hydrated silicates as well as hydrated iron oxide minerals. The few such occurrences examined by the present speaker appear to have an origin differing entirely from that of the laterite itself, being the same as the origin of nodules formed in the laterite matrix by the continuance of weathering action upon the primary laterite, which is itself a residual skeleton derived from the parent rock by removal of the alkalis, alkali earths and combined silica in solution. In the onc instance, the ferruginous nodules have developed in argillaceous sandstone; in the other, they have developed in laterite subsequent to the formation of the laterite; this nodular structure is not a distinguishing characteristic of laterite, although most laterite has developed this structure.

The development of such nodular structures can occur during weathering in any sufficiently porous rock or material, laterite included, provided sparingly soluble matter be present and that climatic and topographic conditions are suitable. The development of nodular structures occurs in a wide variety of materials and is merely indicative of the similarity in response of the various rocks to the same forces of weathering as expressed in similar climates acting in similar topographic situations with like drainage patterns. Different types of nodules are formed depending upon whether a disintegrative or accretionary action is involved and this, in turn, depends upon the whole of the environment in all its complexity.

Before closing, I wish to express my thanks to the Director of the Government Chemical Laboratories, Mr. H. P. Rowledge, for his kind permission to use the facilities of thc Mineral Division outside office hours in order to carry out ccrtain phases of this investigation, which is still in progress. My thanks are also due to Miss Ethel Curran, late of Perth Modern School, for the basic translation of the Latin of Wallerius, and to Mr. and Mrs. Mira Liber for their valued help in the translation from the German of various articles such as those of Johannes Walther and Max Bauer. Lastly, I thank you for your kind attention to-night.

2.—Studies in the Water Relations of Plants

I.—*Transpiration of Western Australian (Swan Plain) Sclerophylls*

By B. J. Grieve*

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The water economy of character plants of the hard-leaved evergreen vegetation on the Perth coastal plain has been studied to obtain information on their behaviour both before and during the long dry summer. With the exception of *Eucalyptus marginata*, all the sclerophylls so far tested *(e.g., Banksia menziesii* and *B. attenuata, Stirlingia latifolia, Hibbertia hypericoides, Bossiaea eriocarpa, Hardenbergia comptoniana, Kennedya prostrata, Eucalyptus calophylla, Xanthorrhoea preissii, Petrophila linearis)* showed in greater or less degree decreasing rates of transpiration with increasing dry conditions. In the spring, transpiration was high, curves being of the one-peak type in *Bossiaea, Kennedya, Banksia attenuata, Hardenbergia* and *Stirlingia*. In summer, curves were commonly of the two-peak type, while in late summer values for some plants remained very low throughout the day after an early morning peak. Average rates of water loss seldom exceeded 5-6 mg./g./min. during the summer. The relatively shallow rooting *Hibbertia* and *Bossiaea* in particular showed very low values and passed into a state of near domancy in late summer. The moisture content of soil at this time is low, while the soil suction force rises above the osmotic values of the leaves. The plants remain in a condition of severe water stress until the break of season rains. The tree sclerophylls, *Banksia* spp. and *Eucalyptus calophylla*, and the shrubs, *Stirlingia, Hardenbergia* and *Kennedya*, with both a shallow and a deep root system, reduced their transpiration rate in summer but were not under conditions of marked water stress. Stomatal movements in some plants *(e.g. Hibbertia, Bossiaea)* showed reasonable correlation with rate of water loss; in others *(e.g. Stirlingia)* stomata remained open at the University station while transpiration rate was falling. Under the more desiccating conditions at the Cannington station they remained closed during the day. A higher rate of transpiration was found in older leaves (as against those of the current season flush of growth) in such plants as *Banksia* and *Stirlingia*. Slower photo and hydro-reactions were observed in stomata of such older leaves. Cuticular transpiration was found to proceed at a low level in the more highly cutinized sclerophylls. The osmotic values of leaves rose with advancing summer, while a rapid return to lower values occurred with break of season rains. Experiments to determine relative xerophytism have so far yielded inconclusive results owing to difficulties with water uptake by the cut-off leaves. Collateral studies on non-sclerophyllous shrubs which grow on the Perth coastal plain, indicate that a considerable degree of physiological diversity exists. *Phyllanthus*, for example, with its soft thin leaves shows a high rate of water loss in spring and early summer. With increasing dryness it maintains its water balance by shedding its leaves. A mesomorph, *Erechthites hispidula* maintained a high rate of transpiration in spring and in summer up to the time it died off.

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Introduction

Relatively little information is available on the water economy of Australian sclerophylls under field conditions, the work of Wood (1923, 1924, 1934) in South Australia, standing alone in this regard.

In an effort to extend our knowledge of this aspect of the physiology of the sclerophyll plants of Western Australia, transpiration and associated studies were planned for stations passing progressively inland from Perth on the western coast towards the Eremaea. From these experiments it is hoped to determine the degree of physiological diversity existing among the sclerophylls and to ascertain the nature of possible ecological adaptations. In the present paper the results obtained for the first stations on the Swan Coastal Plain are presented.

The Research Area—Its Vegetation and Soils

The affinities of the sclerophyllous trees and shrubs of the Swan Coastal Plain were indicated by Diels (1906) who referred to them as "thick shrub growths which can be compared with the maquis of the Mediterranean or better still with the stiff-leaved scrub of the Cape." The plants are predominantly hard-leaved and evergreen, herbaceous plants being poorly represented. Two stations were selected for the study of character plants—one in the vicinity of the University, and the other at Cannington a few miles south-east of Perth—so that these observations are representative of the vegetation of the metropolitan sector of the Swan Plain.

The tree community near the University is of mixed Jarrah *(Eucalyptus marginata)*, Marri *(Eucalyptus calophylla)*, Banksia and Casuarina. The associated shrub layer consists mainly of sclerophyllous plants varying from tall shrubs ($\pm$10 feet in height) down to shrubs ($\pm$ 2-3 feet in height). Herbs, varying in height from two to three feet down to a few inches, occur in the shrub layer.

The soil at the University station may be described as greyish-yellow to yellow sand (Karrakatta Sand). It is neutral or very slightly acid in reaction and the surface soil is darkened with organic matter. The soil profile in the main area of study is as follows:—

Sparse litter

Greyish black—0in.-8in. Coarse sand containing organic matter

Greyish yellow—8in.-18in. Coarse sand

Light brownish-yellow to yellowish-white, changing to yellow with depth—18in.-84in. Coarse sand containing a moderate amount of ferric oxide.

The climax community on the sandy ridges at Cannington is Banksia low scrub forest with associated shrub and herb layers. A typical soil profile (Speck, 1952) in the Muchea sands of the area is as follows:—

A_0 Sparse litter

A_1 0in.- 3in.—Grey sand with little organic matter

A_2 3in.- 8in.—Light grey sand—becoming leached

8in.-60in.—Highly leached white sand

B_1 60in.-70in.—Definitely darkened layer of brown sand suggesting a slight tendency towards formation of Coffee rock

70in.-80in.—Yellow brown clay streaked with blue at depth

Several of the species selected for study were common to each station. Those at Cannington showed in general a higher degree of xeromorphy.

Climate

The Perth area possesses a typical Mediterranean climate, the summers being long and dry, while the rain falls during the mild winter period. The rains commence in May and increase in intensity during June and July. In August there is a slight falling off and during September and October the rainfall decreases still further. This winter rainfall accounts for just over 30in. of the annual average of 34.7 in. Scanty rain (mean value rather less than 1in.) occurs during November, while December, January, February, March and most of April are dry months with rainfall average usually well under 1in. Evaporation figures during this period are high. Gentilli (1948, 1950) from a study of climatic data considered that under the conditions of high evapo-transpiration and little rainfall of the five summer months, the native vegetation in the Perth area would be under stress. Speck (1952) from observations on soil moisture content in the Cannington area in early summer also suggested that plants there would be subject to conditions of water stress for several months.

Methods

Measurement of Transpiration

Transpiration measurements were made using Huber's (1927) "quick weighing" method in which the loss of weight in the first 2-3 minutes after the leaf has been severed from the plant is considered to represent the natural transpiration. This method has been widely used in ecological and physiological work but has been the subject of much discussion and criticism. The main criticism has been that with the rupture of the water columns, on cutting, the release of stress would cause the water to rush upwards so that the leaf would temporarily be supplied with more water, leading to heightened transpiration. Ivanoff (1928) found such an increase in transpiration and various other workers including Kamp (1930) Weinmann and Le Roux (1946) and Anderson, Hertz and Rufelt (1954), have also recorded such an effect. Rouschal (1938) working with northern Mediterranean sclerophylls reported that with one exception there was a regular fall on weighing after abscission, while Oppenheimer (1953) working with similar plants in Palestine reported a regular decrease with time in some species tested and considerable irregularity in others. Our experience here has been that some species tested in summer showed a slow consistent decline in weight over successive two-minute periods, e.g., *Hardenbergia*, *Bossiaea*, *Phyllanthus;* while others sometimes showed a suggestion of the Ivanoff type of increase followed by a consistent fall, e.g., *Hibbertia*. In others again (and this applied more particularly when older leaves were under test) the rate of water loss was somewhat irregular, but remained fairly high over a period of several minutes, e.g. *Stirlingia*, *Banksia*. Typical results for water loss over the first few minutes are given in Table I.

TABLE I

Water Loss from Freshly Cut Leaves

Hardenbergia comptoniana		*Bossiaea eriocarpa*		*Hibbertia hypericoides*				*Stirlingia latifolia*		*Banksia attenuata*	
Time	Loss (mg.)	Time	Loss (mg.)	Time	Loss (mg.)	Time	Loss (mg.)	Time	Loss (mg.)	Time	Loss (mg.)
12·10	....	15·5	....	14·50	....	12·10	....	16·10	....	12·40	....
12·12	2·1	15·7	1·8	14·52	2·0	12·12	1·5	16·12	3·0	12·42	9·3
12·14	1·8	15·9	1·2	14·54	1·7	12·14	1·2	16·14	2·8	12·44	8·3
12·16	1·7	15·11	0·4	14·56	2·3	12·16	1·1	16·16	3·1	12·46	8·2
12·18	1·3	15·13	0·2	14·58	1·2	12·18	1·0	16·18	2·6	12·48	8·2
12·20	1·3	....	....	15·00	1·0	12·20	1·0	16·20	2·7	12·50	8·1
12·22	0·9	....	....	....	....	12·22	0·7	16·22	2·4	12·52	6·1
....	....	....	....	....	....	12·24	0·6	16·24	2·1	....	....
....	....	....	....	....	....	....	....	16·26	2·4	....	....

From these and other results it was considered that the most reasonable measure of the rate of transpiration for the purposes of this ecological study would be during the first two minutes. The downward trend was fairly general after this time, while the Ivanoff type of increase, when it occured, was seldom apparent before the first two minute reading. It is held that the method is basically sound as well as being at present the most appropriate for field studies on transpiration.

The torsion balance used by the author was an Oertling P type (100 mg.) with a milligram scale and mirror so that readings could be made to an accuracy of 0.2 mg. Leaves were cut from the plant with a vaseline smeared razor blade and suspended from the balance hook by means of standard weight cotton threads. Hinged compartments on the balance eliminated wind effects on leaves and counterpoises at the moments of original and final weighing, the leaves being fully exposed for the 2 (or in some experiments, 3) minutes specified. A stop watch was used for timing. Parallel measurements, with as short a time as possible between them, were made with at least two leaves (opposite leaflets in the case of *Hardenbergia* and *Kennedya*) which were similar in age, and position on the test plant.

Transpiration rate is expressed in terms of fresh weight as mg./g./min., and in terms of surface area [total area of leaf (cf. Rouschal, 1938)] as mg./sq. dm./min. where the leaf outline could conveniently be drawn and its area obtained with a planimeter Transpiration records were obtained on selected days during most months of the year. More numerous experiments were done during the period of change from the wet to the dry season.

Evaporation

Evaporation was measured using Stocker's method (1929) as revised by Stahlfelt (1932). The evaporation from a filter paper disk (area 27.7 sq. cm.) during a period of 1-2 minutes was obtained, readings being made at hourly or other intervals as required. These served to give values which were more readily comparable with transpiration from test plants. Piché atmometers as described by Walter (1929) were used to obtain a continuous record of evaporation.

Water Saturation Deficit

Stocker's method (1929) was followed for the determination of the water saturation deficit with the modification that the petioles were cut once only. After a saturation period of 24 hours the leaves were re-weighed and then dried to constant weight at 100°C. The initial and maximum water contents were obtained by subtracting the dry weight from the initial and maximum fresh weights and the water saturation deficit calculated as follows:—

$$\text{W.S.D.} = \frac{\text{Maximum water content} - \text{Initial or field water content}}{\text{Maximum water content}} \times 100$$

Sub-Lethal Water Deficit

As well as determining the Water Saturation Deficit of the leaves in the course of a day during summer, it is necessary to know how much water the leaf is able to give off without undergoing severe injury. This necessitates the continuation of a drying out process sufficiently long for the first signs of death of cells to be recognized. Oppenheimer (1932) coined the expression Sub-lethal Deficit for this and Rouschal (1938) applied the method in detail to the sclerophyll vegetation near Rovigno on the north-eastern Adriatic coast. The Sub-lethal Deficit may be defined as the maximum water deficit which the leaf will stand without death of more than ±5% of leaf tissue. The concept is useful in that it allows us to determine how close to the actual danger point natural water loss from the leaf may go and thus gives more precise meaning to the leaf Water Saturation Deficit.

Following Rouschal (1938), the procedure was adopted of rapid torsion balance weighing of 8-10 separate leaves of a selected plant, then allowing them to dry gradually in air. Periodically (intervals of 30 minutes were in general found to be suitable) a leaf was taken and re-weighed, notes being made on changes in colour or appearance. The petiole was then slit longitudinally and the leaf placed in water. After 2-3 hours under humid conditions it was re-weighed to determine whether water uptake was occurring and finally it was dried to constant weight. This procedure was continued for successive leaves until the point was found where even while some water was still being taken up, death of ±5% of cells was occurring. Determination of this sub-lethal point presented some difficulty as Rouschal's criteria for estimating death of cells namely healthy tissue appearing clear, and moribund tissue cloudy when viewed in transmitted light, proved unsuitable for most of the sclerophylls examined. Parker's tetrazolium chloride test (1951, 1952) while offering advantages for precise measurement of the lethal level was unsuitable for the determination of the sub-lethal level required. Reliance was finally placed upon changes in shape and colour in the leaves and on marked diminution of their ability to take up water after a certain period of drying out.

$$\text{Sub-lethal Deficit} = \frac{\underset{\text{(Max. water content)}}{\text{Saturation water content}} - \underset{(\pm 5\%\ \text{cells dead})}{\text{Dried out water content}}}{\text{Maximum water content}} \times 100$$

The natural Water Saturation Deficit, which is obtained from additional leaves at the same time as the above, may then be compared with the Sub-lethal Deficit and expressed in per cent of this, i.e.

$$\frac{\text{Natural Water Saturation Deficit}}{\text{Sub-lethal Deficit}} \times 100$$

Stomatal Aperture

Schorn's (1929) series of infiltration liquids (isobutyl alcohol and ethylene glycol in 11 mixtures varying from pure isobutyl alcohol, through isobutyl alcohol 9: ethylene glycol 1, isobutyl alcohol 8: ethylene glycol 2, etc. to pure ethylene glycol) was found to be reasonably successful for a number of sclerophylls.

Alvim and Havis's (1954) method of using *n*-dodecane-nujol in a series of ten concentrations in steps of 10% by volume from pure *n*-

dodecane to pure nujol was also used in later experiments and proved valuable in demonstrating smaller stomatal apertures than the Schorn series could record. It also gave more detailed information on slight changes in stomatal aperture. With some plants, however, difficulty was experienced in obtaining as clear a reading as with the Schorn series because of the lack of contrast between the infiltrated and non-infiltrated areas.

Light Intensity

Light intensity was measured in foot candles by means of an EEL photoelectric meter fitted with suitable filters.

Temperature and Relative Humidity

Temperature and relative humidity of the air were measured using a Sling Psychrometer. Instead of Relative Humidity, results are expressed in percentage Saturation Deficit (100-RH) as this latter, as Oppenheimer and Mendel (1939) point out, is in direct relationship to the intensity of transpiration and evaporation.

Soil Suction Force

The suction force of the soil was determined using the method of Gradmann as modified by Heilig (1931). The method proved suitable when the moisture content of soils was reasonably low, but in the absence of a suitable constant temperature room difficulty was experienced in making measurements of low suction tensions because of the condensation of moisture on the walls of the vessels and on the strips of filter paper when the vessels were taken out of the incubator to carry out weighings. It is believed that moisture in soils at this stage is readily available to the plant, forces of not more than 2 atmospheres being involved in binding the moisture to the soil.

Soil Moisture Content

Samples were taken at 1 foot and 2 feet depth in the vicinity of test plants. 10 g. of soil were weighed, then dried to constant weight. The difference between the fresh weight and the dry weight multiplied by 10 gave the percentage of moisture in the soil (Piper, 1944).

Periodicity, Leaf Anatomy and Root Systems

The following sclerophylls were used in this study of water economy:— *Banksia menziesii, B. attenuata, Stirlingia latifolia, Bossiaea eriocarpa, Hibbertia hypericoides, Eucalyptus calophylla*, (these species were common to both the University and Cannington stations), *Eucalyptus marginata, Hardenbergia comptoniana, Kennedya prostrata.* In addition periodic observations were made on sclerophylls such as *Daviesia nudiflora, Xanthorrhoea preissii, Acacia cyanophylla* and *Conostephium pendulum* and on the tomentose succulent *Scaevola canescens*, together with the glabrous, semi-succulent *Scaevola paludosa. Phyllanthus calycinus* (a soft-leaved but xerophytic plant), and the mesophyte *Erechthites hispidula* completed the types of plant studied.

Periodicity

A feature of the growth of sclerophylls such as *Banksia* spp. is the spring flush of growth which continues into early summer by which time the leaves are reaching maturity and have become thick and hard. *Hibbertia, Bossiaea* and *Phyllanthus* commence their new growth early in winter and continue through to early summer, while in *Stirlingia* the growth flush begins in late spring or early summer and leaf development continues well into the dry season. *Hardenbergia* shows no marked periodicity of growth, new leaves continuing to appear throughout the summer.

Ecological Anatomy—Structure

The mature leaves of *Banksia* species show a thick cuticle on the upper surface and densely matted hairs covering stomata on the lower surface; *Hibbertia, Bossiaea, Hardenbergia* and both species of *Eucalyptus* studied show a strong development of cuticle with stomata restricted to the lower surface; *Stirlingia* with vertically growing leaves and overall cutinization has stomata present on both surfaces; older *Kennedya* leaves are strongly thickened with stomata present on both surfaces but more numerous per unit area on the lower surface, while in *Phyllanthus* the leaves are thin and soft, the relatively few stomata per unit area being restricted to the under surface. In Table II the structural characteristics of the sclerophylls tested are given according to the scheme of Evenari (1938).

TABLE II

Anatomical Features of Sclerophylls

	Banksia menziesii	*Banksia attenuata*	*Stirlingia latifolia*	*Hibbertia hypericoides*	*Bossiaea eriocarpa*	*Eucalyptus calophylla*	*Eucalyptus marginata*	*Hardenbergia comptoniana*	*Kennedya prostrata*
Thick and cutinized epidermis	+	+	+	+	+	+	+	+	+
Cover of thick hairs on lower surface of leaf	+	+	—	Dense stellate hairs	—	—	—	—	—
Depression of stomata	±	±	—	—	—	—	—	—	—
Small inter-cellular spaces	+	+	+	+	+	+	+	+	+
Well developed mechanical tissues	+	+	+	+	+	+	+	+	+
Isobilateral structure of leaves	—	—	+	—	—	—	±	—	—
Reduction in size of leaves	—	—	—	+	+	—	—	—	—
High number of stomates per unit area (sq. mm.)	+	+	—	—	+	+	Medium	Medium	Medium

Root System

In *Hibbertia* the root system is relatively shallow, being contained in the first two feet of sandy soil. In *Bossiaea* and *Kennedya* the roots are somewhat deeper penetrating, while in *Stirlingia* in addition to a well branched shallow rooting system a main root goes down to considerable depth. In one instance such a root was traced to over 8 feet without appreciable diminution in its diameter. *Hardenbergia* possesses a root stock structure present at shallow depth but from it a strongly developed root goes down deep into the soil. *Phyllanthus* also possesses a well-defined root stock and a dense clump of roots which, however, remain relatively shallow. *Erechthites* possesses a shallow rooting system. The tree types, *Banksia* and *Eucalyptus* spp. possess both a shallow widely spreading root system and a deeper penetrating one.

Transpiration

The results of a number of transpiration studies are presented in Figures 1 to 8. The purpose is to show the course of transpiration and water balance of elements of the Swan Plain scrub vegetation on passing from spring to the dry summer conditions. Each point in the curves represents the mean water loss of two separate leaves (or in the case of *Hibbertia, Bossiaea* and *Phyllanthus*, of small twigs bearing several leaves).

Stirlingia latifolia

This plant is characterised by fairly high transpiration losses when water supply and atmospheric conditions are favourable. In early spring maximum rates as high as 14-15 mg./g./min. have been recorded (Fig. 1A), but in the majority of the experiments the highest values found did not exceed 10 mg./g./min. The average rate (8 a.m. to 5 p.m.) obtained from a number of experiments carried out during early and late spring periods was 4.7 mg./g./min. Rates after the break of season rains in May and on dry days throughout the winter when evaporation was low, remained below those of spring. Passing from late spring into summer, rate of water loss gradually fell, maximum rates recorded being below 4 mg./g./min. in late summer, (Fig. 1B). A daily two-peak curve is characteristic during the dry period and is to be contrasted with the typical single peak curve found in winter and spring experiments. The average daily rate during dry summers was found to lie between 2 and 2.5 mg./g./min. in the University station and was lower (1.2 mg./g./min.) at the Cannington station.

As will be described in more detail later, the rate of water loss from young leaves is much lower than that from mature leaves. As the amount of new growth in *Stirlingia* in a given season is generally small however, and as the reduced transpiration effect tends to be minimized as the spring flush leaves mature in summer it is considered unlikely that water loss differences between young and old leaves exercise any marked influence upon the overall summertime water economy of the plant.

Observations on stomatal opening in mature leaves during spring and early summer months showed some parallelism with transpiration trends while in young leaves there was evidence of a high degree of parallelism. Passing into mid and late summer, mature and maturing leaves of plants at the University station showed much less correspondence between stomatal opening and rate of water loss. On several occasions stomata were found to remain widely open while transpiration was falling. The hydro-reaction of stomata in mature leaves was found by separate experiment to be very sluggish. Stomata towards the base of such leaves were less responsive than those nearer the apical part. Young *Stirlingia* leaves showed an interesting variation in degree of stomatal aperture along their length. In the early afternoon stomata towards the apex of the leaf were closed, those in the mid section were open to a medium degree and those towards the basal part were widely open. In the late afternoon the apical stomata opened widely while those lower down tended to close. Use of the much more delicate *n*-dodecane-nujol infiltration series facilitated the study of these changes. In the more desiccating environment at Cannington during late summer, stomata were frequently found to be closed to isobutyl alcohol throughout the major portion of the day.

The *n*-dodecane series was not then in use, but in the light of comparative tests since carried out it is likely that stomata may have been recorded as open to 2 or 3 of this series. The low transpiration rate recorded may thus represent more than cuticular transpiration.

The water saturation deficit (W.S.D.) was examined in the Cannington experiments and was found to remain low during the day with a maximum of 6.9% and an average of 6.4%. In most experiments in summer similar low W.S.D. values were obtained. An exception occured in a test plant in February when a maximum of 17.2% and an average of 11.1% for the day, was recorded. The W.S.D. during the spring showed no marked increase during the day indicating that water is absorbed almost as fast as it is transpired. A similar picture was found in early summer, but as atmospheric and soil conditions worsened in late summer, the W.S.D. tended to rise during the morning hours. When a critical low water content was reached, transpiration began to fall. With the building up of water content transpiration rose to give the second peak as illustrated in Figure 1B.

For *Stirlingia* the relatively low value of W.S.D. extending into late summer indicated that even though a large number of the more shallow roots were non-functional due to dried-out soil, the deep main root system ensured that the plant was not subject to great water stress.

Hardenbergia comptoniana

Hardenbergia shows a fairly high transpiration rate in spring when abundant soil moisture is present, but with advancing summer the rate of water loss falls to quite low levels. The transpiration curves in spring are of the one-peak type and follow approximately the course of evaporation and saturation deficit during the day (Fig 2A). Maximum transpiration rates of about 10 mg./g./min. have been recorded while the daily average lies between 5 and 6 mg./g./min., the peak of the curve generally occurring between 12 noon and 2 p.m. In early summer the peak of transpiration, while approximately of the same magnitude as in spring, is found to occur much earlier in the day. Despite rising evaporation and increasing saturation deficit, the transpiration rate tended to fall to a relatively low and fairly constant level during the day. Later on under the more severe mid-summer conditions the morning peak became much shallower (Fig. 2B) and the water loss during the rest of the day fell to quite low levels (maximum 2.6 mg./g./min., average 1.5 mg./g./min.). The mean daily value from a number of experiments during late summer was 1.3 mg./g./min. Water saturation deficit remained quite low, maximum values not exceeding 8%. This plant with advancing summer limits its transpiration so that water loss is fairly rapidly made good by absorption through the deep root system. There is therefore no difficulty with water balance. The infiltration technique for ascertaining stomatal aperture could not be used in the case of *Hardenbergia*, the leaf being of the heterobaric type.

In late summer, tests of stomatal conductance using the cobalt chloride paper method (Milthorpe 1955) showed very low values associated with low transpiration rates as determined by the torsion balance method. It is likely that during the summer the stomata exercise control over water loss in *Hardenbergia*.

Banksia menziesii *and* B. attenuata

These two species presented a contrast in that while *B. menziesii* showed quite a high rate of water loss in late spring (maximum daily rate 11.5; average rate 7.6 mg./g./min.; Fig. 3A), *B. attenuata* lost water at a much lower rate (maximum 5.2, average 3.5 mg./g./min., Fig. 4A).

Passing into summer *B. menziesii* tended to reduce its transpiration rate to a relatively low level (daily average 1.7 mg./g./min. Fig., 3B) earlier than did *B. attenuata* where the rate in early summer (average 11.1 mg./g./min.) rose well above that recorded in spring (Fig. 4B). It was only in the later part of summer that *B. attenuata* reduced its water loss and even then the average daily value was high at 4.2 mg./g./min. Considerable difficulty was experienced in endeavouring to obtain a clear picture of water saturation deficit for both species of *Banksia*. Considerable variability was found to exist, even between matched leaves, in their ability to take up water after the 2-3 minutes of exposure needed for initial weighings. It is therefore reported with caution that the maximum value obtained did not exceed 8% in mature leaves and 20% in cutinized but not fully mature leaves.

In both of the above species of *Banksia* the lower surfaces of the leaves are covered with a dense felt of hairs and the infiltration technique of determining stomatal aperture could not be employed.

Hibbertia hypericoides *and* Bossiaea eriocarpa

Hibbertia, a fairly shallow rooting plant and *Bossiaea*, whose root system has been found to penetrate to 4 feet, both possess the small ericoid type of leaf. Owing to the small size of the leaf, transpiration experiments were conducted using twigs with several leaves attached. The rates of transpiration in spring were moderately high (see Figs. 5A and 6A). Transpiration rates increased on passing from spring into early summer, while adequate soil moisture was still present and evaporation was not unduly high. With advancing summer the transpiration rate of both plants markedly declined and by late summer both showed quite low average rates of transpiration (Figs. 5B and 6B). *Hibbertia* in late summer at the University station gave average rates of 2.2 mg./g./min. Under the more desiccating conditions of the Cannington area, leaves of *Hibbertia* plants became very revolute and turned a yellowish colour, water loss being very low. When twigs were cut and placed in water the leaves took up water and recovered their green colour within 2-3 days. This recovery from yellow to normal green occurs in nature after the infrequent summer rains and regularly after the break of season rains. Using the infiltration method stomatal aperture in *Hibbertia* could be followed reasonably well during spring and early summer, but some difficulty was experienced in the really dry period. Recurving of leaf margins and the closer packing of the stellate hairs then made it difficult to ascertain whether the stomata were slightly open or completely closed. The water saturation deficit in *Hibbertia* increased with advancing season. In spring maximum deficits of 9.6% were recorded with an average of 7.3%.

FIGURES 1-8 INCLUSIVE

The following symbols are used throughout these figures:—

T.	◊	Temperature
S.D.	□	Saturation Deficit
E.	△	Evaporation
TR.	— o —	Transpiration mg./g./min.
	- - ● - -	,, ,,
	- - ■ - -	,, mg./sq.dm./min.
ST.	- - ● - -	Stomatal aperture
	- - - - -	Light intensity

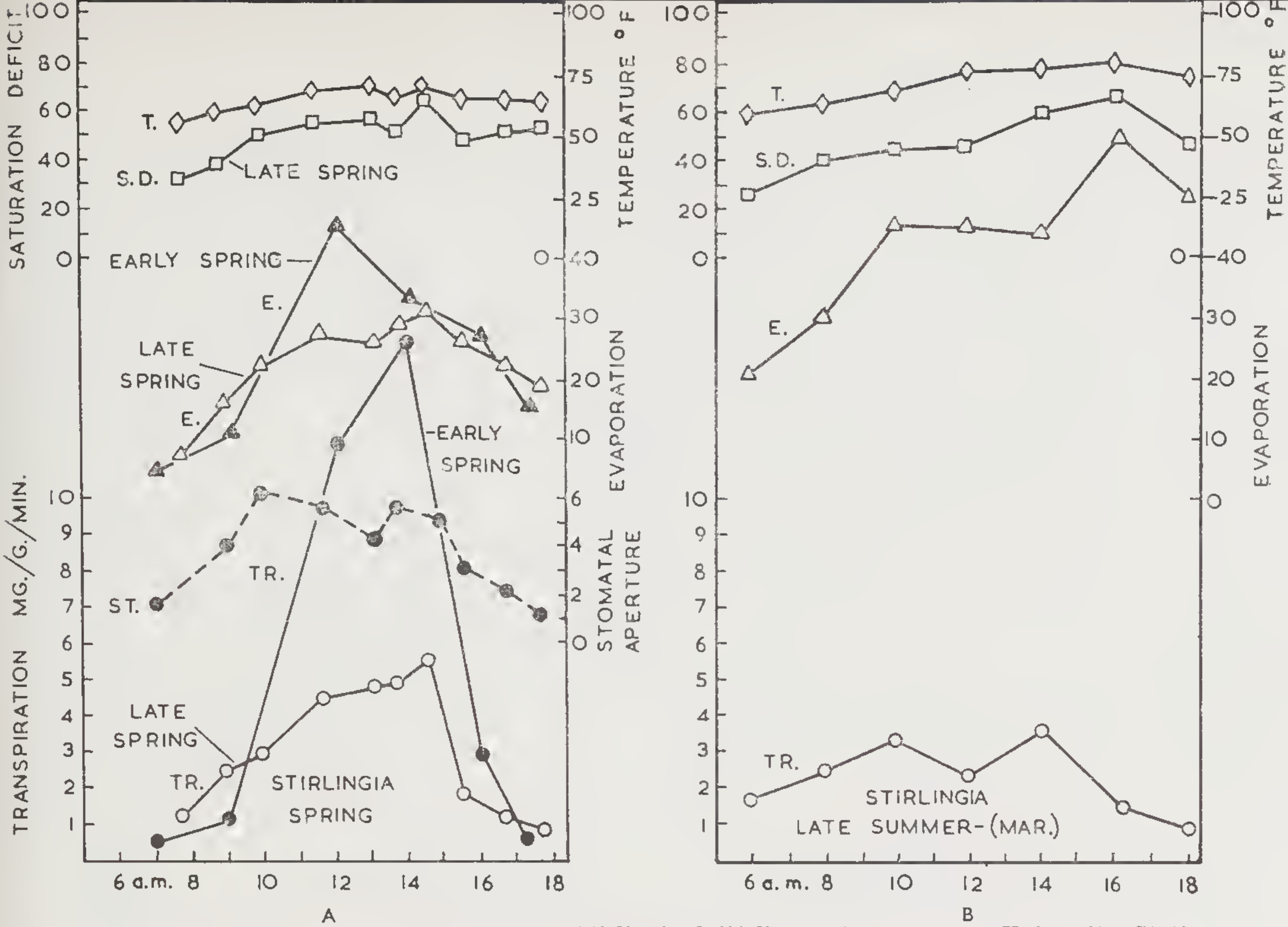

FIG. 1.—Daily march of transpiration in *Stirlingia latifolia*—mature leaves. University Station. (A) Early and late Spring, (B) Late Summer.

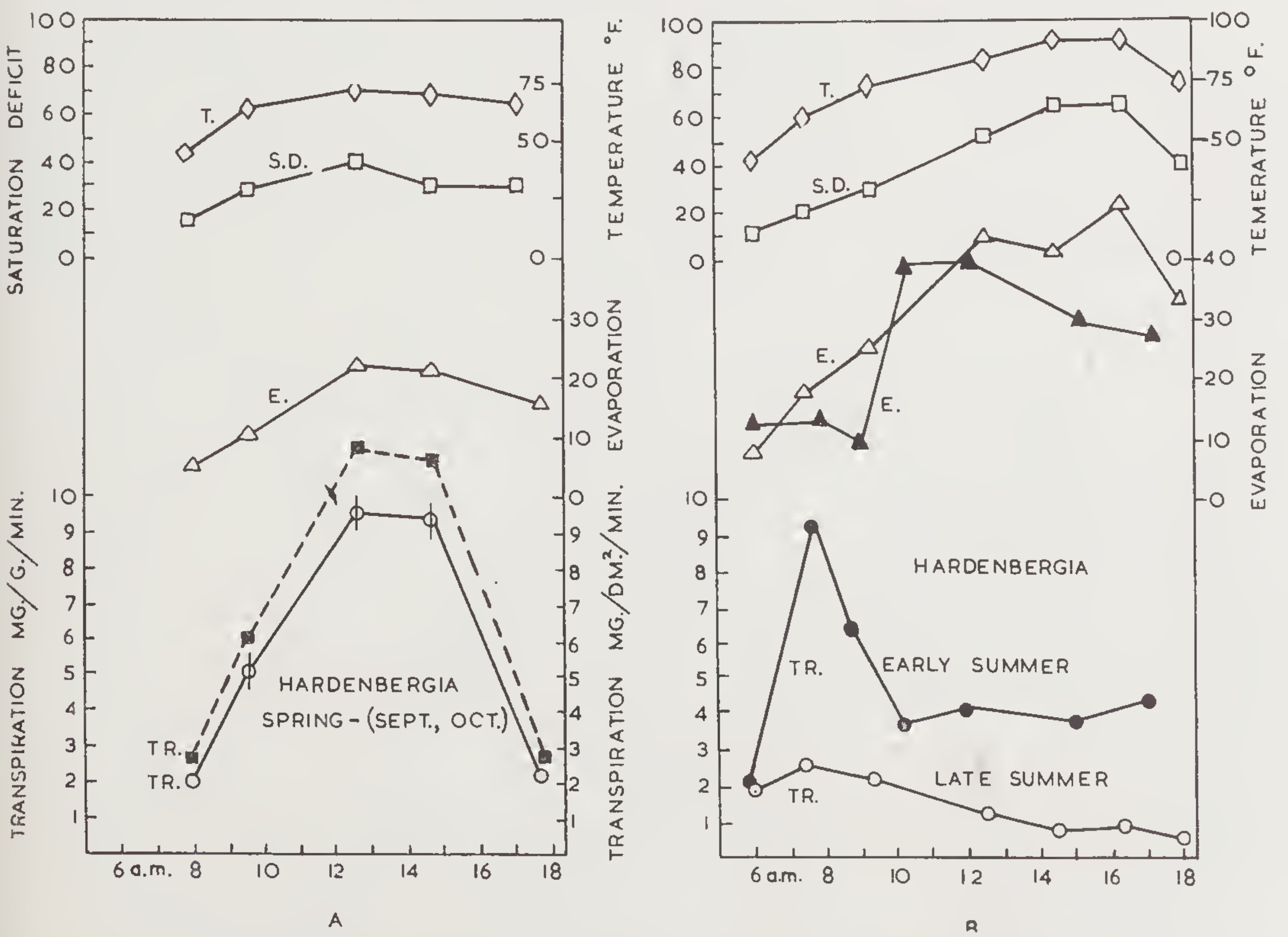

FIG. 2.—Daily march of transpiration in *Hardenbergia comptoniana* in (A) Spring and (B) Early and Late Summer.
In Fig. 2B:—Early Summer, ▲ and ●
Late Summer, △ and ○

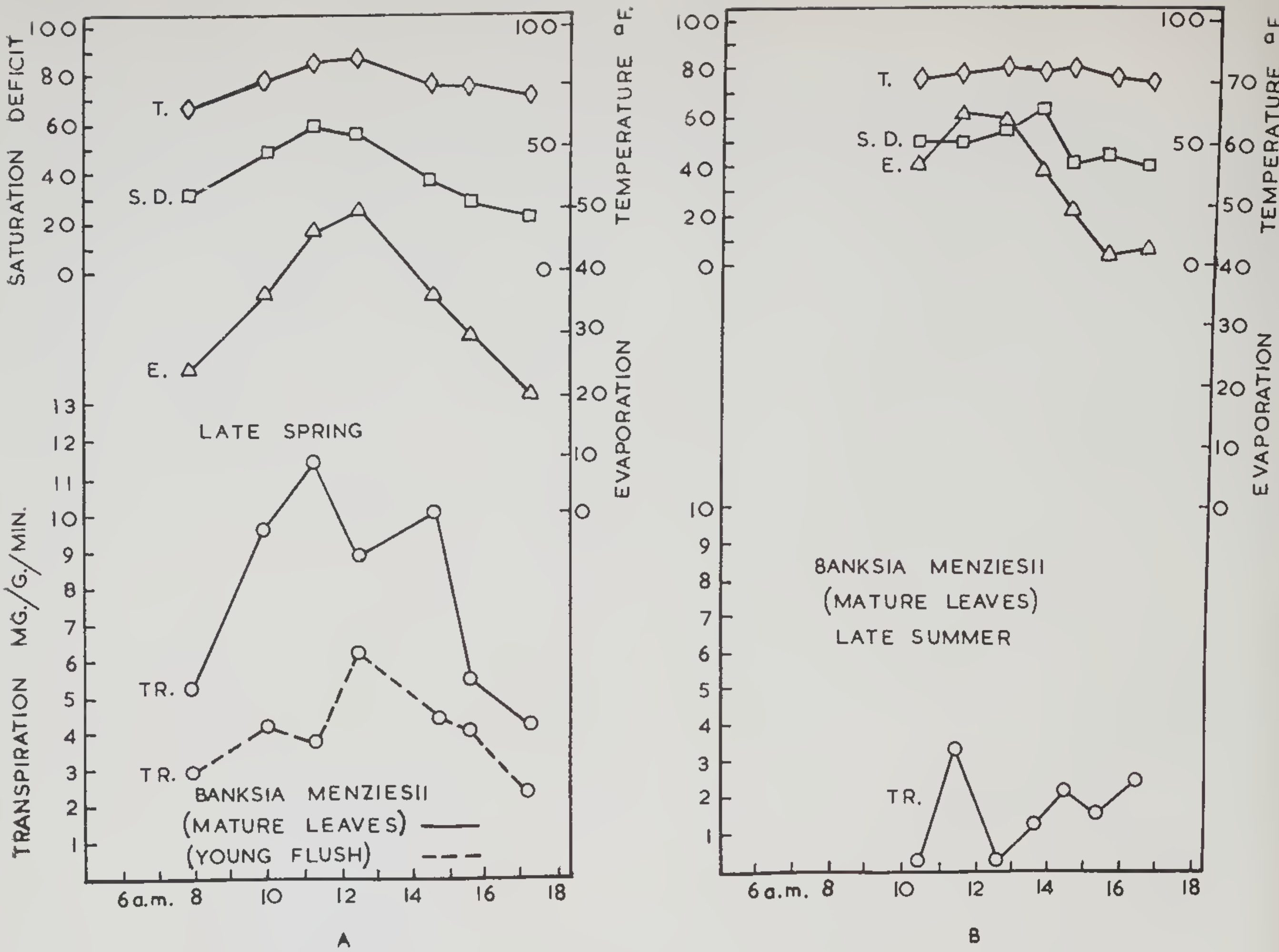

FIG. 3.—Daily march of transpiration in mature and young flush leaves of *Banksia menziesii* in (A) Late Spring and (B) Late Summer.

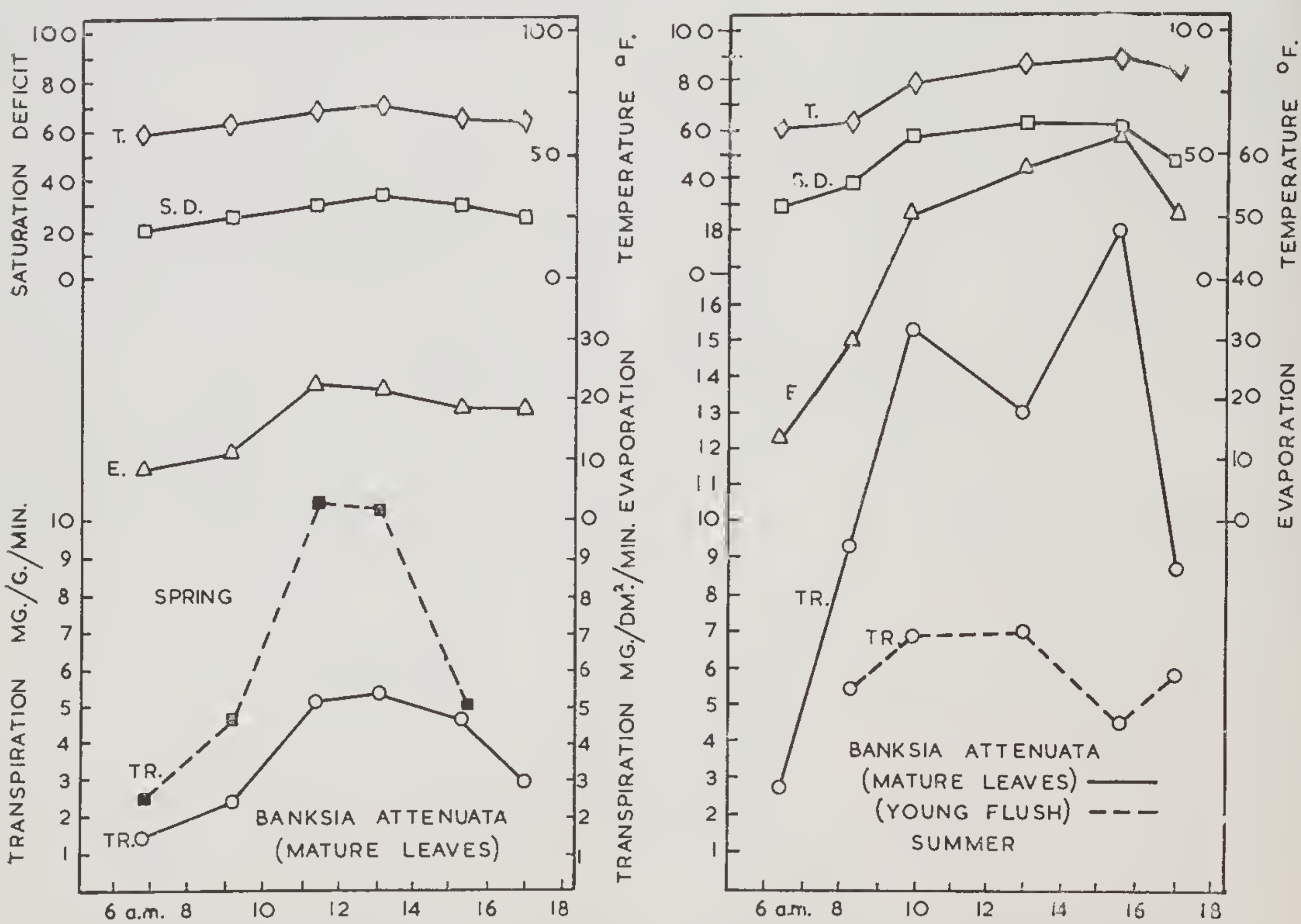

FIG. 4.—Daily march of transpiration in mature and young flush leaves of *Banksia attenuata*, in (A) Spring and (B) Summer.

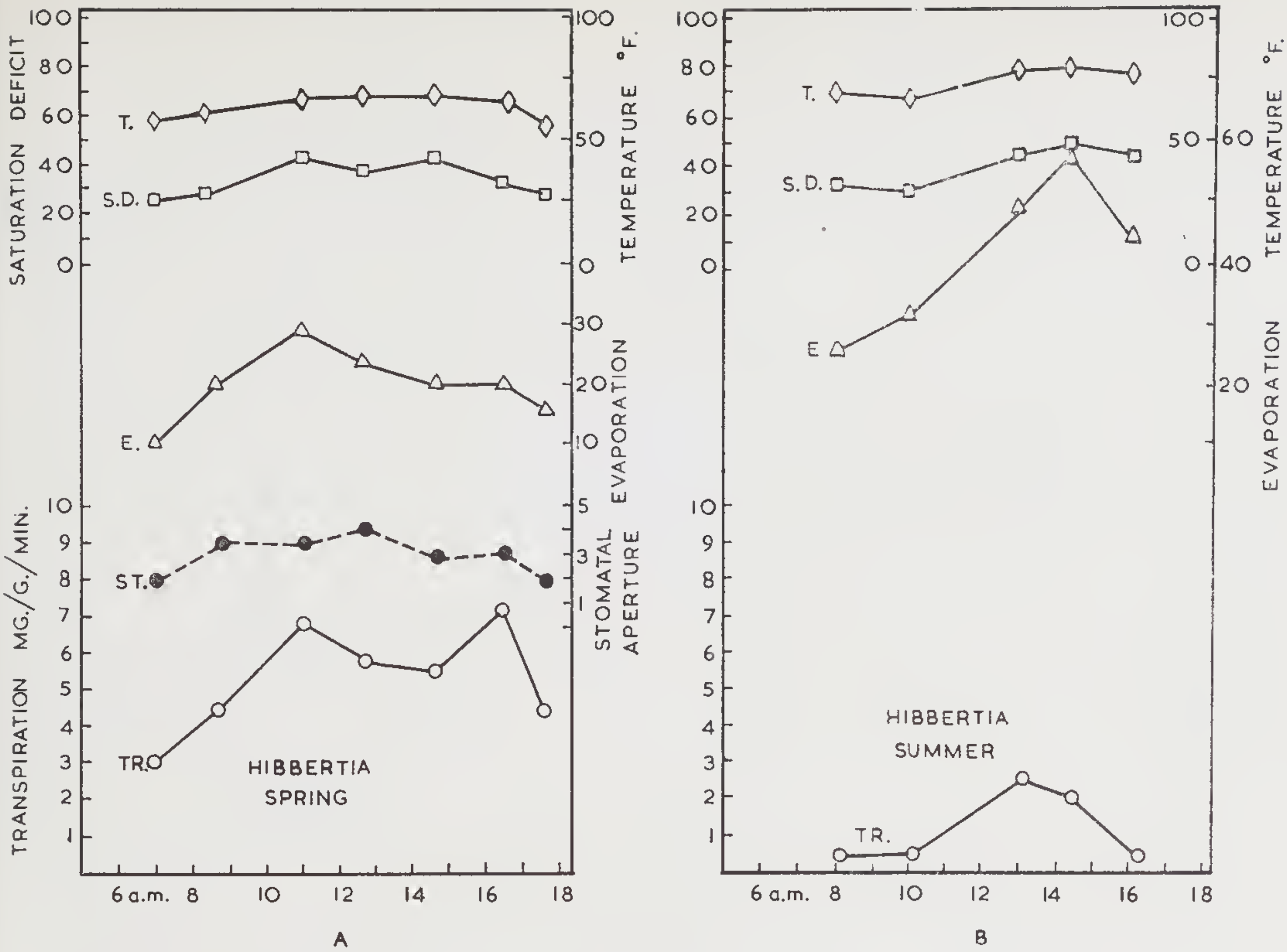

FIG. 5.—Daily march of transpiration in *Hibbertia hypericoides,* in (A) Spring and (B) Summer.

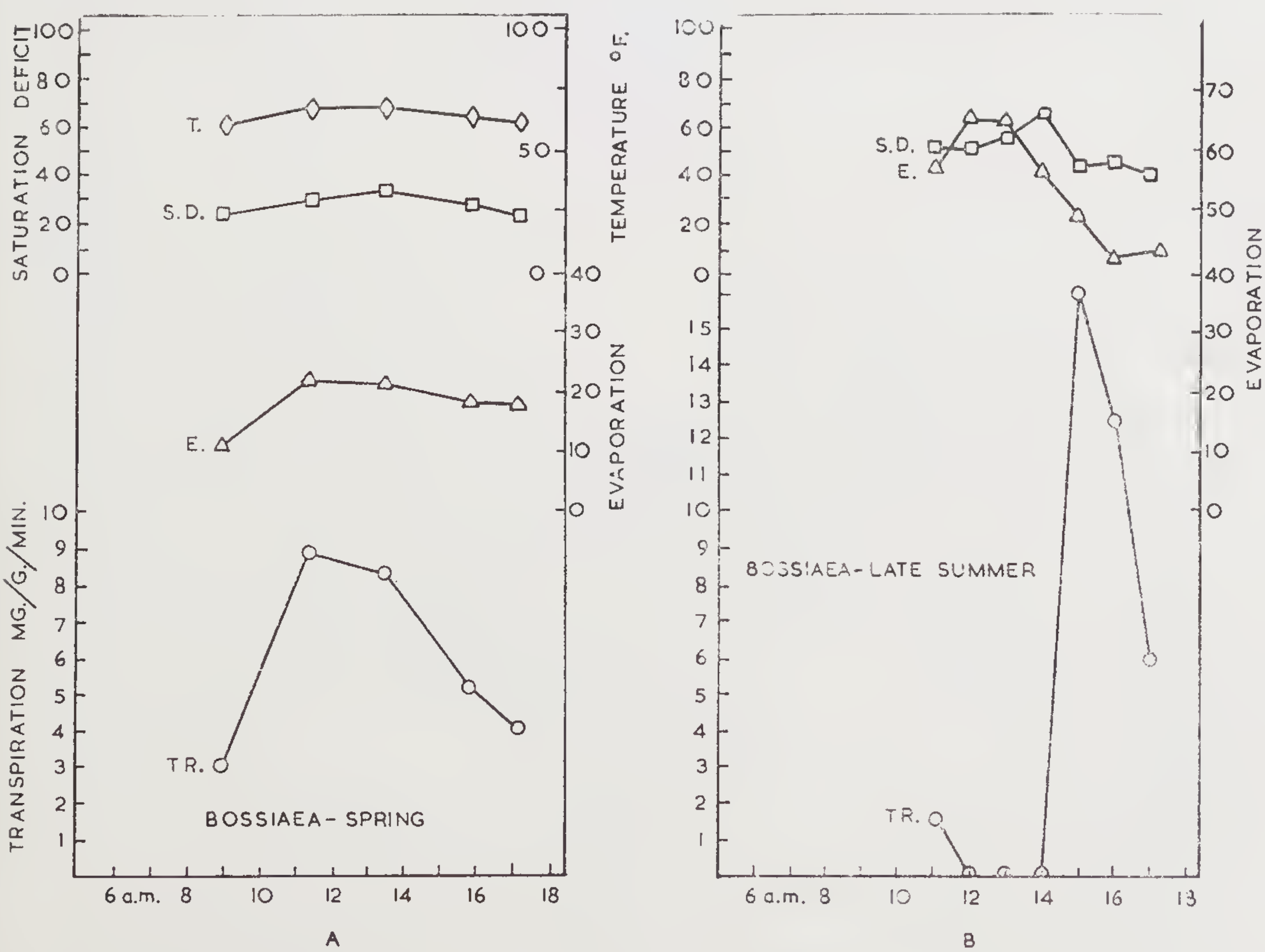

FIG. 6.—Daily march of transpiration in *Bossiaea eriocarpa* in (A) Spring and (B) Late Summer.

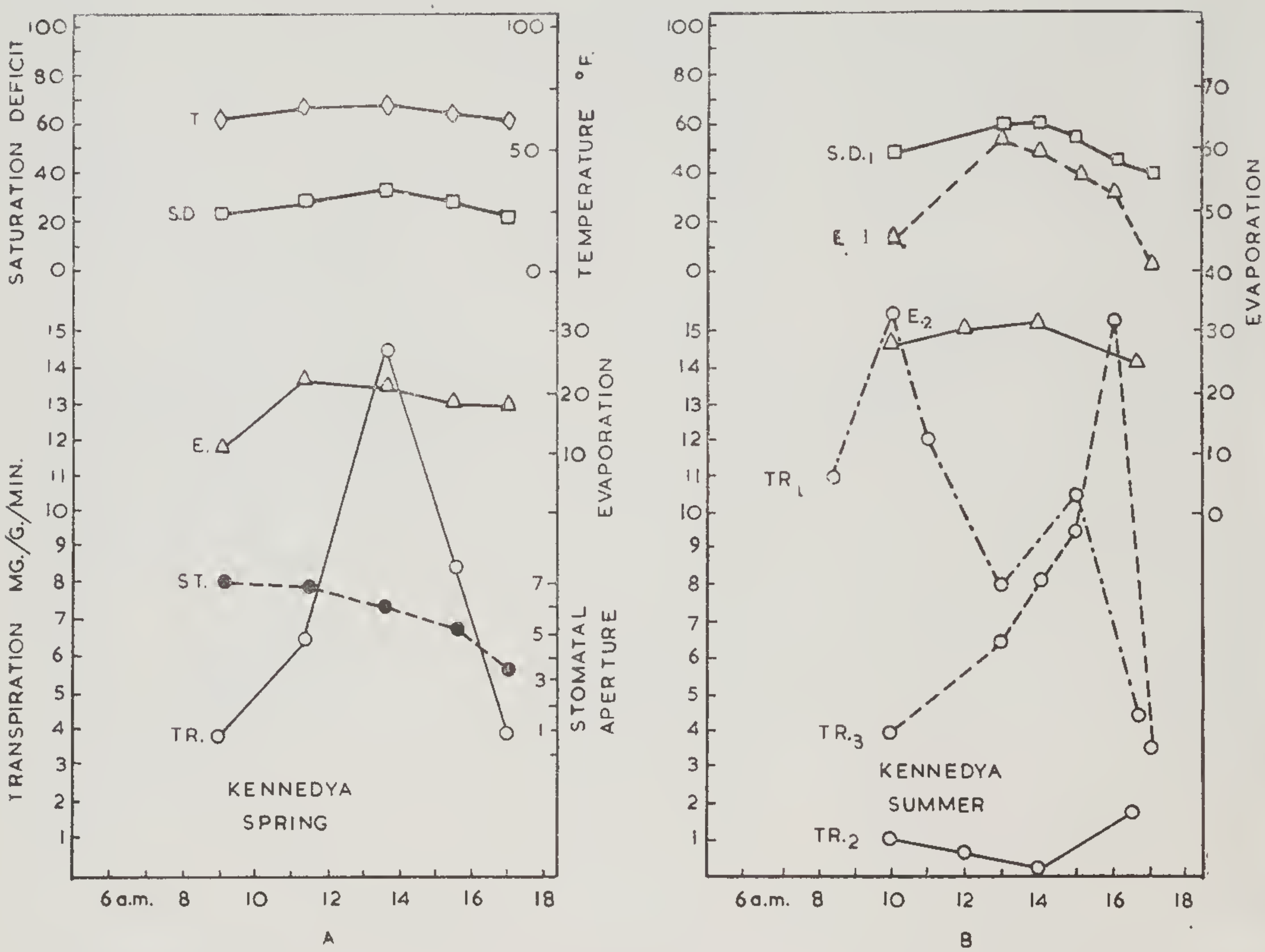

FIG. 7.—Daily march of transpiration in *Kennedya prostrata,* in (A) Spring and (B) Summer.
Early Summer:—E_1 and TR_1
Late Summer:— E_2 and TR_2
Summer (after rainfall):—TR_3

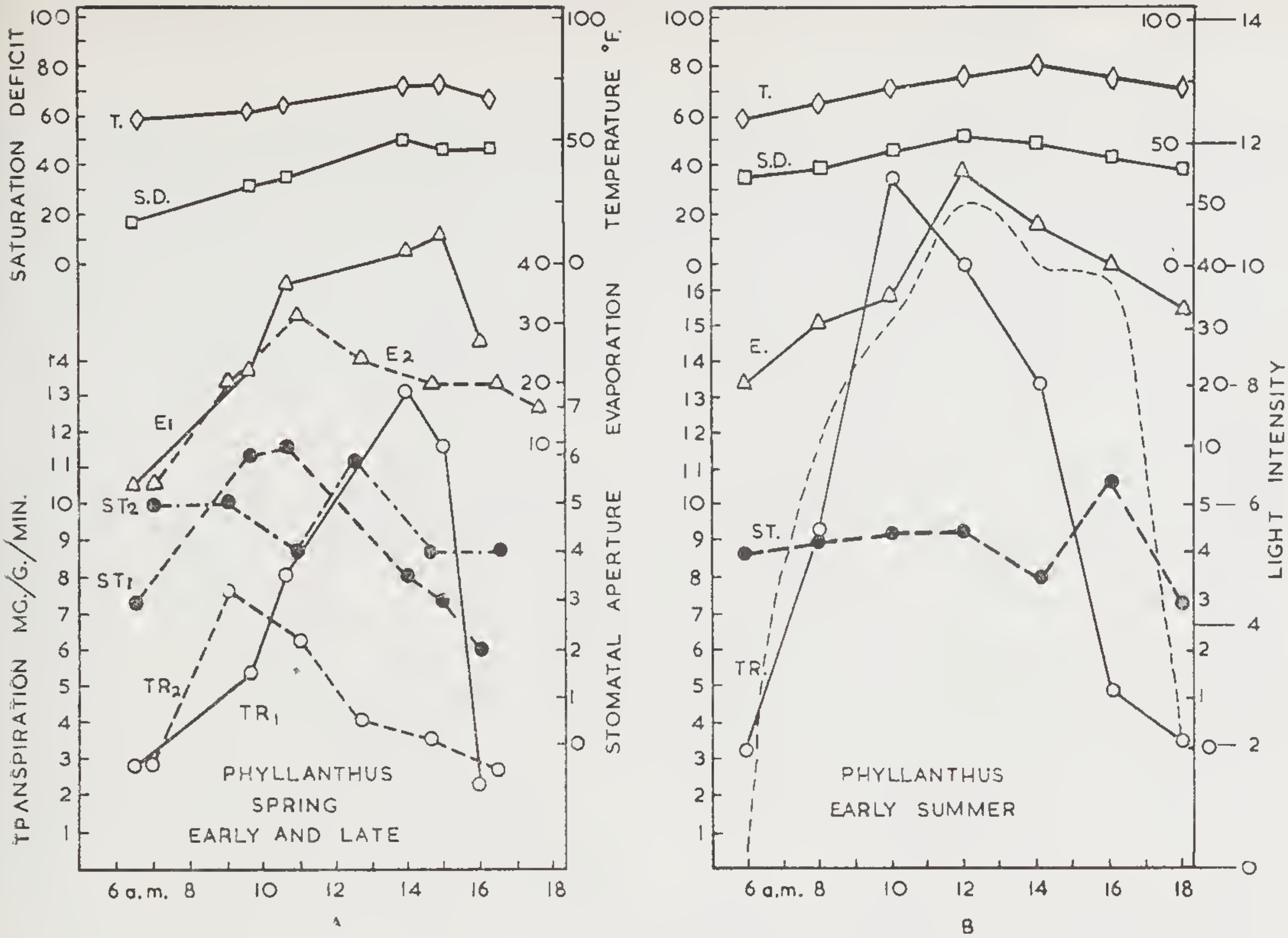

FIG. 8.—Daily march of transpiration in *Phyllanthus calycinus*, in (A) Early and Late Spring, and (B) Early Summer.

Early Spring:—E_1,ST_1 and TR_1
Late Spring:— E_2,ST_2 and TR_2

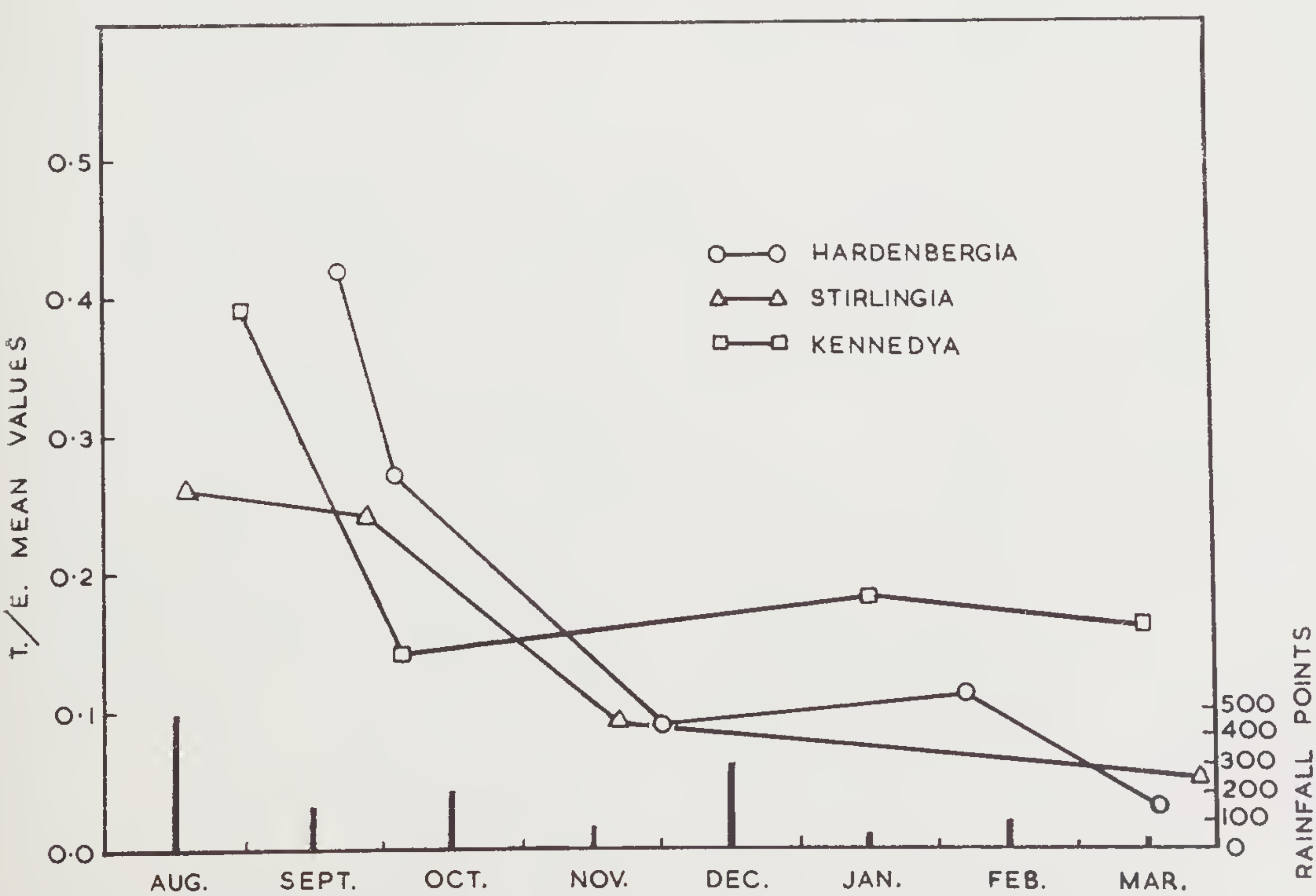

FIG. 9.—Relative transpiration (T/E) of selected plants passing from Spring into Summer, and monthly rainfall data.

In late summer maximum deficits of 25 to 26% were recorded. In spring no significant increase in water saturation deficit occurred during the day indicating that water uptake was keeping pace approximately with transpiration. With advancing summer the water saturation deficit rose during the day, the maximum value often not being reached until 2 or 3 p.m. With the transpiration peak being reached at 8 or 9 a.m. it is clear that during late summer the plant is for some time during each day under considerable stress.

High osmotic values obtained for extracted leaf juice at this time confirm the condition of stress. The plant reacts to this stress by the recurving and incurving of the leaf margins so that the stellate hairs are pressed close together. With closure of stomata water loss is reduced to a low level.

Bossiaea eriocarpa showed the lowest daily average transpiration in late summer of any plant tested in this series, namely 0.3 mg./g./min. For long periods at a time during a hot day no evidence of water loss could be obtained with the torsion balance. The rate might then rise very suddenly, water vapor being released as it were in a burst (Fig. 6B). A close correspondence between stomatal aperture and water loss in *Bossiaea* was established. Where the water loss was negligible, stomata were found to be completely closed to isobutyl alcohol, but when the transpiration burst occurred the stomata could be shown to be open to 1 or 2 of the infiltration series. The stomata of *Bossiaea* react very rapidly in the hydro-reaction test. Within three minutes stomatal apertures have been observed to close down from 5 to 3 on the isobutyl alcohol-ethylene glycol scale; in another three minutes to 1, followed within a further three minutes by complete closure. The water saturation deficit in summer was found to be high with an average of 49% and a maximum of 57%. This, together with the fact that the osmotic value of the leaves rose considerably during the summer months indicated a considerable degree of stress even though some roots have been observed to go down to 4 feet in the sand.

Kennedya prostrata

As may be seen from Fig. 7A, which is typical of several experiments performed, *Kennedya* shows a one-peak curve in spring with high maximum and average daily rates of water loss. Stomata which are present both on the upper and lower surface show gradual closure during the day but appear during this period to have little controlling effect upon rate of water loss. Thus even when transpiration was reduced to 3.8 mg./g./min. at 5 p.m. (Fig. 7A) stomata still remained fairly widely open. Passing into early and mid summer, transpiration rates frequently remained quite high and curves were of the two-peak type. With increasing dry conditions in late summer low transpiration rates were recorded (Fig. 7B, Tr_2). Stomata were closed to isobutyl alcohol series throughout the day. Water saturation deficit values however remained low, rising only to a maximum value of 9.6%. Rainfall during any part of the summer rapidly resulted in an increase in the transpiration rate with a tendency to return to the single peak curve. No clear overall relationship between stomatal aperture and water loss could be demonstrated under spring and early summer conditions, but in late summer stomatal closure was an effective factor in reducing water loss. The hydro-reaction of stomata in *Kennedya* was quite rapid.

Eucalyptus marginata *and* E. calophylla

Marked differences were observed in the transpiration rates of these two Eucalypts. *Eucalyptus marginata* (Jarrah) frequently showed a high rate of water loss in summer (average 7.2 mg./g./min.), stomata often being widely open. Under similar conditions *E. calophylla* showed a relatively low rate of water loss (average value 4.2 mg./g./min.) and the stomata during the hotter part of the day were closed to isobutyl alcohol. At such times the rate of water loss was restricted to 0.3 mg./g./min. *E. marginata* may be regarded as being prodigal of water. Due to its deep rooting system adequate water is available even in late summer. *E. calophylla* even though possessing an extensive root system is more sparing of water in summer.

Xanthorrhoea preissii, Petrophila linearis, Daviesia nudiflora, Conostephium pendulum.

These sclerophylls which were growing at the University station were tested from time to time. They showed fairly high rates of water loss in spring but by mid summer the average rates of water loss were markedly reduced.

Phyllanthus calycinus *(soft-leaved xerophyte)*

Phyllanthus is unusual in having quite thin and soft though small, leaves, and yet occurring as a character plant among the sclerophylls. In late winter and early spring the rate of water loss is high (maximum values of 17.7 mg./g./min. and average daily values of 7.2 mg./g./min. were recorded in August-September). By late spring although the type of curve was still single peaked the time of reaching maximum rate had moved back to much earlier in the day and the peak was lower (Fig. 8A). *Phyllanthus* showed very clear infiltration reactions to both the isobutyl alcohol-ethylene glycol series and the *n*-dodecane-nujol series. In early spring experiments the stomata showed some degree of closure while transpiration rate was still rising. Stomatal aperture then remained relatively constant until late in the day by which time transpiration rate had fallen to quite low levels. In late spring and early summer stomatal apertures were still found to remain at fairly constant aperture while transpiration was rising or falling.

In early summer the rate of water loss remained as high as in late spring, but as atmospheric and soil moisture conditions worsened, defoliation of *Phyllanthus* plants commenced and continued up the stems until by mid-summer (late January and early February) very few leaves were left. Even at the stage where lower leaves were commencing to yellow and fall, the stomata on all green leaves remained fairly widely open during hot days and closure did not occur until late in the evening. The stomata were characterized by very slow hydro-reactions. Photo-reactions were faster but as cloudless conditions are usual this reaction appears to have no ecological significance.

The water saturation deficit of green leaves still attached, while defoliation was occuring lower down on the stem, showed low values up to 2.8%. Owing to the fact that a milky latex is present in *Phyllanthus* and that this may have affected water uptake in the saturating experiments, the above low values must be viewed with caution. It seems significant, however, that leaves of *Phyllanthus* although so soft and thin, do not show wilting.

From these results it appears that *Phyllanthus* is prodigal in the use of water and only balances its water budget and survives the summer by drastically reducing its transpiring surface.

Erechthites hispidula *(mesomorph)*

The water loss of *Erechthites hispidula* a soft-leaved mesomorph growing at the University station was tested for comparison with the sclerophylls. It showed very high transpiration rates through spring (average 10.7 mg./g./min.) and summer (average 13.3 mg./g./min.), up to the time when it wilted irreversibly and died. Stomata appeared to have little controlling influence on transpiration throughout the major portion of the day.

Rate of Water Loss in Mature versus *Young Leaves*

In the course of preliminary transpiration experiments using leaves from different parts of *Stirlingia*, it was observed that the rate of water loss was much higher from mature leaves than from young leaves of the current season flush of growth.

As this ran counter to the commonly expressed view in transpiration literature that young leaves transpired faster, further studies were made of *Stirlingia* and the work was extended to include the two species of *Banksia*. These further tests confirmed the original observation and it was found that the mature leaves lost water at a much higher rate (both in terms of fresh weight and area) during the hotter parts of the day in spring and early summer (see Figs. 3 and 4 and Table III). With advancing summer the spring flush of leaves gradually assumed the normal highly sclerophyllous form and the differences between the rates of water loss became less apparent.

TABLE III

Rate of Water Loss From Young and Mature Leaves

		Spring. mg./g./min.	Early Summer mg./g./min.
Stirlingia latifolia	Young	6·8	7·2
	Mature	12·6	12·3
Banksia menziesii	Young	4·5	4·0
	Mature	9·0	11·0
Banksia attenuata	Young	2·0	7·0
	Mature	4·9	15·8

The lower rate in the young leaves is due, at least in part, to the better stomatal control associated with greater mobility of their guard cells before the processes of lignification and cutinization develop too far. Experiments described earlier dealing with the degree of stomatal aperture in young versus old *Stirlingia* leaves during the day, showed that young leaves were much more responsive to changes in atmospheric conditions and in water content of leaves. The hydro-reactions of mature leaves were also very sluggish as compared with those of young leaves.

Cuticular Transpiration

Cuticular transpiration in *Hardenbergia, Hibbertia, Bossiaea,* and *Eucalyptus* species tested in early summer was found to be quite low, varying from 0.1 to 0.3 mg./g./min. The ratio of cuticular to overall transpiration was highest in *Eucalyptus calophylla* (1 : 60). The lowest ratio under the conditions of these experiments was found in *Banksia attenuata* (1 : 36). Owing, however, to the difficulty for *Banksia* of completely covering the felted hairs on the lower surface with vaseline, (particularly near the recurved leaf margins) it is believed that the water loss recorded may not have been completely restricted to cuticular transpiration. Of the above listed sclerophylls it has been shown for *Hibbertia, Bossiaea* and *Eucalyptus calophylla* that they can completely close down their stomata under desiccating conditions. The first two named also achieve more efficient protection by strong leaf inrolling. Thus with low cuticular transpiration, water loss may be reduced to a minimum. *Stirlingia* and *Kennedya* which bear stomata on both leaf surfaces could not be satisfactorily tested for cuticular transpiration. It may be noted, however, that mature *Stirlingia* leaves are heavily cutinized on both surfaces and it seems reasonable to assume that where stomata do close completely under late summer conditions cuticular transpiration would be slight. *Kennedya* leaves are lightly cutinized on the upper surface and dense hairs are present on the lower surface. Under desiccating conditions the leaf margins tend to roll upward and inward. Transpiration experiments in late summer where stomata were recorded as closed to isobutyl alcohol, showed a fairly high transpiration rate early in the morning. This declined progressively until 2 p.m. with rising evaporation. Subsequent tests suggested that the stomata would have been open to at least 3 on the more delicate *n*-dodecane-nujol series at the start of the experiment and that gradual closure would have occurred associated with some decline in the rate of water loss. The hairs on the lower surface would further help to reduce transpiration and the upward and inward rolling of the leaf would also give some protection to the upper surface. Their combined operation would tend to offset the lack of cuticular development in *Kennedya* and would result in the low transpiration rate recorded.

Course of the Transpiration Curves

Examination of the spring curves plotted in Figs. 1 to 8 shows that with adequate moisture in the soil at all levels and favourable climatic conditions, transpiration in general is high. The curves tend to run parallel to those for evaporation and atmospheric saturation deficit. Passing into summer, with increasing evaporation, higher atmospheric saturation deficits and drier soil, transpiration of the sclerophylls is seen to be gradually restricted. In the case of *Hardenbergia* and *Hibbertia* the late summer curves are of the one-peak type and fall as evaporation rises during the later morning and early afternoon hours.

Stirlingia, Kennedya, Bossiaea and *Banksia* show two-peak curves. The first is in the early morning then with rising evaporation the rate of water loss drops. The second peak in the afternoon may occur while evaporation is still either rising, maintaining a high level, or falling. The increased rate of water loss at this time may be associated with a build up of water content in the leaf tissues but it was not possible to obtain evidence of this.

When relative transpiration, T/E (used in a restricted sense) was plotted against month of year, commencing in spring, the decreasing transpiration with passage into summer became apparent (Fig. 9). It is noteworthy that the steepest fall in relative transpiration occurs by early summer. By this time the soil at the University station at the 2 foot level is drying out (moisture content 1.3%, suction force 50 atmospheres). This affects a large part of the root system of all the plants tested. The shallow rooting *Hibbertia* and *Phyllanthus* and to a lesser extent *Bossiaea* suffer from some water lack at this stage. *Stirlingia, Hardenbergia,* the banksias and the eucalypts all possess as well a deep rooting system. In all cases, however, with the exception of *Eucalyptus marginata*, restriction of transpiration occurred with rising evaporation giving low values for T/E. With more desiccating atmospheric and soil conditions passing into late summer, *Hibbertia* passed into a state of anabiosis, while *Phyllanthus* retained only a few yellowish leaves. *Kennedya* after the first drop, maintained fairly high T/E values passing into late summer, while *Hardenbergia* and *Stirlingia* fell to rather low levels.

Osmotic Values

Detailed observations on the osmotic values of leaves of sclerophylls will be reported elsewhere. It will suffice here to note that osmotic values rose with advancing summer while in general a rapid return to lower values occurred with break of season rains. *Hibbertia* showed the highest values at 25-27 atmospheres. Possibly higher values would have been obtained in later summer but the leaves were so dry that, with the existing sap-press, juice could not be squeezed from them. *Bossiaea* also gave high values up to 21 atmospheres. Here again higher values would no doubt have been obtained in late summer if sap could have been extracted from the leaves.

Stirlingia, Banksia and *Kennedya* gave values up to 21 atmospheres (in one instance a value of 28 atmospheres was recorded for *B. menziesii*) and sap could still be extracted although with some difficulty throughout the summer. Osmotic values up to 16 atmospheres were recorded for *Hardenbergia* in late summer. The figures for *Hibbertia* and *Bossiaea* taken together with the dry nature of the leaves and the high water saturation deficit mentioned earlier, suggest a strained water balance in late summer. The values for the deeper rooting *Stirlingia* and *Hardenbergia* were not unduly high. This fact, together with the lower water saturation deficit observed in these plants, suggests that they possess a reasonably balanced water budget.

Soil Moisture and Soil Suction Force

Soil moisture values showed continuous decline from spring into summer while soil suction force rose. Typical results at 1 foot depth are given in Table IV.

TABLE IV

Soil Moisture and Soil Suction Force at 1-foot Depth

		Sept.	Nov.	Dec.	Jan.	Feb.
Soil Moisture (%)	University ..	3·0	1·8	1·4	1·35	1·3
	Cannington ...	4·1	1·6	....	0·3	....
Suction Force	University	4·5	....	28·1	42·5	50·0
(Atm.)	Cannington ...	3·8	7·6	....	>100	...

At a depth of 2 feet the moisture content at the University station had by late January fallen to 1.09% and the suction force risen to 75 atmospheres.

For shallow rooting plants—in particular *Hibbertia* and *Phyllanthus*—the decrease in soil moisture and increase in soil suction force has considerable significance. By late summer the suction force at the 2 foot level was reaching values which made it impossible for the plants to absorb water. *Hibbertia* whose roots lay in this zone, after progressively reducing its transpiration loss to low values passed into an almost anabiotic state, while *Phyllanthus* having gradually lost more and more leaves as soil and atmospheric conditions worsened, passed the summer in a defoliated state.

With increasing depth the moisture content of the soil at the University station in late summer remained high as the values in Table V indicate.

TABLE V

Soil Moisture at University Station, Late Summer

Depth of Soil Sample	Soil Moisture (%)	Suction Force (Atm.)
1 foot	1·3	50
4 feet	2·5	10
11 feet	4·0	Zero

The main roots of *Stirlingia* and *Hardenbergia* have been traced down to 8 feet in sandy soil and judging from their thickness at that depth could well continue down several feet further. Clearly although the surface lateral roots may be put out of action by rising suction forces at the two foot level, the possession of a deeper penetrating main root means that these plants are unlikely to suffer from severe water stress. The reduction in transpiration rate in summer may be related to slower water movement through the diffuse porous vessels of the deep growing main root with its subsidiary lateral system.

Discussion

All of the sclerophylls examined with one exception, were found to reduce their rate of water loss when passing into the dry summer period irrespective of whether they were (a) relatively shallow rooting types as in *Hibbertia* and *Bossiaea*, or (b) ones which possessed a combination of shallow and deeper extending roots as in *Stirlingia, Hardenbergia* and *Kennedya*, or (c) the trees *Banksia menziesii, B. attenuata* and *Eucalyptus calophylla*.

Plants of type (a) are clearly sensitive to soil drought, while types (b) and (c) are only partially affected. *Eucalyptus marginata* alone among the sclerophylls so far examined, maintained a high level of water loss during summer. The shallow rooting soft-leaved xerophyte *Phyllanthus calycinus* and the mesophyte *Erechthites hispidula* also showed no tendency to restrict water loss with advancing season, but under conditions of soil drought almost complete defoliation occurred in the former, while in the latter case the plant finally died.

Comparative studies of water loss of sclerophylls during different seasons are not available for other parts of Australia, but Wood (1923, 1924) has worked on the transpiration of sclerophylls during summer in arid inland South Australia. He showed that while there was considerable individual variation, their average rates of water loss were low (*Eremophila scoparia* 1.15 mg./sq.dm./min.; *Casuarina lepidophloia* 2.25 mg./sq.dm./min.; *Acacia aneura* 1.38 mg./sq.dm./min.). The mesophyte *Senecio magnificus* showed a rate of water loss well above that of all sclerophylls in the area. This high rate of water loss is paralleled by that of the mesomorph, *Erechthites hispidula* in the Swan Plain area. The rate of loss for this mesomorph is far higher during spring and summer than that of any Swan Plain sclerophyll tested. Under the field conditions near Perth the xerophytic sclerophylls therefore do not conform to Maximov's experience at Tiflis (1929). Wood (1934) however, found high values for three Mount Lofty sclerophylls, *Eucalyptus leucoxylon, Acacia pycnantha* and *Hakea rugosa*. In field studies of similar types of plant in Victoria and Western Australia, the author has so far not found such high values (Grieve, 1955).

In other areas of Mediterranean climate many investigations on sclerophylls and associated plants have been made. The sclerophylls of the Swan Plain are similar in their water loss behaviour in summer to those from Rovigno (Rouschal, 1938), Palestine (Oppenheimer, 1932, 1953) and Algeria (Killian, 1931, 1932).

The osmotic values of Swan Plain sclerophylls so far examined agree fairly well with Braun-Blanquet and Walter's (1931) statement that optimum figures lie between 18 and 26 atmospheres. No exceptionally high osmotic values such as Rouschal (1938) and Oppenheimer (1953) record for two or three maquis type shrubs, have so far been found. The values obtained by Wood (1934) for sclerophylls in the Mount Lofty area near Adelaide agree quite well with those obtained near Perth. As might be expected Wood obtained considerably higher values for sclerophylls of arid inland South Australia.

The rise in osmotic values of Swan Plain sclerophylls on passing from spring to summer is similar to that recorded for sclerophylls in the Mediterranean area (Rouschal (1938); Oppenheimer (1953).

Oppenheimer (1932, 1953) distinguishes four types of Mediterranean maquis vegetation, based on their water balance. Of these we may name three into which most Swan Plain sclerophylls and associated plants fit:

1.—*Deciduous plants failing to show appreciable stress throughout the summer*—In the Mediterranean area trees occur in this class, but the closest Swan Plain equivalent is the soft-leaved xerophyte, *Phyllanthus calycinus* which avoids stress by defoliating during summer.

2.—*Evergreen trees and shrubs physiologically active throughout the summer* — *Eucalyptus marginata* is the only sclerophyll so far worked on in the Swan Plain area which fits into this group. It maintains a fairly high rate of water loss.

3.—*Evergreen species restricting their physiological activity considerably thus avoiding losses of irreplaceable water, and finally reaching a state of near dormancy*—The two relatively shallow rooting genera, *Hibbertia* and *Bossiaea* fit well into this category. Both reduce their water loss drastically in late summer, have high water saturation deficits and high osmotic values. *Hibbertia* in particular passes into a condition of apparent anabiosis until the break of season rains.

It seems that the Swan Plain sclerophyll types such as *Stirlingia, Hardenbergia*, and *Eucalyptus calophylla*, which possess a shallow and a deep rooting system, which have medium water saturation deficits and medium osmotic vaues, but which do not go into dormancy during summer, must form a separate group. They appear to come within Rouschal's Group 2 (1938) in that control of water loss by stomatal closure, or by the operation of some other internal factor, occurs even when adequate moisture is available in the soil, at least to the deeper penetrating part of the root system.

The findings of von Guttenberg (1927) and of Oppenheimer (1953) that stomata of the sclerophyllous evergreens remained wide open in spring, but practically closed during the day in a dry summer, could not be duplicated for all groups of Swan Plain sclerophylls. It is true that *Hibbertia* and *Bossiaea* may close their stomata completely, but in *Stirlingia* the stomata frequently remained open during hot days at the University station, while water loss was reduced. Only under the more desiccating conditions in late summer at Cannington were the stomata of *Stirlingia* found to be closed during most of the day. This at least suggests that once conditions become too extreme closure of stomata takes place and only cuticular transpiration occurs.

The difference in rate of water loss between young flush and mature leaves of sclerophylls appears to have been observed hitherto only by Henrici (1946) in South Africa, although Rouschal (1938) did show similar differences between one year old and two year old leaves of sclerophylls at Rovigno. Henrici noted that for the introduced *Eucalyptus stuartiana* on bright days the young leaves always transpired less than the old. Owing to the fact that adequate soil moisture was present at all times on hot days during her experiments, the results do not appear to be explainable on the grounds of difference in stomatal behaviour between the young flush and mature leaves as is the case in the Swan Plain sclerophyll, *Stirlingia*.

The difficulties encountered in determining water saturation deficits in some sclerophylls have been indicated. These difficulties affected also the attempt to apply the concept of sub-lethal deficits (Oppenheimer 1932, Rouschal 1938) to indicate relative drought resistance in Swan Plain sclerophylls. Inconclusive results for mature leaves of *Banksia* and *Stirlingia* were obtained because very often the leaves either failed to absorb water or absorbed it irregularly. It was observed that even with petioles in water rapid death of such leaves often occurred. Before reaching the conclusion that *Banksia* and *Stirlingia* have a low degree of drought resistance from such results, further experiments on infiltrating such leaves under pressure need to be done. *Hardenbergia* presented no difficulties with water uptake by leaves and the sub-lethal deficit here indicated that this plant would have a high degree of drought resistance.

Acknowledgments

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3.—Atapozoa marshi, a compound Ascidian from Western Australia

By Beryl I. Brewin*

Manuscript accepted—17th May, 1955

A new sub-family Atapozoinae of the family Clavelinidae is erected to house a new compound ascidian *Atapozoa marshi*, from Western Australia. In general features the zooids resemble those of the genus *Eudistoma* Caullery, 1909, but the presence of a stalked brood pouch and of *two* median suckers in the tadpole clearly separate the genera.

Order *Aplousobranchia* Lahille, 1866
Family *Clavelinidae* Forbes and Hanley, 1848
Sub-Family *Atapozoinae*, a new sub-family

Compound ascidians. No common cloacal apertures. Zooids with atrial siphons independent and with a specialised brood pouch that arises at thoracic level.

Berrill (1950) recognises three sub-families of the Clavelinidae—Polycitorinae, Clavelininae and Holozoinae. The species described below belongs to none of the existing sub-families, being separated from the first two by the possession of a brood pouch and from the last by independent opening of the atrial siphon and the consequent absence of common cloacal apertures.

Genus *Atapozoa*, n.gen.

Colonies pedunculate or sessile. Both atrial and branchial siphons opening on the surface of the colony, no common cloacal aperture. Zooids hermaphrodite. A specialized brood pouch developing at the thoracic level. Tadpole with two median suckers.

Atapozoa marshi, n.sp. (Fig. 1)

Colonies (Fig. 1A) large, fleshy, pedunculate. Stalk tapering, up to 4.5 cm. long, 2.0 cm. wide at base, 1.0 cm. wide at junction with head. Head up to 4.0 cm. long, 2.8 cm. wide. Test light greenish brown, firm, with numerous irregularly-shaped test cells and containing also round brown "kotballen"—masses of foreign material. Zooids opening only on head region over which they are evenly and regularly distributed. Pharyngeal region salmon pink, abdominial region green (due to contents).

Zooids (Fig. 1B) up to 3.5 mm. long, 2.2 mm. wide in pharyngeal region which has 18 fine longitudinal muscle bands of 4 to 6 fibres. Rectal-oesophageal region short. Abdominal region about half the width of pharyngeal. A long vascular process with a central septum projects from abdominal region (Fig. 1E). Branchial and atrial apertures each with six short lobes.

Pharynx with 24 tentacles of three orders of size, regularly arranged. On the inner wall of the pharynx two distinct transverse folds from each of which a long lappet curves backwards at the level of the fourth stigmata from the mid-dorsal line. 3 rows of 28 to 29 stigmata, 8 to 15 times as long as wide. Parastigmatic vessels absent. Oesophagus narrow; stomach short, smooth-walled, very curved (Fig. 1G); intestine long, narrow; anal aperture smooth-edged.

Zooids hermaphrodite. In specimens collected 22nd October, 1952, testis in the form of a rosette of 8-14 pear-shaped lobes situated on right of intestinal loop just below stomach (Fig. 1B). Though the rudimentary brood pouch is present in these specimens the ovary could not be identified with certainty. Nor was it apparent in specimens collected 1st November, 1952, or 20th December, 1952. It is suspected from the number of layers on the wall of the brood pouch that the ovary is situated in the lower region of the atrial chamber, as it is in *Sydneioides tamaramae* Kesteven, and that the brood pouch develops around the ovary, but the proof of this could not be obtained (Fig. 1F).

Never more than one tadpole per brood pouch. Brood pouches become large and remain attached to zooids (Fig. 1C). Largest tadpoles (in brood pouches of colonies collected 20.xii.51) 2.4 mm. wide in head region, 6.8 mm. long (4.0 mm. being occupied by the tail). Tadpoles peculiar in the possesssion of *two* elongated suckers which lie one below the other at the extreme anterior end (Figs. 1C, 1D). Tadpoles with well developed stigmata and eye spot show no sign of stolon or buds. This species is quite unlike any hitherto described. Its resemblance to *Colella claviformis* Herdman is only superficial. I am indebted to the Australian Museum for permission to examine the type specimen of the latter. The main differences between it and *Atapozoa marshi* lie in the structure of brood pouch (which in *Colella claviformis* is merely an outbulging of the atrial wall), the number of embryos per brood pouch, and the arrangement of zooids in the colony—those of *Atapozoa marshi* being all at the one stage of sexual maturity, whereas those of *Colella claviformis* are at different stages of sexual maturity in the distal and proximal regions of the head. The stalked ascidians collected on reefs at Roebuck Bay near Broome and depicted by Savile-Kent (1897) resemble this species in form of colony but differ markedly in colour from the specimens in the present collection. Savile-Kent describes them as being a "transparent grey hue, sprinkled throughout their lower inflated areas with minute bright blue spots. These spots . . . are found to represent the separate bodies of the many hundred zooids . . .". Great colour range is known for many species of ascidians and may also occur in *Atapozoa marshi*.

Distribution.—Trigg Island, near Perth, Western Australia. Collected by Mrs. L. Marsh from the roofs of caverns under reefs.

Type specimen.—Deposited in the Australian Museum, Sydney, No. U3843.

Acknowledgment

I am greatly indebted to Mrs. L. Marsh for a very well preserved material, gathered from a comparatively inaccessible locality at different periods in the hope that a seasonal range could be studied. However, it is apparent that the questions of position of the ovary and size of the ovum can be solved only by local scientists with more or less daily access to material. The life cycle of this ascidian will form a rewarding study.

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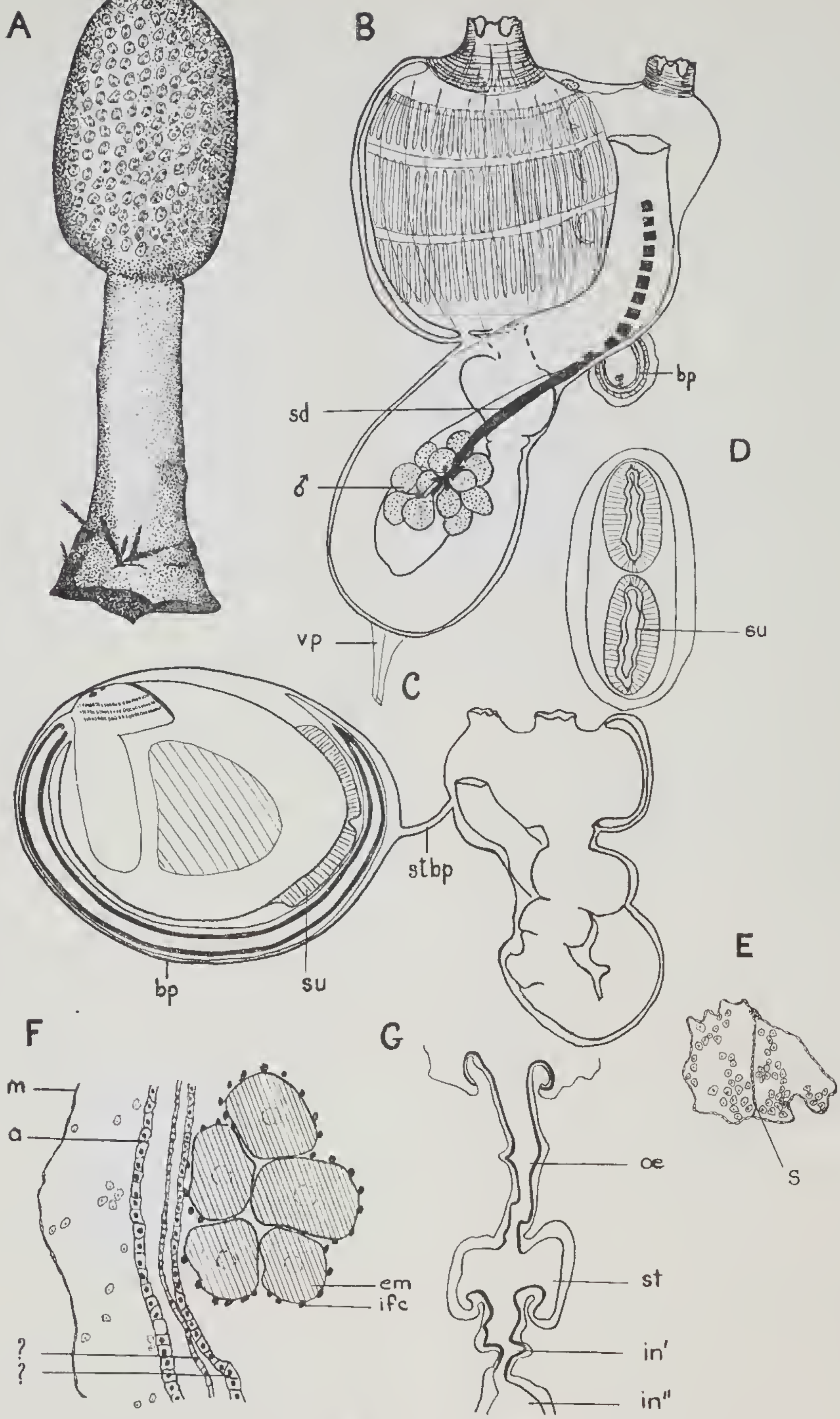

Fig. 1.—*Atapozoa marshi.* A—Colony ×1. B—Left side of zooid with small brood pouch ×20. C—Right side of zooid with large brood pouch in which is held an almost mature tadpole ×20. D—Anterior end of tadpole showing suckers ×20. E—T.S. vascular process. F—Wall of brood pouch ×380. G—L.S. stomach of zooid.

Explanation of Lettering

a—atrial lining.
bp—brood pouch.
em—cells of embryo
ifc—?inner follicle cells.
in'—first portion of intestine.
in"—second portion of intestine.
œ—œsophagus.
m—mantle wall.
s—septum.
sd—sperm duct.
st—stomach.
stbp—stalk of brood pouch.
su—sucker.
vp—vascular process.
♂—testis.

4.—Crustacea from the Cretaceous and Eocene of Western Australia

By M. F. Glaessner*

Manuscript accepted—24th August, 1954

A Cretaceous Cirripede peduncle with heavily calcified integument from the Lower Senonian of Gingin and a new species of Decapod Crustacean *(Protocallianassa australica* n.sp.) from the Eocene strata at 1505 feet in the South Perth Bore are described.

A Cirripede Peduncle from the Gingin Chalk

Some time ago a peculiar fossil from the Senonian (Santonian) chalk of McIntyre Gully, Gingin, was submitted for identification by Dr. C. Teichert (Melbourne University Geology Department Coll. No. 1993). The nature of this fossil became obvious when Withers (1951) described for the first time calcareous Cirripede peduncles which he assigned to the genus *Euscalpellum* Hoek. Though the new fossil differs from all four species described by Withers it will not be given a new name as its relations to another Cirripede whose capitular valves occur in the Gingin Chalk are not at present clearly definable.

The calcarcous stalk (plate, 2 a-d) is cylindrical, about 40mm. long, gently curved, narrowing gradually towards it upper end, with two or three slight constrictions in the upper half, and with the upper end slightly dilated to an elliptical shape 15.5 $\times$ 18 mm. The lower end, probably a fracture plane, is flat (plate, 2d). Its outline is elliptical, measuring 19.2 $\times$ 21.2 mm., with an elliptical opening (5.5 $\times$ 7.0 mm.) situated near the inner end of the shorter diameter of the basal eclipse, which is nearer the concave side of the longitudinal curvature of the stalk. The upper end is funnel-shaped with an irregular outline. The maximum width is 17mm., and a larger opening corresponds in position to the smaller one at the lower end. The walls of the stalk are thick and solid. An incomplete division into plates is faintly indicated by about 25 short radial furrows on the outer cdge of the upper surface. The outer surface of the stalk shows wavy sub-parallel growth lines. On its lower half there are a few widely scattered outlines of peduncle plates. They become more frequent on the upper half and cover almost completely this portion of the stalk where they form several imbricating rows. The plates are irregularly triangular in external view, with a wide convex base and a rounded narrow upper end. The umbo is produced below the apex into a sharp pointed spine or hook which curves outward and slightly downward, particularly at the concave side of the curvature of the peduncle. The plates are completely fused with each other and with the undivided calcareous matter of the peduncle through which they are scattered in the lower portion of the fossil.

The peduncle from the Gingin Chalk resembles *Euscalpellum zelandicum* Withers in its curvature but differs in the outline of the plates. They are elongated in the New Zealand species, with parallel sides. According to Withers they are regularly developed near the base and occur sporadically near the top. The second of these characters depends on the orientation of the specimen, but in any case the first seems to exclude the possibility of specific identity. The other species described by Withers, *E. antarcticum* Withers from the Upper Senonian of Graham Land, *E. eocenense* (Meyer) from the Eocene of the Gulf Coast of the U.S.A., *E. crassissimum* Withers from the Upper Eocene of Tierra del Fuego, differ in the shape and character of their plates, *E. antarcticum* being closest to *E. zelandicum* and the present species.

The generic identification of the peduncles described by Withers as *Euscalpellum* was based on the occurence of capitular valves belonging to *E. eocenense* together with a "strongly plated" peduncle. This species, however, differs most markedly in the shape of the number of peduncle plates from the present fossil. Scalpellid capitular plates are unknown from the other localities from which "monstrously developed" peduncles have been described. Two Cirripede species occur at Gingin, *Zeugmatolepas australis* Withers and *Scalpellum (Neoscalpellum) glauerti* Withers. The sub-genus *Neoscalpellum* is characterised by reduced calcification of valves which makes it unlikely that the heavily calcified peduncle belongs to this species. On the available evidence a relation between *Zeugmatolepas australis* and the present specimen cannot be excluded. The genus *Zeugmatolepas* possesses "three or more whorls of subtriangular lower latera with V-shaped growth lines" (Withers 1935, p. 79). The lower latera of the type species, *Z. mockleri* Withers, are "sub-triangular, with angularly rounded growth lines".

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They resemble strikingly the uppermost peduncle plates of the new specimen. In *Z. australis* the lower latera are described as "triangular, some acutely triangular and bowed outwards" (Withers 1935, p. 94). This similarity in shape between the lower latera of *Zeugmatolepas* and the peduncle plates of the new specimen does not prove specific or generic identity, particularly when the difference in size and also in shape between the peduncle plates and lower latera in the Jurassic *Z. concinna* (Morris) (Withers 1928, p. 103) is taken into consideration. Moreover, the valves in *Zeugmatolepas* are comparatively thin (Withers 1928, p. 98). Nevertheless, a taxonomic relation between these fossils which occur together is more likely than one between the "monstrously developed" stalks which differ widely in the structure of their peduncle plates. The naming of the specimen will depend on further discoveries of either similar fossil peduncles in their original connection with capitular valves or at least of loose capitular valves at one or more of the other localities at which scalpellid Cirripedes are at present represented only by "monstrous" peduncles.

A Decapod Crustacean from the South Perth Bore

In 1899 the late A. Gibb Maitland sent a number of Crustacean remains from bores in the Perth area to R. Etheridge jun. for identification. Twenty years later, Maitland (1919) referred to *"Tellina, Fusus* or *Triton,* and *Callianassa* or *Thalassina"* from depths of between 1505 and 1831 feet in the South Perth Bore.

The Palaeontological Collection of the Australian Museum in Sydney contains a Crustacean on the surface of a core taken at a depth of 1505 feet from this bore (No. F5993, "presented by A. G. Maitland 1899"). This is one of the specimens examined by Etheridge and named *"Callianassa* or *Thalassina."* As it is almost complete and identifiable and comes from a formation from which only foraminifera have been described, it is desirable to give a full account of this fossil.

The fossil is preserved as a rather shadowy, dark, flattened pellicular body, probably chitinous and almost completely uncalcified with the exception of the finger tips. The matrix is a dark grey laminated shale, slightly sandy and glauconitic, with interbedded lighter bands and with microfossils including foraminifera, sponge spicules, bryozoa and ostracodes, and organic debris, visible under the low-power microscope on some bedding planes. These planes show a clear dip of 10°. The fossil is flattened, lying on its side on a bedding plane on which few microfossils, probably ostracodes, are indistinctly visible.

Protocallianassa australica nov. sp.
Plate, 1

Description.—The abdomen and thoracopods are clearly visible but not all the legs can be identified and the carapace is not in its normal position in relation to the rest of the body. A sharp semi-elliptical ridge above the merus of the larger cheliped may represent a cast of the cervical groove and obscure remnants of the carapace seem to extend upward from this line, suggesting that the fossil is preserved in moulting position (Glaessner 1929). Neither the rostrum nor the areas on which lineae could be seen are preserved.

The abdomen is almost completely preserved in a strongly flexed position. The pleurae of segments 2 to 5 are well developed, terminating in rounded lobes. Only the pleurae of the right side are visible and it is uncertain whether the visible dorsal outline of the flattened abdomen is in its median line. The outlines of the first segment and the tail fan are not clearly preserved because of overlapping by the pereiopods.

The first pereiopods are heterochelous. The right chela is larger, with an apparently gently convex dorsal edge of the propodus which, however, could be slightly modified by its flattening. The ventral edge of which only the distal part is clearly preserved is straight and probably ridged. The proximal edge is very slightly inclined downward and forward. The immovable finger is straight and narrow and equals in length the dactylus which is wide (dorso-ventrally) at its base, with a straight ventral and a very strongly curved dorsal edge. No teeth are visible and it is probable that none were present. The carpus was much shorter and probably narrower than the propodus. Only its distal and dorsal outlines are clearly visible. The outline of the merus is irregularly lozenge-shaped. The ischium was apparently rectangular and narrow. The left chela is much smaller and its dactylus is slender but not much shorter than that of the right chela. The immovable finger is shorter than the dactylus. The carpus shows clearly a regularly curved edge extending from the proximal joint to the ventral edge of the propodus. The terminal joints of the remaining pereiopods are not visible. The last pereiopods are preserved in a dorsally flexed position as in living specimens of Callianassa.

Measurements (in mm.)

Length of abdomen (measured along dorsal curvature)	37
Larger (right) first cheliped	
Length from base to tip of dactylus	39
Length of propodus	17
Height of propodus	10
Length of dorsal edge of propodus	12
Length of dactylus	9
Length of carpus (dorsal)	5
Length of merus	8
Height of merus	5
Length of ischium	5
Smaller (left) first pereiopod	
Length of propodus	11
Heigth of propodus	5
Length of dorsal edge of propodus	6
Length of dactylus	7.5
Length of carpus (dorsal)	4.5

Comparisons.—The new species is placed in the genus *Protocallianassa* Beurlen 1930, Type species *P. archiaci* (H. Milne Edwards), which is distinguished by a linea thalassinica on the carapace together with well developed pleurae on the third to sixth abdominal segments, uropods without diaeresis, and large heterochelous first chelipeds. It was considered by Beurlen as intermediate between the Axiidae and Callianassidae but was placed in the latter family as the sole representative of a subfamily Protocallianassinae (Beurlen 1930, p. 332). Mertin (1941) described several species from the Upper Cretaceous of Europe and referred to the same genus two species from the Upper Cretaceous of North America. He noted that the Lower Cretaceous *"Callianassa" uncifera* Harbort closely resembles the Upper Cretaceous species of *Protocallianassa* to which genus the only other European Lower Cretaceous species described as *Callianassa (C. neocomiensis* Woodward and *C. urgoniensis* Lorenthey) are also likely to belong. The new species is distinguished from all these species by the outlines of the carpus and propodus of its chelipeds and also by its rounded second, third and fifth abdominal pleurae. It differs from *Callianassa bakeri* Glaessner (Eocene of Victoria) of which only the chelae are known, in their shape and ornamentation.

Mertin (1941, p. 209) has pointed out that the genus *Protocallianassa* may well extend its range into the Cainozoic. Few complete Tertiary specimens of Thalassinids are known and many of the numerous species of *Callianassa* based on chelae of widely varying shapes cannot be definitely assigned to this genus. The present specimen is the first definite record of a Thalassinid with well developed abdominal pleurae from the Eocene.

Age.—The Eocene age of the strata at 1505 feet in the South Perth Bore is proved by the occurrence of a distinctive fauna of smaller foraminifera in the core which contains *Protocallianassa australica.* Its microfauna includes:

Textularia sp.

Quinqueloculina sp.

Lenticulina sp.

Angulogerina cf. *subangularis* Parr

"*Discorbis assulatus* Cushman" (as figured by Parr)

Eponides sp.

Alabamina westraliensis (Parr)

Anomalina cf. *glabrata* Cushman

Cibicides umbonifer Parr

Cibicides spp.

Globigerina aff. *bulloides* d'Orb.

Globigerina mexicana Cushman

Globorotalia chapmani Parr

Gumbelina rugosa Parr

Ostracode fragments

Sponge spicules

Bryozoa

Fish teeth

This assemblage resembles closely the fauna described by Parr (1938) and later studied by Coleman (1950). It is at present the lowest known occurence of an Eocene fauna in the Perth Basin.

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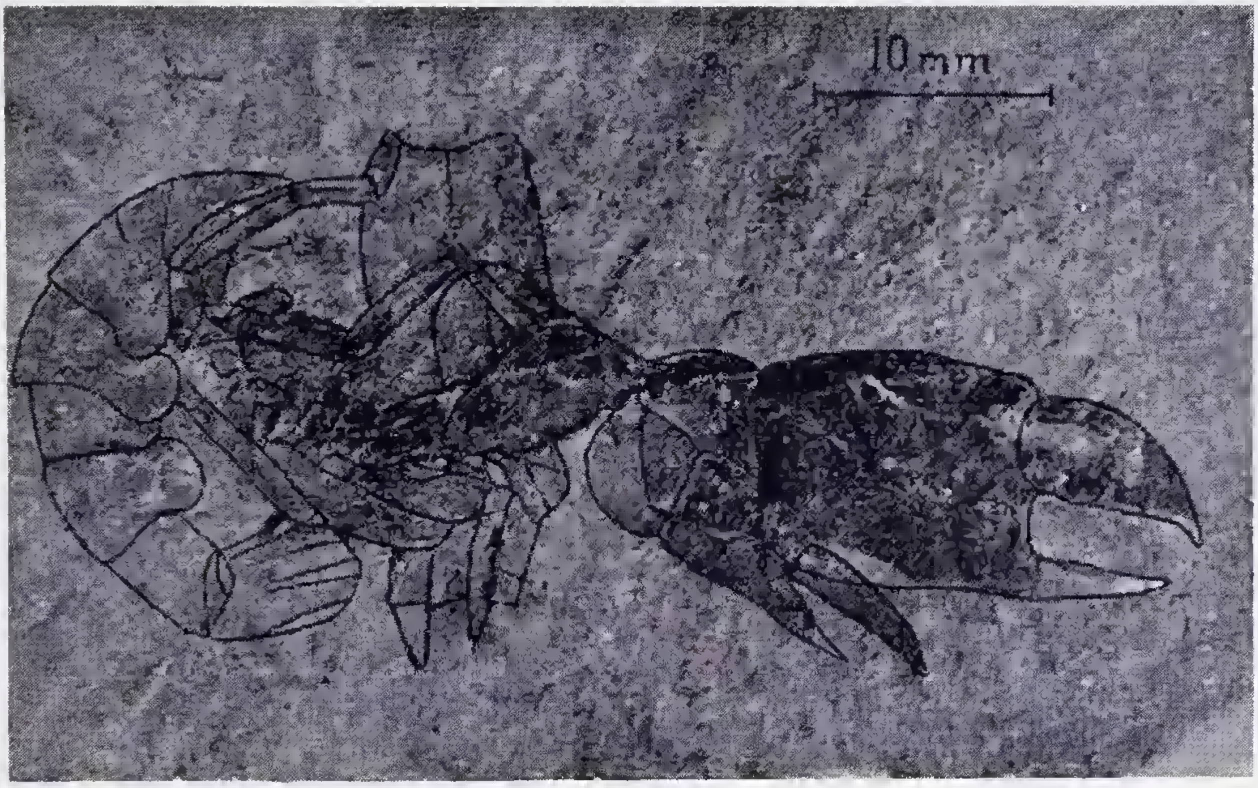

1

2a

2b

2c

2d

Explanation of Plate

1.—*Protocallianassa australica* nov. sp. Holotype. South Perth Bore, Core from 1505 ft. Australian Museum, Sydney, No. F5993.

2, a-d.—Cirripede peduncle. McIntyre Gully, Gingin, Western Australia. Lower Senonian. Melbourne University Geology Department, No. 1993. 2a-2c × 2.5, 2d nat. size.

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5.— The Reaction of Plants to Growth Regulators with particular reference to Weed Control

Presidential Address, 1955

By G. R. W. Meadly, M.Sc.*

Delivered—18th July, 1955

The discovery, functions and composition of plant hormones are reviewed, along with the morphological and physiological responses of plants to related chemicals. The use of these chemicals in agriculture, particularly for weed control, is discussed and the results of work on weed and crop reaction in Western Australia outlined.

Introduction

About a century ago Julius Sachs deduced from his experiments on plants that special substances are responsible for the formation and growth of different organs. Sixty years later Fitting (1909) made the first efforts to determine the chemical nature of plant growth stimulators after finding that water extracts of dead pollen initiated swelling of the ovaries of orchids. He made several attempts to fractionate the pollen extract but no further advance was made until Laibach (1933) showed that the active pollen substance was probably identical with one of the auxins.

Over the same period discoveries were being made in another field of plant physiology dealing with tropisms. Darwin (1880) showed that some influence is transmitted from the upper to the lower part of seedlings when they are exposed to one sided illumination. Boysen-Jensen (1913) demonstrated that this stimulus can be transmitted through a gelatin layer by cutting off the tips of *Avena* coleoptiles and pasting them on again with gelatin. Six years later Paal (1919) showed that the stimulus did not cross a layer of cocoa butter, mica or platinum foil and that a tip placed on one side of the coleoptile caused curvatures similar to those seen in phototropic experiments. He postulated the existence of a diffusible correlation carrier which is produced in the tip and moves downward. Phototropic effects were explained by an interruption in the normal flow of the substance through interference with its action due to some change in the protoplasm.

Went (1926) was the first to collect the active material when he found that it diffused into gelatin from living oat coleoptile tips. This made possible the development of a technique for the quantitative measurement of the growth substance before it had been isolated chemically. An agar block containing the active material is placed on one side of the cut coleoptile surface after removing the tip and the amount of curvature caused by the growth difference of the two sides is measured. Up to a certain concentration the curvatures are proportional to the amount of growth substance applied. This *Avena* test has a high degree of sensitivity, one twenty millionth of a milligramme of growth substance giving a curvature of about 10 degrees.

Went's test was of considerable assistance to workers endeavouring to isolate and define growth substances. In 1928 Nielsen found that two pathogenic fungi produced in the nutrient medium, substances which were strongly active to the *Avena* test and shortly afterwards auxin production was associated with other fungi and bacteria. Attempts to isolate these substances were deferred when the *Avena* coleoptile was found to react strongly to urine. By 1934 three active substances had been isolated—auxin-a, auxin-b and 3-indolylacetic acid. The latter acid was subsequently isolated from yeast and *Rhizopus* and for some time was considered to be restricted to lower organisms. Evidence to the contrary, however, continued to increase and it was finally isolated from wheat and maize by several workers.

Use of Growth Regulators

Following the synthesis of growth regulating substances, applied experimental work was undertaken in a number of directions and plants were found to react in a variety of ways. One of the first practical uses was associated with vegetative propagation. With many plants that are difficult to strike, root development may be hastened and increased by treating the cuttings with growth regulating substances. These

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chemicals are being used by nurserymen without a great deal being known concerning their physiological action.

The theory that a natural root inducing factor moves from the leaves to the base of the cutting causing root initiation has been favoured for some time. When, for some reason this factor does not operate it is possible for it to be replaced by a synthetic growth regulator. Among the better known root inducing substances are indolylbutyric acid, naphthylacetic acid and naphthylacetamide.

Treatment of flowers such as those of the tomato, has under certain conditions, prolonged development resulting in larger fruits which may be seedless. With beans, maturation has been hastened and at the same time the size increased. The rate of ripening of formed fruits can also be hastened and it is not necessary for them to remain attached to the trees. Apples, pears, peaches and bananas have been stimulated by very small quantities —a few parts per million—of naphthylacetic acid and related chemicals.

An accepted practice to improve the fruit set of the Zante currant is to cincture or girdle the main stem of the vine, removing a narrow strip of the inner bark. It is thought that this restricts the downward movement of soluble food materials and results in a concentration above the cincture. The currant fruit is normally seedless and apparently this stimulus is needed to induce satisfactory fruit set and fruit size. With cincturing of weaker vines a marked deterioration of vigour may occur and an alternative method of improving fruit set has been sought. Work undertaken by L. T. Jones (1953) in the Swan Valley has shown that satisfactory setting has followed spraying with a solution containing 20 to 40 parts per million of *p*-chlorophenoxyacetic acid. 2, 4-dichlorophenoxyacetic acid was somewhat less effective and, at times, caused damage to the bunches.

Abscission of flowers has been both retarded and accelerated by the same growth regulator. The reaction of greenhouse tomatoes, however, has been sufficiently uniform for them to be treated commercially to prevent flowers from falling and these substances have also been used to replace pollination. Careful control of the treatment is essential as relatively small quantities are lethal to tomatoes.

Spraying to bring about thinning when excessive flowering of fruit trees occurs, takes advantage of the conditions when floral abscission is increased. The same variation occurs with leaves and fruits but detailed investigations have allowed growth regulators to be used in some cases for retarding fruit drop, a practical application that can be very useful in orchards. The stage of fruit development at the time of application is important.

Although the properties of growth regulating substances already mentioned are important, their herbicidal effects are of outstanding significance. The major portion of the address will be devoted to this aspect.

Herbicides

Chemistry

It is now generally recognised that indolylacetic acid is one of the important hormones found in plants and as it can also be synthesized in the laboratory, it has been an important starting point for the preparation of substances likely to have herbicidal properties.

Studies began at the Jealotts Hill Research Station, England, in 1936, the earliest work dealing with stimulation of the rooting of cuttings. It was soon extended to include the effects of 3-indolylacetic acid and 1-naphthylacetic acid at different concentrations upon seed germination, seedling development and the growth of established plants of many species. The results of these experiments showed that the higher concentrations of growth substances actually depressed growth. These observations together with a knowledge of the variation in root formation and deformation effects produced with different species led to the assumption that these growth substances in higher concentrations would have selective phytocidal action.

Slade, Templeman and Sexton (1945) found in 1940 that applications of 25lbs. naphthylacetic acid per acre to oats weedy with charlock (*Brassica sinapis*) killed the charlock. The oats received only a slight check and recovered fully. 84% of the charlock failed to germinate and seedlings that emerged soon died. Other experiments indicated that wheat, barley and rye behaved similarly to oats while large plantain (*Plantago major*) and yarrow or milfoil (*Achillea millefolium*) resembled charlock in their responses.

These results confirmed the selective phytocidal properties of certain growth substances and initiated the search for cheaper and more active chemicals than naphthylacetic acid. Within two years of this work investigators in both England and America had recognised the strong growth regulatory and herbicidal effects of chlorinated phenoxyacetic acids.

Even during the early investigations a considerable number of chemicals were screened. In America the derivatives of 2, 4-dichlorophenoxyacetic acid (2, 4-D) were favoured while in England, where exploratory work commenced several years earlier, the compound selected for development was 2-methyl-4-chlorophenoxyacetic acid (M.C.P.A.). This was due in part at least to the greater availability in England of chloro-cresol as opposed to chloro-phenol. Of the many other related chemicals that have been tried 2,4,5-trichlorophenoxyacetic acid (2,4,5-T) has proved of greatest practical value forming the basis of preparations for treating woody plants.

It is interesting to note the similarity in the structural formula of indolylacetic acid and the synthetic hormone-like substances such as the chlorinated phenoxyacetic acids. The main difference in structure is that the $-CH_2COOH$ group of indolylacetic acid is attached to the benzene ring through a pyrrole ring while with the chlorinated phenoxyacetic acids this group is attached through an oxygen atom.

2,4-D acid is only slightly soluble in water and for herbicidal purposes its derivatives are the important chemicals. The most widely used are the sodium and triethanolamine salts and the esters. The sodium salt is moderately soluble in water but "hard water" having a high calcium or magnesium content may cause a precipitate that will clog the filters and spraying nozzles. The amine salts are soluble in all proportions in water and are therefore well adapted to the low volume spraying equipment, even when high rates of chemical are required. The ester compounds are only slightly soluble in water but may be dissolved in some petroleum oils. By the use of suitable emulsifiers the minute oil droplets containing the ester can be kept in suspension in a suitable form for spraying purposes. The esters are synthesized by the reaction between 2,4-D acid and an alcohol. As a large range of alcohols is available it is potentially possible to have a large range of 2,4-D esters, although naturally the cheaper and more readily available alcohols are mainly used, e.g., methyl, ethyl, isopropyl and butyl. The length and structure of the alcohol portion of the 2,4-D ester molecule affects its vapour pressure and in consequence, the volatility. In general, the longer the carbon chain in the part of the molecule contributed by the alcohol the lower the volatility. Where low volatility is important, high molecular weight alcohols have been used but they are more expensive. M.C.P.A. has been used mainly as the sodium salt and has similar properties to 2,4-D. With 2,4,5-T, the ester is the main formulation, in some cases high molecular weight alcohols being used to reduce volatility.

As the components of proprietary lines of herbicides have different molecular weights and are also prepared in different concentrations it is essential to be able to compare the active chemical content of preparations and to have a uniform method of expressing rates of application. The term acid equivalent is used and refers to that part of a 2,4-D formulation that theoretically could be converted to the acid. The acid equivalent may be stated as a percentage by weight or the weight of 2,4-D acid in a given volume.

2,4-D may be classed as a non-toxic substance. Cows and sheep were not affected by feeding on pasture sprayed with 2,4-D and no harmful results followed daily doses of 5.5 grams to a cow for 106 days. The 2,4-D was not excreted in the milk, nor was it found in the blood serum of a calf given milk from the test cow. There is some evidence that the growth of aerobic micro-organisms may be inhibited while some groups of anaerobic organisms may be stimulated. At the usual rates of application 2,4-D does not generally reduce the total number in the soil.

Morphological Effects

The effect on plants depends primarily on the quantity applied and absorbed but is also influenced by a number of other factors including the growth stage of the plant, the rate of growth at the time of spraying and climatic conditions, particularly temperature. As already mentioned, at controlled rates, the growth regulating properties are apparent at much lower concentrations than the toxic effects. The first reaction is often a twisting or bending of the stems and leaves resulting from differential growth rates in petioles and elongating regions of the stem. Leaves may become thickened and an increase in turgor often results in a propping appearance. Colour changes similar to autumn leaves may occur. Stems also become thickened and often split. The extreme response is a cessation of growth followed by a characteristic browning of the foliage and stems associated with the dying of the tissue.

With sublethal doses the reaction of the plant takes a number of forms. Besides the twisting of the stems already mentioned, leaves produced after the application may assume unusual shapes. Entire leaves become deeply divided and those normally having broad lobes may be reduced to narrow segments. Proliferation of floral parts is not uncommon and fasciations are also caused as well as adventitious roots. Parthenocarpy may be induced resulting in seedless fruits. In the case of cereals, irregular spikelets and empty florets occur. These responses can be attributed to the interference of hormonal action in the young structures by the synthetic growth regulating substances. 2,4-D appears to concentrate in the young embryonic or meristematic tissues that are in a rapid state of metabolic activity, affecting them more than mature or relatively inactive young tissues.

Physiological Effects

Although the physiology underlying the effects of synthetic growth substances on plants is far from being fully understood and applied studies have been given more attention than fundamental research, part of the story can be told. The severe and diversified effects indicate that they exert an influence on some general and basic metabolic process. As pointed out by Bonner and Bandurski (1952), according to this view, the observed response, whether growth by elongation, production of roots, suppression of lateral buds or of flowering, increase in rate of protoplasmic streaming or production of changes in chemical composition, would be the visible manifestation of the effects on this common basic process. A ready and simple explanation would be an essential relationship between enzymes and growth regulating substances. It has been shown that the action of numerous enzymes are influenced by these substances, some being increased and others inhibited, but information available gives only partial support to this theory.

A number of effects on chemical composition and physiological processes have been recorded. Respiration may be stimulated or retarded, the reaction apparently depending on the concentration in relation to the susceptibility of the plant. Kelly *et al.* (1949) showed that the rate of respiration in pea seedlings was increased by concentrations within the range of 0.001 to more than 100 parts per million of 2,4-D while 1,000 parts per million reduced the rate by 40 per cent. On the other hand a 20 per cent. stimulation with oat seedlings required at least

1,000 times as much 2,4-D as for the same stimulation in pea seedlings. Even when lethal doses are applied an initial increase in respiration may occur followed by a reduction as the plant approaches death. The influence on the respiration rate is considered by some workers to be linked with the effect of 2,4-D on water uptake.

By some means not fully understood 2,4-D upsets the balance between synthesis and use of plant food, particularly carbohydrates. After application in herbicidal quantities there is a slight decrease in the rate of photosynthesis associated with a steady loss in total dry weight due mainly to a decline in the weight of starch and starch-like substances. Usually there is an initial increase in the sugars followed by a rapid and steady decline. There is still some doubt whether the depletion of sugars is sufficient to cause death of the plant.

Both increases and decreases in the protein content of wheat grain have been recorded with increases predominating. When higher percentages have been recorded some doubt has existed whether there was increased synthesis of the proteins or whether a decrease in total seed weight accounted for the proportional increase. There are indications of a lowering of the nitrogen and potassium absorption and treatment with 2,4-D has also reduced the upward movement of radioactive phosphorus to the leaves and modified the distribution and accumulation pattern of this radical.

It has been proposed by van Overbeek (1947) that 2,4-D, like natural auxin, might affect oxidative assimilation in the cell but unlike auxins might escape inactivation by oxidases that normally regulate metabolism. The resultant increase in the catabolic processes in the cells while the anabolic system was blocked would cause rapid injury to the plant. Johnson and Fults (1952) have shown that once it has entered cells, 2,4-D stimulates the production of scopoletin, a coumarin-like compound that is highly toxic.

Although the actual cause of plant mortality following the application of growth regulating substances has not been defined with certainty there is no doubt that they disorganise a number of metabolic processes.

Absorption and Transloeation

It is already apparent that growth regulating substances applied to plants produce effects at some distance from the point of application. This involves both absorption and translocation. Hormones may be transported in plants by three different mechanisms. Following absorption by the roots they move in the xylem transpiration stream to the leaves. In the process they may be absorbed selectively and accumulated in adjacent active tissue such as xylem, parenchyma and cambium. Hormone molecules in leaves move with carbohydrates into the phloem where they are carried in the assimilation stream to regions where foods are being used or stored. In living parenchyma hormones may move from cell to cell by a polar mechanism.

Researches undertaken by many independent workers indicate a decided similarity between the movement of plant hormones and 2,4-D substances. It is generally accepted that chemicals in aqueous solution do not enter the leaf through the stomata but diffuse through the cuticle. Crafts (1948) suggested that, for ready entry through the cuticle, herbicides should be in a non-polar form. This would explain why the non-polar esters of 2,4-D pass through a waxy cuticle more rapidly than the polar salts.

Having penetrated the cuticle the 2,4-D molecules pass from a lipoidal medium into the aqueous medium of the mesophyll cells where somewhat polar properties are required to facilitate translocation. Experiments undertaken by Crafts (1952) have shown that 2,4-D ions of the sodium salt enter leaves slowly; aliphatic esters enter rapidly but do not part from the cuticle and translocate well; and 2,4-D acid and heavy ester molecules pass through cutiele, mesophyll and phloem with relative ease. Having reached the phloem without causing immediate damage to the intervening tissue they are translocated with synthesized food materials to regions where it is being used. The affects of the 2,4-D are therefore likely to be felt at the most vital points and deep penetration of perennial rooting systems is often possible.

Translocation can be quite rapid. Although one to two hours may be required for the chemical to penetrate the cuticle and move across the mesophyll, Day (1950) has shown that in the phloem it may move at rates from 20 to 160 cm. per hour. The rate of movement is not related to concentration of 2,4-D but is influenced by the rate of food movements. High concentrations can impede or arrest translocation by acting as contact herbicides and killing the conducting tissue.

Differential Action

For the agriculturist the most important characteristic of synthetic growth regulators is their selective action on plants. Although in general, grasses are resistant and broad leaved dicotyledons are susceptible there are many exceptions involving variation in tolerance of different species and even different varieties. Undoubtedly a number of factors contribute to the variation in reaction.

A waxy cuticle, particularly when associated with close parallel venation as with cereals, causes many spray droplets to bounce and run off. On the other hand broad leaved plants have leaf surfaces that are more readily wet by sprays which may spread as a thin film or retain contact over a large proportion of the surface in the form of fine droplets. The upright habit of grasses, especially cereals, also causes more run off than leaves that are disposed in a more or less horizontal position. Again, in the case of grasses the growing points are located in the crown of the plant, at or below soil level and are therefore protected by foliage. With broad leaved weeds the growing points at the tips of the shoots and in the leaf axils are usually exposed.

Selective action may also be influenced by factors affecting absorption and translocation. Reference has been made to the fact that these processes are affected by the relative polarity of the chemical and the tissue. Absorption of polar substances through the roots is uninhibited but there may be some selectivity due to restriction of entry through heavily cutinised cuticles. Variation in translocation which is closely linked with the plant species and stage of growth can also result in differential reaction.

Although morphological characteristics contribute, the main causes of differential action are associated with physiological differences. The story is only partially understood, however, and factors such as differences in enzyme systems, response to pH changes, chemical constitution of the plant and cell metabolism, may be involved. These factors are affected by the age of the plant and also by environmental conditions, such as temperature and available moisture. When physiological processes are slowed down by such factors, reaction to 2,4-D is usually less apparent. There is some systematic correlation between synthetic hormones and plants, e.g., members of the Cruciferae are, in the main, susceptible, while the Polygonaceae which includes many broad leaved types such as docks (*Rumex* spp.) and doublegee (*Emex australis*) are relatively resistant. The correlation does not extend very far, however, as responses have varied with different species and even different varieties of the one species.

Agricultural Application

Although employed primarily as selective herbicides, 2,4-D and related compounds can be used as contact sprays for killing annual and checking perennial weeds, as translocated sprays, particularly for perennials and as temporary soil sterilants. Our main interest, however, is in the selective control of annual weeds in cereal crops. It is proposed to deal with the various factors involved in relation to development and research in Western Australia.

Two of the most widespread and troublesome weeds in this State are wild turnip (*Brassica tournefortii*) and wild radish (*Raphanus raphanistrum*). As these are both annual species of the Cruciferae and are closely related to *Brassica sinapis* with which some of the original experiments were undertaken at Jeallots Hill, trials with them were commenced as soon as the chemicals became available. Much of the subsequent work has been done with these two plants along with doublegee (*Emex australis*).

Type and Quantity of Chemical

The first commercial lines were the sodium salts of M.C.P.A. and 2,4-D. These were soon followed by the triethanolamine salt and various esters of 2,4-D and latterly corresponding compounds of M.C.P.A. have also been formulated. The earlier overseas reports frequently referred to application rates exceeding one pound of acid equivalent per acre. With high average yields of forty bushels or more per acre the cost of such treatments could be absorbed but such rates were difficult to reconcile with the relatively low cereal yields in this State. Meadly (1951) recorded effective control of young wild turnip plants in a cereal crop at Wongan Hills with both two and four ounces acid equivalent per acre, the species being particularly susceptible. Treatment increased the yield of a heavily infested crop on light land from 8.5 bushels to 13.2 bushels per acre. Corresponding yields at Dalwallinu were 5.7 and 11.6 bushels respectively. Other formulations have since been proved effective and four ounces acid equivalent per acre is used for most spraying of wild turnip although, when conditions are favourable, somewhat lower rates have been equally satisfactory.

The story with wild radish has been somewhat different. With the initial trials, using the sodium salts, four ounces acid equivalent per acre checked the plants but a proportion recovered and set seed. Much more satisfactory control was obtained at the eight ounce per acre rate. In the years immediately following, wild radish spraying was undertaken with the amine and sodium salt of 2,4-D and the sodium salt of M.C.P.A. mostly at four ounces of acid equivalent per acre but sometimes at six. During this period a number of indifferent results caused concern among farmers. The reason for some, but by no means all of these could be traced and further detailed investigations were undertaken (Meadly 1954). Chemicals used were the sodium salt of M.C.P.A. and the amine, ethyl ester and butoxyethanol ester of 2,4-D. All were applied at both four and six ounces of acid equivalent in five gallons of water per acre. The four ounces of M.C.P.A. and 2,4-D amine affected a proportion of the wild radish plants but did not give a satisfactory degree of control. The six ounce rate of both gave practical control although some plants recovered and set seed. There was no difference between the two types of ester but the results with four ounces of acid equivalent per acre were somewhat better than those with six ounces of amine and M.C.P.A. The six ounce rate of both esters gave complete control of wild radish. Based on this work the ester is now being used largely by farmers for this weed with increased uniformity of results. It is not usually recommended, however, when the cereal is undersown with a legume and this aspect of crop tolerance will be discussed later.

The habit of doublegee and the fact that it is an annual gave reason to believe that it would be susceptible to moderate rates of application of 2,4-D. This plant has belied its appearance, however, and much research over a period of years has failed to provide a really effective treatment. Meadly and Pearce (1954, 1955) record trials with various formulations of 2,4-D at a wide range of acid equivalent levels. Results were variable and no treatment could be relied upon to give a high degree of control. With heavily infested crops six ounces acid equivalent of 2,4-D ester per acre has suppressed the growth of young doublegees sufficiently to warrant its application but has not prevented seed formation. A second treatment two weeks after the first, even with the lower rates, gave a total kill of doublegees in one trial at Geraldton in 1954, but the same double treatment at Beverley was not effective.

Volume of Application

When hormone-like chemicals were first applied for weed control the volumes used for other herbicides were followed and one hundred gallons or more of solution were applied per acre. Such volumes, although inconvenient, are acceptable for highly productive crops but would present a problem under the conditions applying in this State where large areas require treatment and suitable water is not always readily available. It is simple mathematics to compute that 500 acres, by no means an excessive area for one property, would require 50,000 gallons of water if sprayed at the rate of 100 gallons per acre. This quantity must not only be supplied but transported to the site of operations.

The agriculturist and engineer soon joined forces and overcame this major difficulty by constructing nozzles which, when fitted to booms were capable of an even and effective application with as little as four or five gallons per acre. Later developments include nozzles having spinning discs and rotating brushes and also various types of atomisers. Most of the cereal crop spraying in Western Australia is now being undertaken with six to eight gallons per acre, using booms of 30 feet or more in length and travelling at about four miles per hour. An average coverage is 15 acres per hour.

A more recent development is the application of 2, 4-D by means of aircraft. With Tiger Moths, the main type in use in this State, the tank capacity is approximately 30 gallons and therefore the rate used with low-volume booms is scarcely practicable, as it would entail landing and refilling after four or five acres of spraying. A specially designed nozzle, however, has made possible a satisfactory application of two gallons per acre enabling 15 acres to be treated with each flight. Much work has been involved in calibrating aircraft, including determining the effective spraying swathe and ensuring an even dispersal of an adequate number of spray droplets.

Droplet Size

When considering droplet size two important factors are involved. The spray must be in such a form that it actually reaches the plant under average conditions of wind, temperature and humidity and upon making contact permits absorption of the chemical by the plant. Fisher *et al.* (1952) reported that coarse droplets estimated to be 450-500 microns gave somewhat higher kills of mesquite *(Prosopis juliflora)* than either fine or medium-coarse droplets, both of which gave comparable results. Other workers, however, including Mullison (1953) consider that the herbicidal effect is controlled by the amount of 2,4-D applied rather than the number or size of the droplets. All are agreed that the droplet size must be such that it does not evaporate or be dispersed by wind between boom and weed.

The amount of potential drift depends on wind velocity and droplet size. A still atmosphere is the ideal but in practice it is necessary to operate with a low velocity wind. With ground machines the effect can be minimised by having the boom as near the target as possible. In order to obtain complete coverage, however, the distance is seldom less than one foot and with some nozzles may be two feet. With aircraft operating in Western Australia the boom is usually six to ten feet above the crop. Maximum wind velocities suggested are 12 miles per hour for ground machines and seven to eight miles per hour for aircraft.

An interesting chart published by Edwards and Ripper (1953) shows the relation between droplet size and distance of drift under different conditions. Droplets having a mass medium diameter of 50 microns while settling 10 feet will drift 500 feet in a 10 m.p.h. breeze, and 200 feet in a 3 m.p.h. breeze. The corresponding figures for droplets having a m.m.d. of 400 microns were 30 feet and less than 10 feet. The need for a large droplet size with aircraft application is obvious but the m.m.d. is limited by the economic application rate and the likelihood of missing some of the weeds if the figure is too high. With aerial spraying the tendency is to produce coarse droplets with m.m.d. about 300-450 microns while with low volume ground units the figure usually varies from 90-120 microns.

Growth Stage of Plant

Plants, in general, are most vulnerable to hormone-like substances when at the seedling stage. Later, reaction may be closely correlated with the rate of growth. Plants checked by adverse conditions such as low temperatures and lack of moisture tend to be more resistant and difficult to kill. This would appear to be due to the greater susceptibility of active meristematic tissue.

The greatest benefit to cereal yields can also be expected from early removal of weed competition. It is necessary to ensure, however, that a more or less complete emergence of the target weed has occurred before spraying and also that the crop is at a tolerant growth stage.

Weather Conditions

As already discussed, strong winds are very undesirable as they accentuate spray drift, particularly with aircraft application. An additional hazard to nearby susceptible crops is presented by nozzle drooling when ferrying or turning near them. This has been reduced by the use of individual cutouts on each boom nozzle, at times supplemented by suction by means of a Venturi device when the main valve is closed. In America the use of volatile esters is not favoured because of the risk of damaging susceptible crops, particularly cotton. In Western Australia, however, cases of injury to crops such as tomatoes and lupins have occurred with the relatively low-volatile preparations and have been due to drift during operations rather than subsequent volatilisation and movement. In America, with aircraft spraying, some particles have been carried by air currents for distances up to four miles while in this State lupins more than one mile away from spraying operations have been damaged severely.

The most adverse combination for aerial spraying is a high wind velocity and temperature associated with low humidity. Besides the drift factor, significant evaporation of droplets can take place during passage from the boom to the herbage. On the other hand higher temperatures favour growth and tend to make the weeds more susceptible to the chemical.

During the winter, mild conditions are more likely to favour than detract from results. Although fine weather is recommended, rain a few hours after treatment, particularly when using 2,4-D ester, is unlikely to affect results.

Tolerance of Crops

Although the selective action of the synthetic hormone-like substances is one of their outstanding characteristics, reference has already been made to the high susceptibility of certain crops and there is by no means complete tolerance in the case of many sprayed extensively for weed control. In this State we are concerned mainly with cereals and a considerable amount of research has been undertaken, to define a safe level of treatment. Although there is some variation in the results reported it is possible to make conclusions of practical value.

Cereals are likely to be affected if sprayed at the seedling stage but develop resistance when tillering or stooling has progressed. Treatment during this early danger period can result in a number of malformations and growth disturbances. Wheat may develop club shaped, twisted and branched ears with an irregular arrangement of spikelets. The glumes may become fused, the number of spikelets in each group reduced and a proportion of the florets aborted. Symptoms also include thickened culms, chlorosis, reduction in height and delayed maturity.

Susceptibility again increases at the "boot" stage when the head is enclosed in the leaf sheath. Risk of damage continues during pollination but decreases at the "milk" and soft dough stages. Late spraying does not usually cause abnormalities but reduced grain setting has been attributed to it. Workers are in general agreement that wheat is least and oats most susceptible with barley occupying an intermediate position. There is also variation in reaction to formulations. The ester of 2,4-D is likely to be most severe, with the sodium salt of M.C.P.A. least harmful.

During 1954, at the Merredin Research Station three wheat varieties—Bungulla, Bencubbin and Wongoondy—were sprayed at the pretillering, early tillering and "boot" stages with eight ounces acid equivalent per acre of 2,4-D amine, 2,4-D ester and sodium M.C.P.A. Yields of grain showed no significant difference due to variety or growth stage although there were indications of reduced yields with the pretillering and "boot" stage treatments. This tendency was more noticeable following the later spraying. With research in other countries cereal damage is usually associated with application rates of one pound or more of acid equivalent per acre. Eight ounces were used in the Merredin trial as higher rates are seldom applied for weed control in cereal crops in Western Australia. There is little doubt that external factors including climatic and soil conditions, by virtue of their influence on the growth processes of cereals can influence results. Some abnormalities have followed field spraying at four ounces acid equivalent per acre of 2,4-D amine but only a small proportion of the plants have been affected.

In a country so dependent on subterranean clover (*Trifolium subterraneum*) as a legume it is important that information should be available concerning its reaction to the various formulations, especially when first sown along with a cereal. Although a considerable amount of work on clover tolerance has been published little of it has dealt specifically with subterranean clover and the results show a decided difference in reaction between species. Again most of the investigations have been undertaken with pastures where clovers tend to be more resistant than when growing in association with a cereal crop.

Some exploratory work undertaken in 1952 on a pasture dominated by the Dwalganup strain of subterranean clover indicated that this species, except at the small seedling stage, is not readily killed by application of 2,4-D, many plants persisting at the 2 lb. per acre acid equivalent rate of M.C.P.A. and $1\frac{1}{2}$ lb. per acre acid equivalent rate of 2,4-D amine. It was apparent, however, that even some of the lighter treatments retarded the date of flowering. This could be vital in districts having a short growing season as it would be equivalent to converting Dwalganup into a later strain from a maturity viewpoint and might prevent effective seed setting. Any reaction of this nature would be of greatest significance in the case of spraying to control weeds in the year of clover establishment. Few, if any, dormant seeds would be present in the soil and regeneration of the clover could only be obtained from seed formed in the season of sowing. As subterranean clover is frequently established along with a cereal crop which would normally be sprayed for weed control the reaction of the clover to chemicals under such conditions is most important.

An experiment was designed to ascertain the effects on seed setting of different formulations applied at various rates to Dwalganup subterranean clover sown along with a crop. It was intended to carry out the experiment at a number of different centres but conditions during 1954 restricted the work to one property in the Toodyay district on land being cropped for the first time. The clover was sown at 8 pounds per acre with a light cover crop of wheat.

The sodium salt of M.C.P.A. and the amine salt and ethyl ester of 2,4-D were applied to the various plots as shown in the table. The required amount of chemical was dissolved in water and applied at 5 gallons per acre through a low-volume boom. At the time of spraying the crop was approximately 9 inches tall and stooling freely while the clover was at the 3 to 4 leaf stage. In order to estimate the effects of the treatment 12 plant counts of one square link were made on each plot. The position of each count was marked and at the end of the season the seed was removed from the individual areas. In this way the seed set by over 2,500 plants was recorded.

Table Showing Seed Formation.

Treatment	Ozs. acid equivalent per acre	No. of seeds set per plant
M.C.P.A. (sodium salt)	4	6.6
,, ...	8	8.5
,, ...	12	7.0
,, ...	16	7.4
,, ...	24	3.2
,, ...	32	4.9
2,4-D/amine (triethanolamine) ..	4	5.7
,, ...	8	4.3
,, ...	12	2.1
,, ...	16	1.0
,, ...	24	0.8
,, ...	32	0.6
2,4-D/ester (ethyl)	4	3.1
,, ...	8	3.0
,, ...	12	1.4
,, ...	16	0.9
,, ...	24	1.1
,, ...	32	1.0
Control	—	8.7

Significant difference between treatments ($P=0.05$) = 3.35.

The results are summarised in the table and illustrated by the graph. With M.C.P.A. the yield of seed per plant was significantly depressed for all treatments above the 16oz. level. In the case of 2,4-D amine the depression occurred with all treatments above the 4oz. level, while with 2,4-D ester all treatments caused a significant reduction in seed yield.

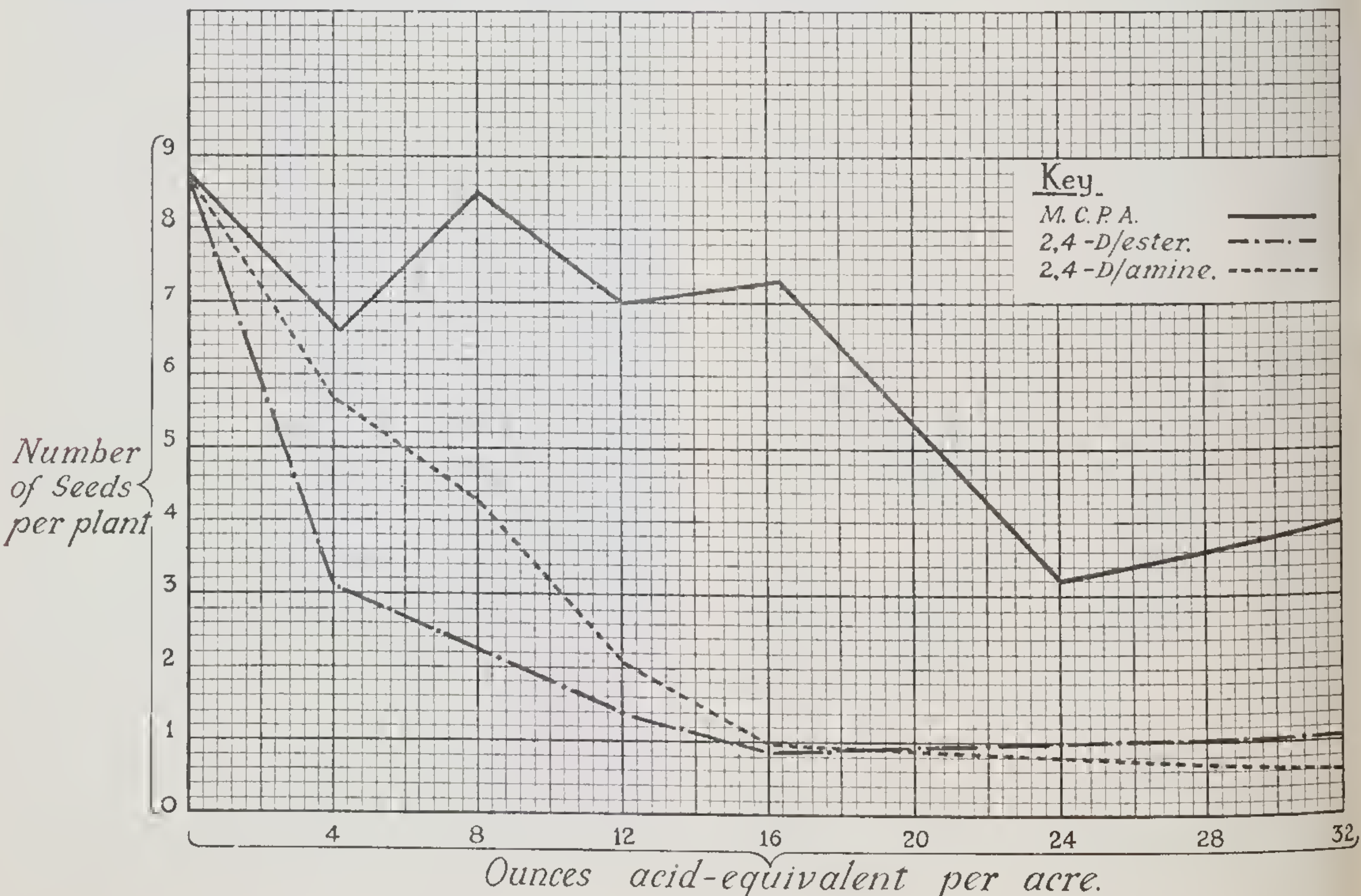
The results have considerable practical value and have made possible tentative recommendations regarding the spraying of cereal crops with undersown clovers (Meadly and Pearce 1955). Further similar trials during 1955 at four different centres should complete the information required and allow details regarding formulations and quantities to be defined.

Other Weeds

The growth regulators have proved very useful for the destruction of other weeds besides those controlled selectively in cereal crops. Cape tulip (*Homeria breyniana* and *H. miniata*) reacts to relatively high rates of application, corm and cormil development being arrested. The most effective formulation, optimum economic dosage and most vulnerable growth stage have been defined by Meadly (1954). The ester of 2,4-D has given best results and the most favourable time for spraying is somewhat later for *H. breyniana* than for *H. miniata*. A number of other troublesome herbaceous weeds are also susceptible.

Among woody plants blackberry (*Rubus fruticosus*) has been treated successfully with the ester of 2,4,5-T. No advantage has been gained by using a mixture with 2,4-D ester. Time of application is significant, treatment at the flowering and fruiting stage in mid-summer being most effective. This is assumed to correspond with active downward movement of food materials in the phloem facilitating translocation and deep penetration by the 2,4,5-T. Although foliage spraying of mesquite (*Prosopis juliflora*), including aerial applications, have not proved effective good results have followed treatment of the basal portion of the stump with a 1% acid equivalent solution of 2,4,5-T in distillate.

Some work has also been undertaken with York Road Poison (*Gastrolobium calycinum*) and regrowth of various *Eucalyptus* species. Results have been very variable and relatively high rates of application are necessary. This method of treatment is not economical for large, dense areas but may prove advantageous under



some conditions such as with poison plants growing in rocky situations where it is difficult to undertake other control measures. In some cases 2,4,5-T has proved more effective and no more costly than bashing for controlling *Eucalyptus* suckers. With *Gastrolobium* species best results have followed the application of 3-4 lb. acid equivalent in 150 gallons of water per acre of vegetation when the plants are flowering in the Spring. With eucalypts autumn treatment has proved more effective.

Conclusion

During the relatively short period that synthetic growth regulating chemicals have been available rapid and spectacular advances have been made. Extensive research has been undertaken in many countries with a natural tendency for the concentration to be on applied rather than fundamental aspects. The need for more basic physiological information is now being felt and this field is receiving more attention.

The use of these chemicals for weed control alone has resulted in enormous savings to the agricultural industry. Figures for Western Australia, although not on the same scale as those for Canada and the United States, underline this statement. In a period of three years the area sprayed for the control of weeds in cereals increased from experimental proportions to an estimated total of 400,000 acres in one season. Based on a conservative estimate of increase in yield due to treatment, the additional annual production approaches one million bushels. Experience in this State gives support to the statement of an eminent scientist that the discovery of the herbicidal properties of growth regulating substances is the greatest scientific contribution to agriculture since superphosphate fertilizer.

It is likely that further researches by the chemist and agriculturist will result in improved formulations that will increase the effectiveness of present work and extend the range of species that can be controlled chemically.

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6.—Plant Ecology of the Coastal Islands near Fremantle, W.A.

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The plant communities of the major coastal islands near Fremantle, W.A., have been described in relation to the soils, climate and geomorphology and a comparison drawn between the island vegetation and that of the adjacent mainland.

The vegetation, which is structurally a *Scrub Formation*, is composed of three well defined sub-formations, viz., tall scrub, scrub and low scrub and several other sub-climax communities of doubtful status.

The island vegetation is of special interest, not only for its density of cover and high frequency of dominants, but also for the paucity of plants of the Myrtaceae, Papilionaceae and Epacridaceae and the complete absence of members of the family Proteaceae.

It has been shown that within one locality the distribution of species is dependent on habitat and for comparable habitats on the islands and the mainland the composition of vegetation is substantially the same. The overall distribution of species is explained by a late Pleistocene land bridge between the islands and the mainland.

Introduction

The vegetation of the coastal islands—Garden, Rottnest and Carnac—is very unusual when compared with that of the adjacent mainland. This fact has long been recognized and commented on both by local and visiting botanists, but apart from notes on brief excursions no account has been written. The object of this paper is to give a description of the vegetation of the islands and to discuss briefly its relationship to the environmental factors. In addition, a comparison is made between the vegetation of the islands and that of the coastal areas on the mainland between Rockingham and Scarborough. This has led to a discussion of the present distribution of species in the area and an interpretation of the past history of the islands in the light of this distribution. The geographic relation of the islands to the mainland is shown in Fig. 1.

Garden Island has been chosen for a more detailed study than the other islands because it has remained almost unchanged by settlement. Rottnest Isand has been inhabited from the early history of the State and so has suffered drastic changes in vegetation; and Carnac Island, though its vegetation is unchanged, is considered too small for any but shoreline conditions to prevail.

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The historical records of these islands can be traced back to 1658 (Heeres 1899), when a Dutch vessel, the *Waekende Boeij*, while looking for survivors of a ship which was wrecked further to the north, anchored to the north of a small island in latitude 31°47′ S. Samuel Volkersen, the captain of the vessel, writing to the Governor of the East India Company in 1659, wrote:—

> In slightly under 32° south latitude there is a large island at about three miles from the mainland of the Southland. The island has high mountains with a good deal of brushwood and many thorn bushes so that it is hard to go over . . . . . Slightly more to the southward is another small island.

There is no doubt that Volkersen referred to Rottnest and Carnac Islands, although they were not named until much later.

In 1696 three vessels under the command of William de Vlamingh, while searching for a lost vessel, arrived at Rottnest Island and Gerrit Collaert, captain of one of the vessels, wrote:—

> On 31st December (1696) I again put on shore with the skipper . . . . . I found several sorts of shrubs the greater part of which were unkown to me . . . . . There were also a variety of trees and among them one sort the wood of which had an aromatic odour . . . . .

and a few days later de Vlamingh wrote of:—

> a very agreeable belt of trees, very thick and about half a league in extent . . . . . We perceived that a very grateful odour came from these trees.

This quotation suggests that the vegetation of Rottnest Island has changed considerably and in fact *Callitris robusta* thickets were probably originally widespread. Garden and Carnac Islands are apparently unchanged and although Garden Island was studied by a zoologist from the French ship *Naturaliste*, little useful information on the vegetation can be obtained from his journal.

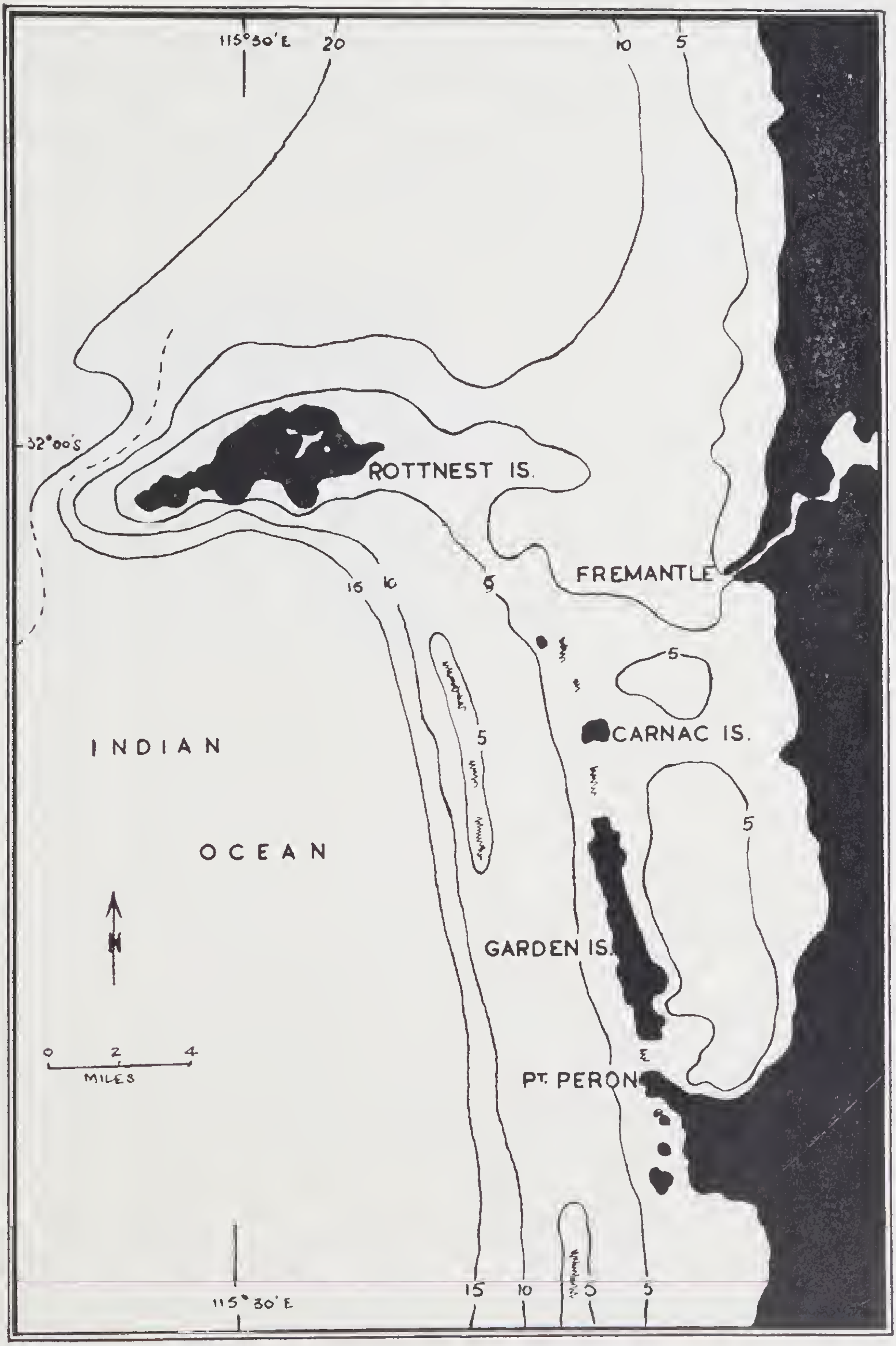


Fig. 1.—Plan showing location of islands and bathymetry of the surrounding ocean.

In 1854 William Harvey visited the area and writing of the vegetation of Rottnest Island said:—

> . . . . its land flora is remarkable for the total absence of Proteaceae and Grass trees and for the paucity of Myrtaceae, Epacridaceae and Leguminosae . . . .

Harvey's statement puts the problem in a nutshell, and it is the consideration of this problem, accompanied by a description of the environmental factors, which make up this paper.

A list of species and their distribution on the islands is given in Appendix I. The authorities for all species are also included in this list.

Geomorphology

The islands under discussion are parts of two physiographically distinct ridges which lie roughly parallel to the mainland coast between 32° and 32°30′ south latitude. The easternmost ridge passes through Murray Reefs, Penguin and Seal Islands, Point Peron, Garden and Carnac Islands and the Stragglers. The other, about two miles further west, passes through Coventry Reef, Hawley and Casuarina Shoals and Rottnest Island. A study of the bathymetry of the region makes this feature even more marked (Fig. 1). These ridges are composed of Pleistocene to Recent aeolianite. They have been described (Teichert, 1947b; Fairbridge 1950) as being the remnants of a peninsula which extended about twenty miles from the present coastline when the level of the sea was considerably lower. With the rising of the sea the ridges have become more and more dissected until now there remain only four major land surfaces and several small rocky islands. Erosion is still going on, but only slowly. Point Peron has since been reunited to the mainland by blown sand (Fairbridge, 1948).

The islands have a hard core of travertinized calcareous dune rock which is generally taken to be late Pleistocene in age (Fairbridge, 1948). This rock is exposed extensively on Rottnest and Carnac Islands while on Garden Island it is largely blanketed by more recent sand dunes.

Exposures in the dunes on Garden Island show the typical cross-bedding of aeolianite. The upper 6-8 feet is still quite loose, but below this there is incipient cementation and a few travertinized root channels (Fig. 2). Analysis has shown that the lower levels are only slightly richer in calcium carbonate than the surface.

Garden Island can be divided into two physiographically distinct areas. The first is the main axis consisting of relatively high steep dunes underlain by limestone and the second is the low flat area making up Colpoys Point. It is suggested that the latter was formed comparatively recently by progressive additions of sand which washes through South Passage. This is indicated by the radial structure of Colpoys Point and the smooth even curve of Careening Bay.

A feature of the coastline, both on the islands and the mainland, is the presence of wave cut platforms at different levels above the existing sea level. Fairbridge (1948) has shown that there is a fair degree of correlation between the raised platforms here and at Houtman's Abrolhos Islands 300 miles to the north. This suggests eustatic changes in sea level. The changes can be roughly referred to world-wide changes since the Pleistocene period (Zeuner, 1945, 1946). This allows of accurate dating of physiographic events in the area, the time of the 10 foot platform having been put at 2,000 B.C. The sea level apparently reached its maximum height at that time and has since dropped, with periods of still-stand at 5 feet and 2 feet. From this it can

Fig. 2.—Soil profile in a cutting through a dune. Solution channels are forming in the lower layers. Garden Island.

be assumed that individual islands and the mainland have not been linked by a direct land bridge for at least 4,000 years, and that probably the time when they were connected lies nearer 100,000 years ago. This would correspond with the Würm exposure of Europe.

There is no permanent fresh water on the islands and no evidence that there has been any in the past. However, the army authorities have put down two deep bores and several wells. The bores are artesian and there is a continuous flow of water to the sea.

Early visitors were unanimous in describing the islands as being mountainous, the steep and densely vegetated dunes giving an exaggerated impression of height when viewed from a distance. However, the highest point on Garden Island is slightly less than 200 feet, while Rottnest Island has a maximum elevation of 130 feet.

Climate

The area in the vicinity of Fremantle has a typically Mediterranean climate. In other words, there is a cool wet period and a warm dry period, with short periods of transition.

Most of the climatic data were obtained from the Rottnest Island weather station (see Appendix II) and it has been assumed that these records apply equally to conditions on Garden and Carnac Islands and Point Peron.

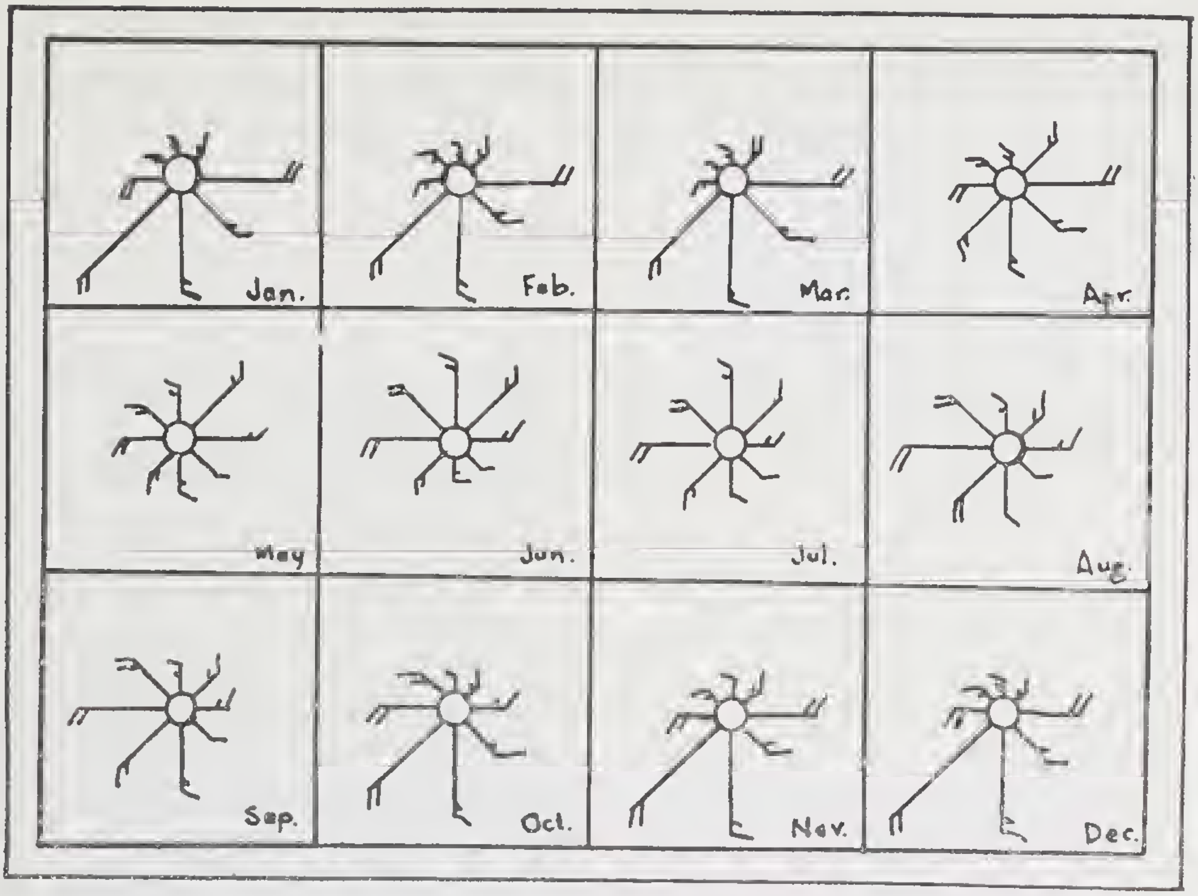


Fig. 3.—Mean monthly wind Roses at Perth Weather Bureau. The length of the arrows represents the mean total number of miles from each direction on a scale of 1in. to 5,000 miles. The feathers indicate the speed of the wind on the Beaufort Scale. North is towards the top of the page.

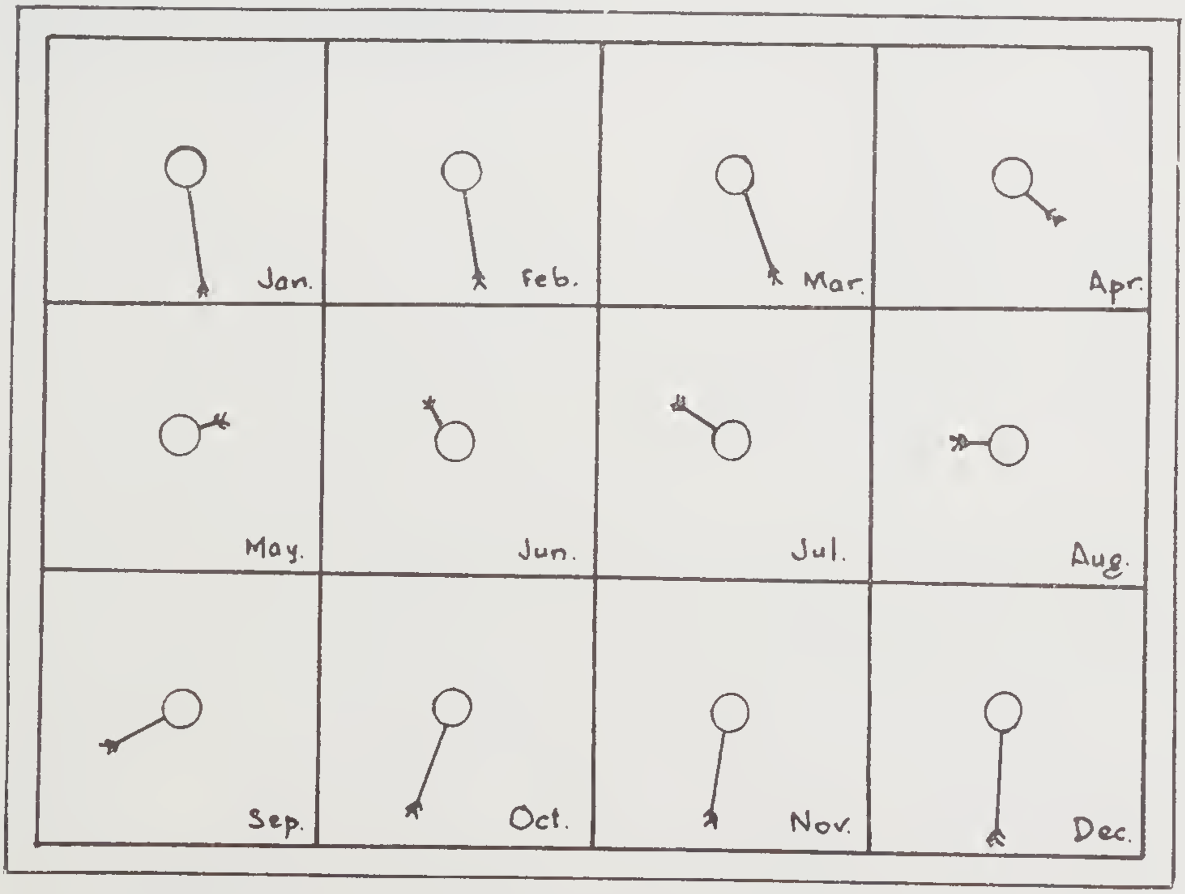


Fig. 4.—Resultant wind. Perth Weather Bureau. The length of the arrows represents the resultant wind on a scale of 1in. to 10,000 miles. North is towards the top of the page.

It is only during the period May-August that the west coast of Australia is subject to any constant rain-bearing wind. Rottnest Island receives 72% of its annual rainfall during these months and 93% during the months of April to October. Thus the distribution of rainfall is more important than the yearly total. During the winter there is a surplus while during the summer there is a marked deficiency. As the main rain comes when evaporation is at a minimum and run off is negligible in the loose sand most of it penetrates the soil. The figures quoted for potential evapo-transpiration (Appendix II) are calculated from a formula proposed by Thornwaite (1948). It is suggested that conditions in undisturbed scrub are such that the actual water loss would be less than the figure calculated.

The effectiveness of the rainfall was calculated using Thornwaite's (1931) formula, which is regarded by Gentilli (1948) as being the most suitable for Australian conditions. Rainfall effectiveness increases very rapidly during the latter part of April and decreases just as rapidly in August. This leaves about half the year when conditions become semi-arid or drier (less than 2.2). There is some lag, however, and it has been shown (Speck, unpublished data) that some soil water is still available until early December. On Garden Island the position of the ground water table varies from 4 feet below the surface in August to 14 feet in March.

It is suggested that plants obtain much of their moisture during the summer months from dew which forms every night, but which is never measurable. Wallabies (*Setonix brachyurus* and *Protemnodon eugenii*) have existed on the islands for centuries without any reliable fresh water supplies, suggesting that in summer the dew must be considerable. The greater part of Garden Island is covered with dense low scrub and this may have the effect of decreasing evaporation from the soil surface.

The lower mean monthly temperature limit for plant growth lies between 45° and 50°F. Since the lowest mean temperature on the coastal islands is 58°F. in July it may be concluded that temperature would, at the most, cause only a slight retardation of growth. It is also significant that the lowest recorded temperature is considerably above freezing point. A striking feature of the temperatures of the islands is the uniformity of the mean temperature. The daily range varies from 10° in July to 13° in February.

Wind data for Western Australia are limited, Perth Observatory being the only coastal station having a continuous record of wind speed and direction. However, it is considered that the wind at Perth would be substantially the same as on the coastal islands, except that sea breezes would begin to blow earlier each day and the velocity of the westerly and south-westerly winds would be greater than at Perth.

It will be seen from the monthly wind roses (Fig. 3) that for the nine months from July to March the greater part of the wind is from the south-western sector. This is due partly to the influence of the local winds, but also to the fact that for some of this period the cyclonic winds coincide with the local winds. During April the predominant wind is from the east and May and June are almost equally windy from all directions. The diagram was constructed from records taken over ten years.

It is significant that the "resultant wind" (Fig. 4), which has been calculated for each month from the wind roses, reflects the control of the local winds for the greater part of the year. The cyclonic winds only become dominant during the winter months. Vegetation on the west coast of Garden Island is often aligned in a south-west north-west direction showing the predominating influence of the local winds (Fig. 5). The fact that the resultant wind makes a complete counter-clockwise rotation during the year is explained by the annual change in position of the belt of high pressure systems.

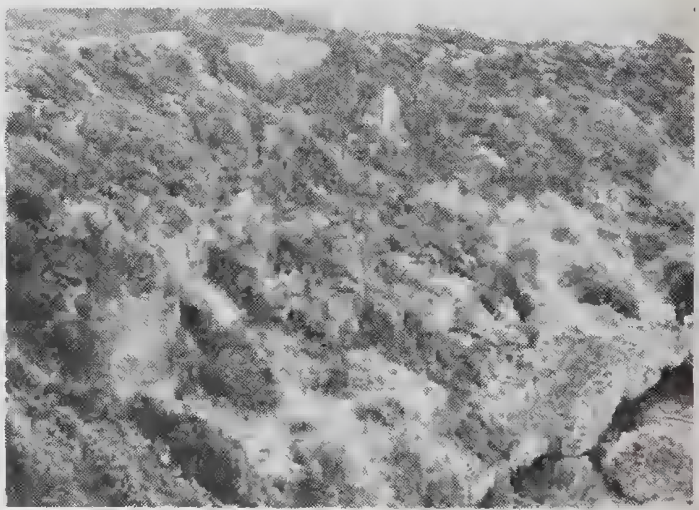


Fig. 5.—Cliff side vegetation, shaped and prostrated by wind action. Pt. Atwick. Garden Island.

The long axis of Garden Island is orientated about 15° west of north, while Rottnest has its greatest extent east-west. The importance of this becomes apparent when the prevailing winds are considered. It means that for Garden Island the maximum length of coastline is almost at right angles to the wind for the greater part of the year, while it is only the south-west portion of Rottnest which is affected.

The contrasting orientation of the islands may explain why Garden Island is largely covered by loose blown sand, while Rottnest has extensive rock outcrops.

On the west coast of Garden Island the effect of wind is very marked. Blow-outs and partial burying of the vegetation (Fig. 6) are common, and it is only those plants which can keep pace with the banking sand which survive. On exposed dunes and cliffs many shrubs have been reduced to a prostrate form by the action of the wind, each bush having a clipped appearance. The effects of salt spray on this vegetation must be considerable, especially where the waves break on rocks and the spray is carried over the land by wind.

Another wind effect may be seen in the orientation of *Callitris robusta* clumps on the north end of Garden Island (Fig. 7). From available evidence it is suggested that this clump has been spread through the seeds being blown by the wind. Ring counts of trees from different parts of the largest clump indicate that the

Fig. 6.—"Blowout" on the west coast of Garden Island. Sand is rapidly encroaching on to stable vegetation.

direction of the spread has been towards the north-east. During the summer months when the seeds are being shed the winds are from the south-west.

In this connection it is of interest to note that on the islands there are other species whose seeds are distributed by the wind. Some of these are *Senecio lautus*, *Arctotheca nivea*, *Clematis microphylla* and *Comesperma integerrimum*.

On the mainland the effect of wind has in certain areas been increased by the action of man. At Point Peron clearing of vegetation has led to mobile sand which is now fairly extensive. Attempts are being made to stabilise this sand by the introduction of Marram grass (*Ammophila arenaria*). Along the coast proper, especially on the wide, sandy beaches, the sand is constantly shifting and blow-outs are frequent.

It can be seen from the foregoing that the wind, although ordinarily not strong enough to uproot trees or break branches, has, by its very constancy, perhaps a greater influence than many of the other factors.

The effects of light, embracing intensity, length of day and duration of sunshine, form an important component of the environmental complex but without controlled conditions it is impossible to isolate its influence. It is reasonable to assume that it is the low light intensity which excludes most undergrowth from the dense *Acacia rostellifera* and *Callitris robusta* communities. On the other hand it is difficult to say whether it is the lack of competition or protection from the sun which allows the small annual *Didiscus* to flourish in the *Callitris robusta* thickets.

The salient point to be made in this very brief discussion of the climatic factor, is the seasonal aspect of the weather. The rain comes in the cooler part of the year when the rate of plant growth is at a minimum with the result that some plant groups are excluded or restricted. The family *Gramineae* for instance, which requires rainfall in the warm season, is represented by only one native species (*Stipa variabilis*).

Garden Island

The vegetation of this island is remarkable for three reasons. Firstly, certain important families of the mainland are either absent (Proteaceae) or present in restricted numbers (Myrtaceae and Papilionaceae). Secondly, the dominant species present show an unusually high frequency, five-sixths of the area available being covered by dense scrub formed by *Acacia rostellifera*, *Callitris robusta* and *Melaleuca huegelii*. The third unusual feature of this vegetation is its structure which is probably unique in Western Australia. In many cases the scrub consists of a single storey of dominants in contrast to the three distinct stories found in the *Eucalyptus marginata* and *E. gomphocephala* communities of the mainland (Speck 1952). The closed canopy of the island vegetation serves further to distinguish it from any other community.

Fig.7.— Lineation of *Callitris* clumps on North end of Garden Island. Traced from an aerial photograph.

The vegetation on the island consists of two ecologically and physiognomically distinct types: a stable central area of dense scrub and an unstable fringing zone. The fringing vegetation is subject to constantly changing conditions and this is reflected both in the structure and composition.

Using the system of classification of Beadle and Costin (1952) the following eight plant communities are recognised on Garden Island:—

(i) *Callitris robusta* association (tall scrub)

(ii) *Acacia rostellifera* association (scrub)

(iii) *Melaleuca huegelii* association (scrub)

(iv) *Myoporum insulare* association (low scrub)

(v) *Acacia heteroclita association* (low scrub)

(vi) *Pittosporum phillyraeoides* association (low scrub)

(vii) Seasonal Communities

(viii) Littoral Vegetation

The following discussions will apply to relatively pure communities although it must be stressed that in respect to the tall scrub and scrub communities there are all combinations from 100% of one to equal proportions of *Acacia rostellifera*, *Callitris robusta* and *Melaleuca huegelii* and often an admixture of *Melaleuca pubescens* and *Spyridium globulosum*.

Description of the Communities

Callitris robusta *Association*.—This community is restricted mainly to a large clump covering about a square mile in the northern part of the island. There are however small clumps in the *Acacia* scrub of the south end of the island and on the eastern extremity of Colpoys Point there is a mixed stand of *Callitris robusta* and *Melaleuca pubescens*. The average height of the trees in these clumps is 17-20 feet although many individual trees in the open grow to 35 feet. The average stem diameter is 2-3 inches and as most of the trees are 30-40 years old it is apparent that the annual increments are very small. In the clumps the trunks are straight and unbranched and the canopy completely closed giving the community the structural characteristics of a forest (Fig. 8). The undergrowth is very limited, *Phyllanthus calycinus* being the only common undershrub. In season, the tiny annual *Didiscus pilosus* flourishes in the *Callitris* community. The lack of light is possibly sufficient to restrict most other plants. There are isolated bushes of *Spyridium globulosum* and rarely *Eremophila brownii* and *Leucopogon richei*. There are

Fig. 8.—*Callitris robusta* association, Garden Island. Note single storey structure.

occasional trees of *Melaleuca pubescens* and *Acacia rostellifera* and these have taken on the same form as the *Callitris* viz. tall and slender with only a tuft on top. The creepers *Cassytha glabella* and *Comesperma integerrimum* are present, but do not attain any large size. Within the community seedling regeneration of *Callitris* appears to be restricted, only a small percentage of those germinated surviving beyond December.

As far as can be seen there is no obvious factor limiting the distribution of *Callitris*. It grows as individual trees and small clumps throughout the *Acacia* scrub. It is scattered through the *Melaleuca huegelii* community and it competes on equal terms with *Melaleuca pubescens*. There is evidence that the *Callitris* is encroaching on the *Acacia* scrub. Ring counts of trees from different parts of a clump show that the age decreases from 40 years in the centre to 22 years at the periphery. This indicates that the spread of the clump has been a gradual process. It is significant that the boundary between these two communities is quite sharp. There is seldom any merging one into the other.

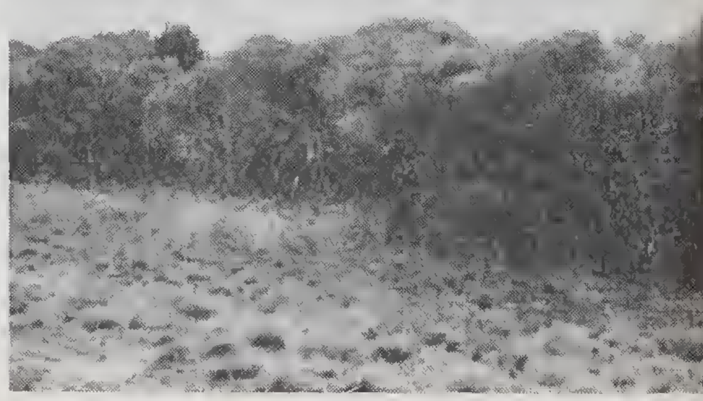


Fig. 9.—*Acacia rostellifera* association showing the dense, uniform canopy. *Stipa variabilis* and *Didiscus coeruleus* are shown at the side of the track. Garden Island.

A feature of the *Callitris* scrub is the thick layer of leaf litter. There is commonly 2-3 inches of undecomposed leaves on the surface below which is about 1-2 inches of decomposing leaves. The soil profile below this is as follows:—

0-1in. Dark grey calcareous sand rich in organic matter

1-6in. Grey-brown calcareous sand

6-45in. Light yellowish grey calcareous sand becoming very light grey with depth

Table I shows that the nutrient status of the soil is very high for natural conditions.

Acacia rostellifera *Association*.—This is the most widespread community on the island. Superficially the impression is given of a pure stand, but *Callitris* occurs throughout and *Melaleuca huegelii* forms an integral part. *Melaleuca pubescens* also appears sporadically, while *Spyridium globulosum*, which often attains a height of 8 feet, must be considered as a co-dominant.

The *Acacia rostellifera* scrub is very uniform in height (8-10 feet) and extremely dense and tangled (Fig. 9). Other species of *Acacia* are present, e.g., *Acacia cyanophylla* and *Acacia heteroclita*. The former, while of rare occurrence, is spread throughout the association, while the latter is mainly present in the vicinity of the mobile dunes.

Undergrowth is usually present even though restricted in many parts to *Stipa variabilis. Phyllanthus calycinus* and *Acanthocarpus preissii* occur in the more open areas. *Leucopogon* spp. and *Diplolaena dampieri* grow where the scrub thins out to separate bushes. *Guichenotia ledifolia* and *Lasiopetalum angustifolium* occur towards the northern end of the island in less dense areas, and *Didiscus coeruleus* (Rottnest Daisy) grows profusely where the scrub has been cleared.

Acacia rostellifera scrub shows a remarkable ability to regenerate vegetatively, exposed or damaged roots giving rise to new bushes. Many roads made by the Army during the period 1939-1945 are now completely over-grown and the scrub constantly encroaches on any cleared area. It appears to be a very vigorous community.

The soil is brown and powdery below the layer of decomposing leaves and at 2 feet is very light grey calcareous sand (Fig. 2). The important point about this soil is that it supports a very dense vigorous vegetation suggesting that the nutrient status is high. Chemical analyses (Table I) show a very high nitrogen level which may be due to symbiotic nitrogen fixation. No clear-cut evidence has been obtained to indicate nodulation here. It may, however, be noted that Wilson (1939) in U.S.A. has shown that some *Acacias* do possess *Rhizobia* as do also some species in Queensland (McKnight 1949). Root nodules have been noted on several species of *Acacia* found in the vicinity of Perth (Parker, personal communication).

Melaleuca huegelii *Association.*—This association is confined to several small areas to the north of Sulphur Jetty near the eastern coast of Garden Island where it is developed on low lying areas. The canopy is very uniform and its density is increased by the creepers, *Cassytha glabella, Clematis microphylla, Comesperma integerrimum, Rhagodia baccata* and *Hardenbergia comptoniana*, which flourish here. There is a well defined under-storey of shrubs consisting of *Eremophila brownii, Phyllanthus calycinus, Acanthocarpus preissii* and *Leucopogon richei*. Below this is a thick mat of moss and in spring the annuals *Didiscus pilosus* and *Parietaria debilis*.

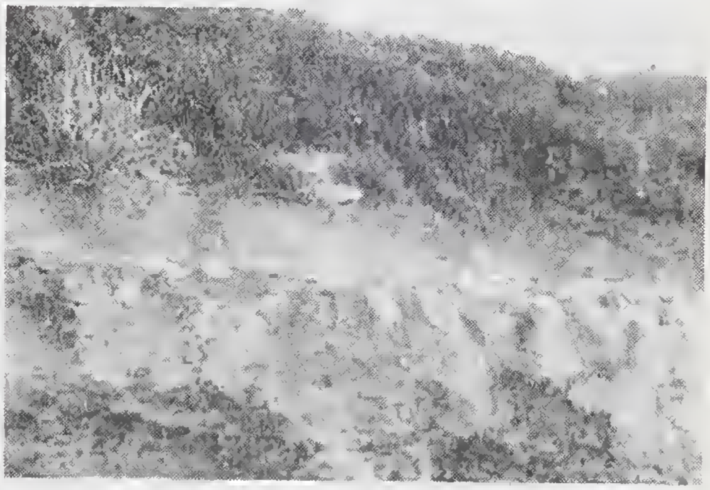
The soil has a fairly high concentration of organic matter below a thin layer of decomposing leaves, but at 2 feet is very light grey sand as in the other communities.

Myoporum insulare *Association.*—This community consists of dense scrub about 6 feet in height and is confined to the southern end of the island where it covers an area of a few acres. Associated with this community are *Acacia cyclopis, Rhagodia baccata* and *Solanum simile*. Undergrowth species are *Eremophila brownii* and more rarely *Solanum nigrum*.

The soil is a very shallow dark grey sand overlying limestone.

Acacia heteroclita *Association.*—*Acacia heteroclita* is the main component of a stand of low scrub restricted to the limestone cliffs near Point Atwick and northward. It stretches inland about a quarter of mile where it merges very gradually into the climax island vegetation.

The main associated plants are *Acacia rostellifera, Spyridium globulosum, Diplolaena dampieri, Leucopogon* spp., *Melaleuca pubescens* and *Exocarpus aphylla*. Below this storey there is a dense growth consisting mainly of *Lepidosperma squamatum* and less commonly of *Stipa variabilis, Phyllanthus calycinus* and *Acanthocarpus preissii. Westringia ridiga, Dodonaea aptera, Alyxia buxifolia, Acrotriche ovalifolia* and *Melaleuca pubescens* also occur near the cliff edge, these bushes often being prostrated and elongated by wind action.



Figg. 10.—*Acacia heteroclita* association developed on shallow soil. Garden Island.

The soil is seldom more than a foot in depth and is fairly rich in organic matter (Fig. 10). This soil is similar to that on the south end of the island and chemical properties would be comparable.

Pittosporum phillyraeoides *Association.*—Near the south-west corner of Garden Island several small areas of *Pittosporum* scrub occur. They consist of thin straggly bushes about 4 feet 6 inches high with the foliage completely restricted to a small tuft on top. The canopy, though only 4-5 feet above the ground is very dense and completely closed. There is very little undergrowth and the soil, below a thick mat of leaves, consists of light brown gritty calcareous sand which becomes gradually lighter in colour with depth.

Seasonal Communities.—These communities are of considerable importance since they are the feeding grounds of the Garden Island Wallaby (*Protemnodon eugenii*). On the northern tip of the island the scrub gives way to an open area covered by *Asphodelus fistulosus, Anthericum divaricatum* and *Stipa variabilis*. The two former components die down to ground level in the summer months and then regenerate in the spring. There seems to be a definite association between these plants and the introduced white land snails (*Bothriembrium bulla*), which congregate thickly on the stems without damaging the plant.

The second seasonal community, a mixed annual meadow occurs on the south end of the island and is developed on shallow dark grey sand overlying limestone. Some chemical properties of this soil are shown in Table I. The annual vegetation is rarely more than 2 inches high and is composed of *Euphorbia drummondii, Geranium pilosum, Erodium cicutarium* and Poa spp. In the late winter it forms a thick mat on the area between the *Acacia* scrub and the cliffs on the southern end of the island. The best development is in the valleys protected from the wind and salt spray. Other common plants here are *Anagallis arvensis, Tripteris clandestina, Solanum simile* and *S. nigrum.*

On the tops of the rocky headlands the vegetation is subject to salt water spray and possibly for this reason the annuals are almost absent. The more salt resistant plants *Carpobrotus acquilaterus, Stipa variabilis* and *Scripus nodosus* make up most of the ground cover and even on these the effects of the salt are shown by necrotic spots. The shallow soil contains many foecal pellets which have been identified as those of insects, probably the larvae of a scarab beetle (Mr. J. Callaby, personal communications).

Littoral Vegetation.—This community is developed on the beaches, cliffs and partially fixed dunes bordering the island. The environmental conditions here are extreme—conditions which are generally recognised as being very unfavourable to plant growth. These include sand blast, desiccation, salt spray, intense light and highly calcareous sand as soil. It is understandable then that only specialised plants, characterised by waxy, hirsute and succulent leaves, can survive.

The limits of this zone are very poorly defined. It grades imperceptibly into the scrub. However, within the zone two fairly distinct habitats occur—the rocky cliffs and talus slopes and the sandy beaches.

Fig. 11.—Cliff side vegetation, Garden Island.

Generally the succulent plants are found on the rocky cliffs. Most common are *Carpobrotus aequilaterus* (Fig. 11), *Tetragonia implexicoma, T. zeheri, Wilsonia backhousii* and *Nitraria schoberi.* Where the cliff is not so steep other plants such as *Westringia rigida, Olearia axillaris, Alyxia buxifolia* and *Boronia alata* occur. Where the soil is deeper and a little more mature *Lepidosperma gladiatum* and *Scirpus nodosus* appear. In this habitat it seems that the wind is the main factor limiting species.

The sandy beaches have different environmental conditions. Salt spray is not so severe but light is very intense. Plants which can withstand sand blast such as *Calocephalus brownii, Angianthus cunninghamii, Arctotheca nivea* and *Spinifex hirsutus* are the most common. Here is opportunity for primary succession and on most beaches there is at least a rough zonation of vegetation.

Discussion of the Soil Properties

The soils of Garden Island are comparable to those of a considerable portion of the west coast of Western Australia and for this reason further discussion is warranted.

Smith (1951), referring to coastal soils in the Margaret River area and Speck (1952) working on similar soils in the vicinity of Perth, have emphasised the high content of calcium carbonate and the consequent alkaline reaction and high loss on ignition.

However, there has been little other recent work and so the present investigation, while not by any means complete, constitutes the first detailed examination of these soils. This work has the further advantage that the soils have been studied under conditions in which the soil-vegetation balance is practically undisturbed.

Table I shows the results of analyses for the major elements, the methods employed being those described by Piper (1947). Figures for phosphorus have been omitted because of lack of agreement between determinations using different analytical methods. Indications were that the surface horizons contained from 0.10 to 0.15% total phosphorus. This high figure may be due in part to calcium phosphate which occurs in some shells and foraminiferal tests.

The most important single factor affecting the soils is the extremely high content of calcium carbonate which commonly makes up 85% of the solum. This means that the reaction is always strongly alkaline and, in fact, the pH is below 8.0 only in the upper organic horizons. The high carbonate content serves to explain the discrepancy between the figures for sodium chloride and total soluble salts, the former usually being about 60-70% of the latter. In this case it is assumed that the total soluble salts include a considerable proportion of bicarbonate ions.

Chemical analyses show an unusually high fertility under virgin conditions in Western Australia. More important, it can be seen that the several communities have significantly different levels, the soil supporting the *Acacia rostellifera* association having an extremely high level. The high nitrogen content in this soil suggests that *Acacia rostellifera* has nitrogen fixing properties.

A remarkable feature of these soils is the A_{00} and A_0 horizons which commonly have a depth of 4 inches. The development and maintenance of these horizons is probably largely due to protection from fires since they are lacking on Rottnest Island where fires have been common. It is suggested also that the protection from sun and wind afforded by the dense canopy may keep surface conditions unfavourable for decomposition. Table I suggests that oxidation of the A_0 horizon has not proceeded very far. It is evident that the bulk of the nutrients are in and immediately below this horizon.

Oosting (1954) and Pidgeon (1950) have shown that the salinity of coastal soils is not as high as would be expected and suggest that soluble salts are removed rapidly, especially during the wet season. Pidgeon further suggests that it is the content of organic matter in the soil which determines the amount of soluble salts which can be retained. In the Garden Island soils, which were sampled after the main winter rains, the relation between these two components is very marked. Analysis of the results shown in Table I give a coefficient of 0.9425 ($p < 0.001$) for organic carbon with soluble salts and 0.9417 ($p < 0.001$) for nitrogen with soluble salts. Thus, taking the organic carbon and nitrogen content as a measure of the soil organic matter, there is a highly significant correlation. This fact needs to be considered in relation to the perennial beach plants, which are probably not halophytic even though they can survive saline conditions for short periods. The annual plants such as *Cakile maritima* and *Arctotheca nivea* are only present on the beaches during the winter when soluble salts would be quickly leached out.

It is of interest to speculate on the rate of soil formation on the calcareous dunes in Western Australia. Burges and Drover (1953) studied the rate of podzol development in beach dunes in New South Wales and concluded that a humus podzol had formed from dunes containing about 3.0% calcium carbonate in about 3,000 years. In the dunes under consideration here the content of calcium carbonate is in the vicinity of 80% and the time required for the soil to reach equilibrium would be much greater. Recent developments in radio-carbon dating of carbonates may enable the relative ages of the coastal dunes and limestone deposits to be established. In a highly calcareous soil a considerable proportion of the calcium carbonate could be leached away without a significant change in the apparent calcium carbonate content. It is evident that the proportion of calcium carbonate remaining to the apparent total weight of soil would remain fairly constant. For example a soil containing 90% calcium carbonate could lose 50% of its original weight and still show an apparent calcium carbonate content of 80%. This argument can be continued until the interstital spaces become filled with the insoluble silica grains.

It seems probable that under the prevailing climatic conditions calcium carbonate would not remain in the solum, but would be leached out and redeposited in the vicinity of the ground water table leaving the upper part of the soil neutral or slightly acid in reaction. Such is the case in the Tuart (*Eucalyptus gomphocephala*) zone of the mainland where there is often ten feet of yellow sand overlying limestone (Speck, 1952). In many places along the mainland coast limestone occurs very near to the surface and it is assumed that this represents a truncated profile, the upper horizons of sand having been removed by wind. This will explain the crust of travertine which occurs so commonly.

Rottnest Island

An account of the overall geology and physiography of the islands has already been given, but further detail is necessary for Rottnest. For the most part it is composed of solid limestone in contrast with the unconsolidated dunes of Garden Island. Another feature is the low topographical level. The highest point is about 130′ above sea level and, more important from the point of view of vegetation there are swamps and permanent lakes which provide completely different environmental conditions.

The relative proportions of species on the island has changed considerably since white man first landed on the island. This has been brought about by burning and clearing and to a lesser extent by the introduction of exotic species. However, the natural vegetation is more affected by the accidentally introduced species than by those intentionally introduced. *Asphodelus fistulosus* and *Anthericum divaricatum* which came originally from the Mediterranean, and *Euphorbia peplis* have spread all over the island. There are also several introduced grasses, *e.g.*, *Poa australis* and *Polypogon maritimus*.

The present vegetation can be divided into several well defined communities and these will be discussed as follows:—

(i) *Melaleuca pubescens* association (forest)
(ii) *Acacia rostellifera* association (scrub)
(iii) *Templetonia retusa* association (scrub)
(iv) *Acacia cuncata* association (low scrub)
(v) *Stipa-Acanthocarpus* community
(vi) Halophytic communities
(vii) Littoral vegetation

Description of the Communities

Melaleuca pubescens *Association*.—This tree forms pure stands of considerable area on Rottnest Island in contrast to Garden Island where only small clumps occur. It seems in some places that *Melaleuca pubescens* is the climax vegetation following a succession from swamps and lakes (Fig. 12) since on the higher ground surrounding these there is often a zone of *Melaleuca pubescens*. However, this tree also grows quite commonly on soils developed over limestone.

This community has a distinctive appearance with its clean straight boles and dense rounded crowns. In typically developed areas the trees are 30—35 feet high and have a dense interlocking canopy. Undergrowth is restricted to a sparse growth of *Stipa variabilis.*

Fig. 12.—*Melaleuca pubescens* association bordering Herschell Lake, Rottnest Island.

Acacia rostellifera *Association.*—This scrub varies in height from 8 to 15 feet and has a completely closed canopy. It is not now very widespread on the island, but appears to be a remnant of some former much larger community. It often occurs in the valleys but on higher ground around the lakes it appears to be a stage in the development of a climax.

There is evidence that *Stipa-Acanthocarpus* community is spreading at the expense of this association. Where the *Acacia* scrub has been burned or cleared the grass takes over before the *Acacia* can regenerate.

Templetonia retusa *Association.*—On Rottnest Island this association covers quite extensive areas mainly in the eastern sector and as on the mainland it is restricted to areas where limestone is at or near the surface (Fig. 13). The scrub is typically 6—8 feet in height and is fairly dense. Undergrowth is quite considerable and consists mainly of *Stipa variabilis* and *Senecio lautus.*

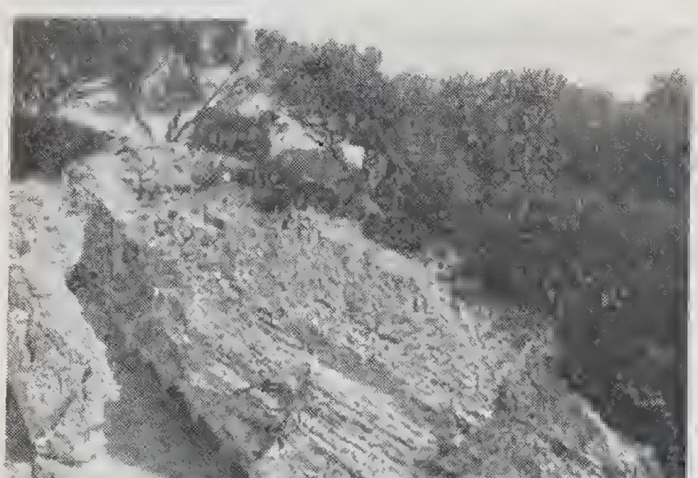


Fig. 13.—*Templetonia retusa* association growing on shallow soil over limestone, Rottnest Island.

Acacia cuneata *Association.*—This low scrub seldom exceeds four feet in height and is very dense. All the bushes are rounded and the branches reach right down to the soil surface allowing only restricted development of undergrowth.

The association is best developed on the western end of the island near the Neck where it grows on recently vegetated sand dunes. Although *Acacia cuneata* is the most abundant component, *Olearia axillaris* and *Westringia rigida* bushes together make up about 50% of the cover. *Scaevola* spp. also occur, especially near the shore. From the shore line there is a fairly well defined zonation of vegetation. *Spinifex longifolia* passes into *Olearia axillaris* which then merges into the *A. cuneata* scrub.

Stipa variabilis—A c a n t h o c a r p u s preissii *Community.*—This is by far the most widespread community on the island and it is probable that the extent can be attributed to man's action in burning the *Acacia rostellifera* scrub (Fig. 14). The community grows apparently equally well on recently colonised sand dunes or on the sparse soil overlying limestone. Generally *Phyllanthus calycinus* is present on the younger soils and again, depending on edaphic factors, both

Fig. 14.—*Stipa variabilis—Acanthocarpus preissii* association which has developed where *Acacia* scrub has been cleared. Rottnest Island.

Thomasia cognata and *Guichenotia ledifolia* may occur. *Thomasia* grows on the shallow soils over limestone and *Guichenotia ledifolia* often occurs in the valleys. However, *Guichenotia* is not restricted to this community; in one place at least it appears to be a stage in the succession from swamp vegetation to *Melaleuca pubescens.* The community is the most important on the island from the viewpoint of food for animals and birds.

The Halophytic Communities.—It is the presence of this type of vegetation on Rottnest Island which makes it so different from Garden Island. The halophytic communities are developed on swamps and lakes which are mainly restricted to the eastern end of the island. The low lying regions give a distinctive appearance to the Rottnest landscape.

Zonation is clearly shown in these areas. Around each lake and swamp there are concentric bands of successively taller vegetation types (Fig. 15). In fact this may be true plant succession.

Fig 15.—Zonation of vegetation bordering a swamp on Rottnest Island. Zones from the water's edge are *Salicornia blackiana*, *Atriplex paludosa*, *Scirpus nodosus*, *Solanum simile* and *Stipa variabilis*.

On the lowest levels the soil is saline (6.25% sodium chloride) calcareous mud containing algal remains and gastropod shells. *Wilsonia humilis* and *Salicornia blackiana* occur on this soil which is waterlogged for the greater part of the year. There is a sharp transition from this zone to a thick mat of *Salicornia* below which the soil, although damp, is not always waterlogged. This soil has 3.3% sodium chloride. The next zone varies considerably in different localities. In some cases the *Salicornia* merges into an *Arthrocnemum bidens* zone and thence into *Melaleuca pubescens* or *Acacia rostellifera* zone. This is generally the case in the swampy areas. However, around the lakes the zone following *Salicornia* is usually a narrow band of *Atriplex paludosa*. Rarely the *Atriplex* may be absent and the *Salicornia* ends abruptly giving way to a dense *Scirpus nodosus* or *Scirpus nodosus-Gahnia trifida* community. The soil in this zone is brown calcareous sand in which the salt content is negligible.

In one instance the *Arthrocnemum bidens* passes into a poorly defined zone of *Stipa variabilis* in which *Guichenotia ledifolia* is also present. However, this may be lacking and either *Melaleuca pubescens* or *Acacia rostellifera* may grow right down to the edge of the swamp. Around the lakes the sequence is more constant and the *Scirpus-Gahnia* zone passes gradually into a narrow band of *Solanum simile*. Where the ground begins to rise this last band disappears and, depending on whether or not the area has been burned, *Stipa—Acanthocarpus* or *Melaleuca pubescens* occur.

Littoral Vegetation.—These communities are similar in all respects to those already described on Garden Island.

Carnac Island

Carnac Island is about two miles north of Garden Island. It forms roughly a square of about 38 acres in area. Except for a sheltered sandy beach on the east and two tiny beaches on the west side the island is bounded by steep limestone cliffs. The highest point is 60 feet and there is very little of the island below 25 feet in height. The uniform topography means that most of the island is exposed to the wind and this fact is reflected in the vegetation. There is no fresh water on the island.

It is to be expected that Carnac Island situated as it is between Garden Island and Rottnest Island would have similar vegetation. However, being such a small island on which no part is more than 200 yards from the sea, it is natural that the dominant plants would be those which are found only on the borders of the larger islands.

The recognisable communities, which are shown in Fig. 16 are as follows:—

(i) *Acacia rostellifera—Olearia axillaris* association (scrub)

(ii) *Olearia axillaris—Scaevola crassifolia* association (low scrub)

(iii) *Frankenia pauciflora—Rhagodia baccata* association (low scrub)

(iv) *Rhagodia baccata* association (low scrub)

(v) *Nitraria schoberi* association (low scrub)

(vi) *Scaevola crassifolia — Calocephalus brownii* association (low scrub)

(vii) *Carpobrotus aequilaterus—Tetragonia* spp.—*Suaeda maritima* mat

(a) Description of the Communities

Acacia rostellifera—Olearia axillaris *Association.*—This community abuts on to the eastern beach and extends about halfway across the island. It appears to be the climax vegetation for this island. *Acacia rostellifera* is the main component, but *Olearia axillaris* is spread uniformly throughout. *Clematis microphylla* does occur here but is never well developed. Undergrowth consists of *Bromus gussonii* and *Lepidosperma gladiatum*.

The soil consists of calcareous fine sand very low in organic matter.

This community merges imperceptibly into the shoreward zone of *Olearia—Scaevola* scrub.

Olearia axillaris—Scaevola crassifolia *Association.*—This is the most variable community on the island, but the two main components occur fairly uniformly throughout (Fig. 17). *Rhagodia baccata* becomes more common near the shoreward cliffs.

The soil is light grey calcareous sand with limestone 8—12 inches below the surface.

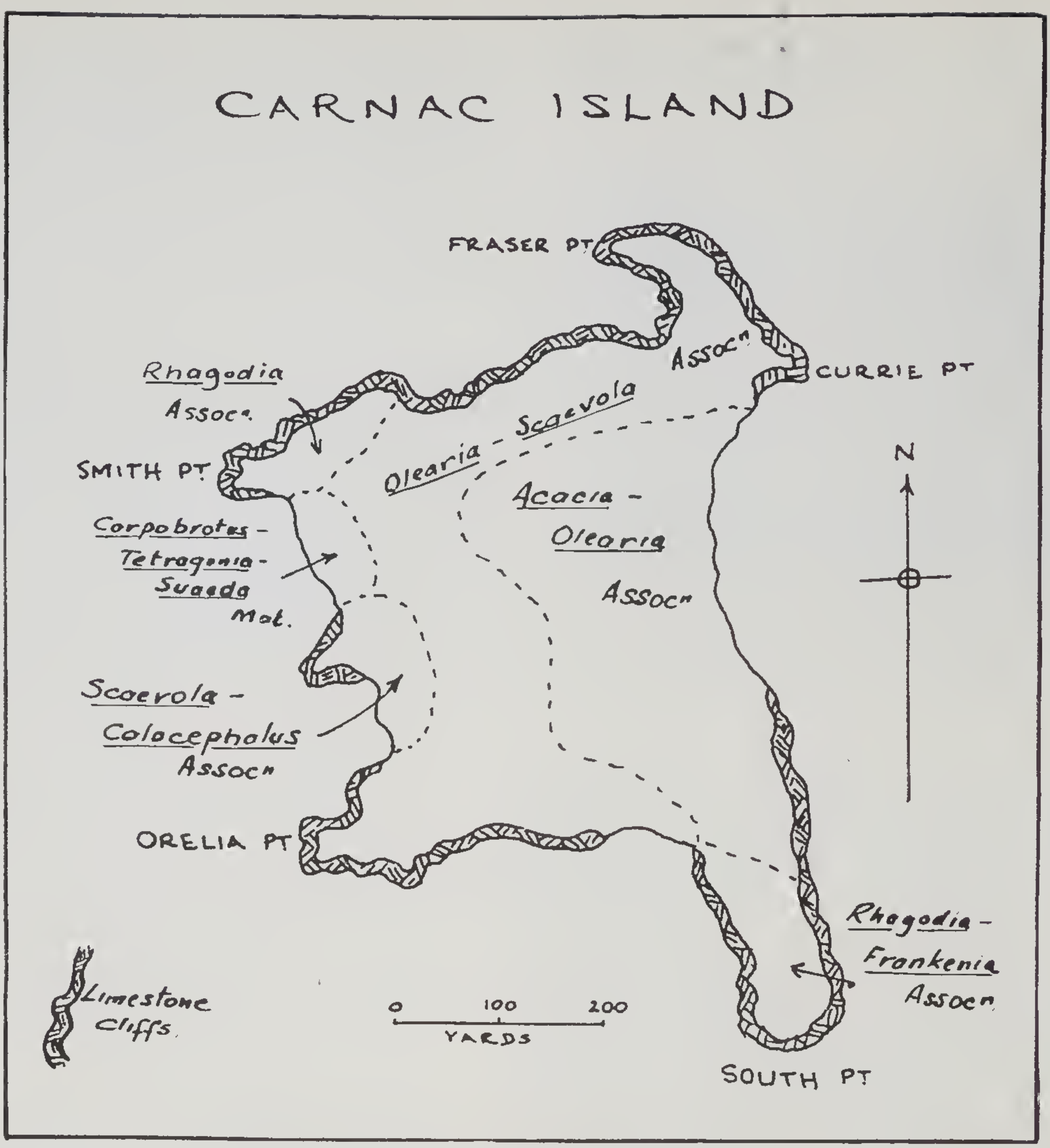


Fig. 16.—The plant communities on Carnac Island.

Frankenia pauciflora—Rhagodia baccata *Association.*—This is a very distinct and sharply defined community restricted to South Point. It is typically 12—18 inches in height and completely covers the soil. The soil consists of a few inches of dark brown calcareous sand overlying travertinized limestone (Fig. 18).

Rhagodia baccata *Association.*—This occupies only a small area near Smith Point (Fig. 19). It grows right up to the cliff edge on the north-west and extends about 50 yards landwards.

It is about two feet in height and is quite dense. The soil is fairly deep and is coarse textured throughout.

Nitraria schoberi *Association.*—On Carnac Island *Nitraria schoberi* forms a dense tangled scrub all along the talus slopes of the cliffs on the northern side. *Rhagodia baccata* occurs but only rarely. The very loose sandy soil of the talus is stabilised mainly by the cover of *Nitraria.*

Fig. 17.—*Olearia axillaris—Scaevola crassifolia* scrub in the foreground merging into *Acacia rostellifera—Olearia axillaris* scrub in the background. Carnac Island.

Fig. 18.—*Frankenia pauciflora*—*Rhagodia baccata* association, Carnac Island.

Fig. 19.—*Rhagodia baccata* scrub on a talus slope, Carnac Island.

Scaevola crassifolia — Calocephalus brownii *Association.*—On the western shore between the two beaches is a small area where *Calocephalus brownii* extends back from the coast and merges with the *Olearia—Scaevola* scrub to form a separate community. This may be only a variant of the *Olearia—Scaevola* scrub, but it appears different enough to warrant separate consideration. *Salicornia blackiana* forms a mat over a small area on the point between the beaches.

Carpobrotus aequilaterus—Tetragonia *spp.*—Suaeda maritima *Mat.*—Fringing the larger of the two western beaches is a thick mat of succulent vegetation. This extends back about 50 yards from the beach. Besides the three main components *Enchylaena tomentosa* occurs frequently. The bank is quite steep but the loose sand is held firmly by the vegetation.

The Mainland

The mainland adjacent to the islands, with an expanding city in its immediate hinterland, has suffered many changes in respect to its vegetation. However, there are remnants of the original vegetation at various points between Point Peron and North Beach and it is the vegetation of these areas which will be compared with that of the islands.

Point Peron, which was formerly a rocky island is now joined to the mainland by blown sand (Fairbridge, 1948). It is controlled by the same environmental conditions as the islands and this is reflected in the vegetation. However, there are some important differences. As would be expected there has been an influx of introduced species such as *Euphorbia* spp., *Bromus gussonii, Solanum sodomaeum, Aster subulatus, Sporobolus virginicus* and *Tripteris clandestina*.

The natural vegetation, though structurally the same as that of the islands, differs in that certain species common to the islands are absent. The most important of these are *Melaleuca pubescens, Guichenotia ledifolia* and *Lasiopetalum angustifolium*. Species common to the understoreys of the *E. gomphocephala* and *E. marginata* associations do not occur on Point Peron. It is assumed then that the absence of these plants on the islands is not due to isolation, but environmental conditions.

The coastal strip between Fremantle and Rockingham was probably originally covered by dense *Acacia rostellifera* scrub similar to that on Garden Island. At present it is much denuded by clearing and fires, but it appears to differ only in that *Xanthorrhoea preissii* occurrs commonly throughout. The remnants of *Callitris robusta* scrub near Naval Base also shows the similarity of this strip to the island vegetation. Relics of a similar vegetation are to be seen along cliff sides of the Swan River at Freshwater Bay, Mosman Bay and Blackwall Reach.

Further to the north at Cottesloe, City Beach, Scarborough and North Beach the vegetation is different, the mature tuart and jarrah forest approaching much nearer to the shoreline, although there is an area of dense *Acacia rostellifera* scrub between City Beach and Scarborough.

One of the most striking features of the beaches of the mainland, particularly City Beach and Scarborough, is the presence of *Arctotheca nivea*, which is most active in stabilising the sand (Fig. 20). This plant keeps pace with the banking sand and in most places the bank is several feet in height. It may well be that this is the first stage in plant succession since this zone is followed by successive zones of *Spinifex hirsutus* and *Olearia axillaris-Scaevola* spp. before reaching the low scrub which is probably the climax dune vegetation. The scrub is made up principally of *Scaevola* spp., *Rhagodia baccata, Myoporum insulare, Olearia axillaris, Scirpus nodosus, Lepidosperma gladiatum* and the creepers *Cassytha glabella* and *Hardenbergia comptoniana*.

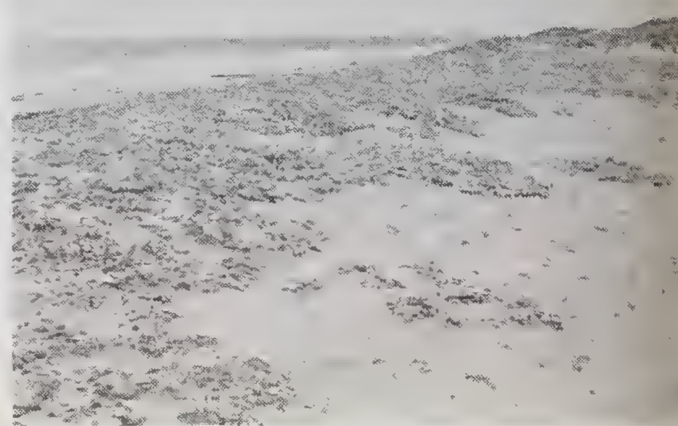


Fig. 20.—Beach sand stabilised by *Arctotheca nivea*, City Beach.

Alyxia buxifolia and *Dodonaea aptera* do not occur in the beach vegetation of the mainland. These are very common on the islands, but apparently occur on the mainland only on Point Peron. Within a short distance of the shoreline in the City Beach-Scarborough area occur many plants not usually associated with beach vegetation. These are *Santalum acuminatum, Hibbertia* spp., *Melaleuca acerosa, Oxylobium capitatum, Gompholobium tomentosum, Acacia pulchella* and *Tersonia brevipes*. The presence of these is a reflection of more mature soil conditions.

It is not until the *E. gomphocephala* zone is reached that significant numbers of Proteaceous and Leguminous plants are found. *Grevillea crithmifolia* and *Petrophila serruriae* occur on the seaward fringe of this zone and then *Banksia* spp. and *Stirlingia latifolia* are associated with the tuart. *Casuarina fraseriana* also occurs as part of the understorey of the tuart, but is not found nearer the shoreline. *Agonis flexuosa* commonly grows on the calcareous dunes of the mainland but is not found on the islands.

It is of interest to note that the coastal vegetation contains many genera and even species which occur much further inland in the Eremean Province. It is evident that the habitats have no obvious common environmental factor, although Gardner (1942) points out that the soils which support these plants are either physically or physiologically dry. It is likely that the solution to this problem will be found only in a study of the physiology of the plants concerned. The presence of calcium carbonate in the profile may be part of the answer, but other factors will also contribute.

Discussion

The vegetation of the islands has distinctive features both structurally and floristically. The undisturbed vegetation as already described consists of dense almost impenetrable scrub in which the upper storey is completely closed and the understorey very sparse or absent. This is in striking contrast to the jarrah (*E. marginata*) and tuart (*E. gomphocephala*) associations of the mainland which have an open tree layer and a rich and varied understorey of small shrubs and harsh woody monocotyledons. These associations are however developed on mature soils such as do not exist on the islands.

The distribution of species both on the islands and the mainland can, with some exceptions, be explained by habitat rather than insularity. Thus the protected sandy beaches on the eastern side of Garden Island, Thompson's Bay on Rottnest Island and Mangles Bay near Rockingham are characterised by a zone of *Spinifex longifolia* which grows at the foot of a low fore-dune, the scrub approaching very near to the beach. The exposed beaches on the western sides of the islands, Shoalwater Bay near Rockingham and metropolitan beaches on the mainland, have a much steeper bank, which is stabilised by *Scirpus nodosus*, *Lepidosperma glaliatum* and then by *Olearia axillaris* and *Scaevola* spp. On the seaward side of the bank *Spinifex hirsutus* and *Arctotheca nivea* are the only plants which can withstand the sand blast, although there may occasionally be *Salsola kali* and *Cakile maritima*.

The rocky cliffs and headlands on the western sides of the islands, and along the mainland coast between the metropolitan beaches, also have a characteristic vegetation—both in species and habit. The salt spray tolerant plants, *Carpobrotus*, *Tetragonia*, *Suaeda*, *Enchylaena* and *Frankenia pauciflora* are very commonly seen clinging to the rocks and *Nitraria* and *Rhagodia* where there is a little more soil. *Calocephalus*, *Angianthus* and *Scaevola crassifolia* are common along the tops of exposed cliffs, but apparently require a few inches of soil to survive. There are some larger bushes such as *Alyxia buxifolia*, *Dodonaea aptera* and *Westringia rigida*, which, when present in this habitat, are wind-shorn and prostrate. Thus on Carnac Island, which is principally bordered by rocky cliffs and of relatively small extent, it is found that the most common plants are *Nitraria*, *Rhagodia*, *Olearia axillaris* and the succulent plants.

The stable dunes on the islands and on parts of the mainland support a dense growth of tall scrub or scrub. This grades shoreward into the low scrub of the recently colonised dunes or the scattered prostrate plants of the tops of the exposed limestone cliffs.

On Rottnest Island and on parts of the mainland coast the limestone comes very near to the surface and such areas are characterised by *Templetonia retusa* and *Thomasia cognata*. *Templetonia retusa* does not occur on Garden Island although there are many places where it would be expected.

Having established that the species distribution within any one area is dependent on habitat, it remains to explain the overall distribution of species, and for the explanation it is necessary to use palaeo-geographical evidence. It has been suggested (Fairbridge 1948) that the whole of the continental shelf became dry land during the period corresponding to the Würm exposure of Europe. This would allow large areas of aeolianite to accumulate and so for a short time coastal conditions extended far beyond the present shoreline allowing migration of typical coastal species. In the ensuing period towards the close of the Pleistocene, the level of the sea rose gradually, the higher parts of the aeolianite being cut off from the mainland. This explains why some of the same species are found on all the islands and the mainland, although there are anomalies such as the absence of *Melaleuca pubescens* on the coast adjacent to the islands.

The absence from the islands of such characteristic Australian families as the Proteaceae and Xanthorrhoeaceae and many of the Myrtaceae is at first sight very striking. However, it is evident that these families are not found on the mainland where conditions approximate to those on the islands. The vegetation development under similar conditions in these two areas is substantially the same and it is the environment rather than isolation which has restricted migration.

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Appendix I

Distribution of Plant Species on the Coastal Islands

	Rottnest Island	Garden Island	Carnac Island
Cupressaceae			
Callitris robusta (R.Br.) Mirb.	x	x	
Typhaceae			
Typha angustifolia Linn.		x	

Appendix 1—*continued.*

	Rottnest Island	Garden Island	Carnac Island
Gramineae			
Spinifex hirsutus Labill.	x	x	
Spinifex longifolius R.Br.	x	x	x
Stipa variabilis Hughes	x	x	
Polypogon maritimus Willd.	x		
Polypogon monspeliensis (L.) Desf.	x		
**Avena fatua* Linn.	x	x	x
Poa annua Linn.	x	x	
**Poa caespitosa* Forst.	x	x	
**Bromus gussonii* Parl.	x	x	x
Cyperaceae			
Scirpus antarcticus Linn.		x	
Scirpus nodosus Rottb.	x	x	x
Lepidosperma gladiatum Labill.	x	x	x
Lepidosperma squamatum Labill.	x	x	
Gahnia trifida Labill.	x		
Liliaceae			
Thysanotus patersoni R.Br.	x	x	
**Asphodelus fistulous* Linn.	x	x	
Asparagus asparagoides Wight		x	
**Anthericum divaricatum* Jacq.	x	x	
Dianella revoluta R.Br.	x	x	
Acanthocarpus preissii Lehm.	x	x	
Amaryllidaceae			
Conostylis candicans Endl.	x	x	
Orchidaceae			
Eriochilus tenuis Lindl.		x	
Urticaceae			
Parietaria debilis Forst.		x	
Santalaceae			
Exorcarpus aphylla R.Br.	x	x	
Leptomeria preissiana (Miq.) D.C.	x	x	
Loranthaceae			
Loranthus miraculocus (Miq.) var. *melaleucae* (Tate) Blakely		x	
Polygonaceae			
**Emex australis* Steinh.	x	x	
Chenopodiaceae			
Rhagodia baccata (Labill.) Miq.	x	x	x
Atriplex isitidia Miq.	x	x	x
Atriplex paludosa R.Br.	x		
Salsola kali Linn.	x	x	x
Salicornia blackiana Ulbrich.	x	x	x
Arthrocnemum bidens Nees.	x		
Enchylaena tomentosa R.Br.	x	x	x
Suaeda maritima (R.Br.) Miq.	x	x	x
**Chenopodium murale* Linn	x	x	
Aizoaceae			
**Tetrogonia zeheri* Fenzl. ex Harv. et Sond.	x	x	x
Tetragonia implexicoma (Miq.) Hook.	x	x	x
Carpobrotus aequilaterus N.E.Br.	x	x	x
Cryophytum crystallinum (L.) N.E.Br.	x		
Raunculaceae			
Clematis microphylla D.C.	x	x	x
Lauraceae			
Cassytha glabella R.Br.	x	x	
Cruciferae			
Cakile maritima Scop.	x	x	x
Pittosporaceae			
Pittosporum phillyraeoides D.C.	x	x	
Mimosaceae			
Acacia rostellifera Benth. ...	x	x	x
Acacia heteroclita Meissn.	x	x	
Acacia cyclopis A. Cunn.		x	x
Acacia cyanophylla Lindl.	x	x	
Acacia cuneata A. Cunn.	x		

Appendix 1—*continued.*

	Rottnest Island	Garden Island	Carnac Island
Papilionaceae			
Hardenbergia comptoniana R.Br.	x	x	
Templetonia retusa R.Br.	x		
Geraniaceae			
Geranium pilosum Forst.	x	x	
Pelargonium australe Wild.	x	x	x
**Erodium cicutarium* (L.) L'Her.	x	x	
Zygophyllaceae			
Nitraria schoberi Linn.	x	x	x
Rutaceae			
Boronia alata Smith	x	x	
Diplolaena dampieri Desf.	x	x	
Polygalaceae			
Comesperma integerrimum Endl		x	
Comesperma confertum Labill.		x	
Euphorbiaceae			
Phyllanthus calycinus Labill. ..	x	x	
**Euphorbia drummondii* Boiss	x	x	
**Ricinus communis* Linn.			
Beyeria viscosa (Labill.) Miq.	x		
Stackhousiaceae			
Stackhousia pubescens A. Rich.	x		
Sapindaceae			
Dodonaea aptera Miq.	x		
Rhamnaceae			
Spyridium globulosum (Labill.) Benth.	x	x	x
Sterculiaceae			
Lasiopetalum angustifolium W. V. Fitz.		x	
Guichenotia ledifolia J. Gray	x	x	
Thomasia cognata Steud. ...	x	x	
Frankeniaceae			
Frankenia pauciflora D.C.	x	x	x
Myrtaceae			
Melaleuca pubescens Schau.	x	x	
Melaleuca huegelii Endl.	x	x	
Onagraceae			
Epilobium glabellum Forst.		x	
Umbelliferae			
Didiscus pilosus Benth.		x	
Didiscus coeruleus D.C.	x	x	
Epacridaceae			
Leucopogon richei (Labill.) R.Br.	x	x	
Leucopogon racemulosus R.Br.	x	x	
Acrotriche ovalifolia R.Br.	x	x	

Appendix 1—*continued.*

	Rottnest Island	Garden Island	Carnac Island
Gentianaceae			
Erythraea centaurium Pers.	x	x	x
Primulaceae			
**Anagallis arvensis* Linn.	x	x	x
Samolus repens (Forst.) Pers.	x	x	
Apocynanceae			
Alyxia buxifolia R.Br.	x	x	
Convolvulaceae			
Wilsonia humilis R.Br.	x		
Wilsonia backhousii Hook.	x	x	
Labiatae			
Westringia rigida R.Br.	x	x	
Solanaceae			
Solanum nigrum Linn.	x	x	x
Solanum simile F. Muell.	x	x	
Scrophulariaceae			
Dischisma capitatum (Thunb.) Chois.	x	x	
Orobanchaceae			
Orobanche australiana F. Muell.	x	x	x
Myoporaceae			
Myoporum insulare R.Br.	x	x	
Myoporum viscosum R.Br.	x		
Eremophila brownii F. Muell.	x	x	
Lobeliaceae			
Lobelia tenuior R.Br.	x	x	
Goodeniaceae			
Scaevola crassifolia Labill.	x	x	x
Compositae			
Olearia axillaris (D.C.) F. Muell.	x	x	x
Senecio lautus Soland. ..	x	x	x
Calocephalus brownii (Cass) F. Muell.	x	x	x
**Arctotheca nivea* (Less) Leeuwin	x	x	
**Cryptostemma calendulaceum* (Linn.) R.Br. ...	x	x	
Athrixia pulverulenta (Lindl.) Druce		x	
**Hypochaeris glabra* Linn.	x	x	
**Sonchus asper* Hill	x	x	x
**Sonchus oleraceus* Linn.	x	x	x
**Tripteris clandestina* Less.	x	x	x
**Erigeron crispens* Ponnet	x	x	
**Angianthus humifusus* (Labill.) Benth		x	
Angianthus cunninghamii (D.C.) Benth.	x	x	x
**Inula graveolens* Desf.	x		

* Introduced species.

Appendix II

Climatological Data, Rottnest Island, W.A.

	Jan.	Feb.	Mar.	Apl.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.	Year.
Absolute Max. Temp. °F.	101·0	99·0	93·0	87·0	78·5	72·4	69·6	71·4	80·0	88·0	92·2	97·4	101·0
Mean Max. Temp. °F.	78·2	78·8	76·6	73·5	68·0	64·1	62·4	63·0	64·8	67·2	72·0	75·4	70·1
Mean Temp.	71·6	72·2	60·4	67·5	62·9	59·6	57·8	58·1	59·5	61·6	65·8	69·1	64·6
Mean Min. Temp. °F.	64·9	65·5	64·1	61·6	57·9	55·1	53·2	53·1	54·2	55·8	59·5	62·8	59·0
Absolute Min. Temp. °F. ..	56·0	55·0	53·8	51·5	48·2	45·8	45·0	44·0	46·0	48·0	50·0	54·0	44·0
Mean Daily Range	13·3	13·3	12·5	11·9	10·1	9·0	9·2	9·2	10·6	11·4	12·5	12·6	11·4
Rel. Hum., 9 a.m. (%)	63	63	67	69	73	76	76	74	73	70	66	63	70
Rel. Hum., 3 p.m. (%)	64	64	65	64	67	69	70	68	69	67	66	65	67
Cloud, 9 a.m. (tenths) ...	3·7	4·0	4·4	5·1	6·0	6·4	6·2	6·0	5·7	5·5	4·8	4·1	5·2
Cloud, 3 p.m. (tenths) ..	3·3	3·7	4·0	4·9	5·9	6·3	6·2	5·8	5·5	5·1	4·2	3·5	4·8
Mean Sat. Deficit (ins. Hg)	0·289	0·285	0·229	0·202	0·152	0·124	0·117	0·126	0·142	0·176	0·223	0·271	0·195
Rainfall (ins.)	0·23	0·38	0·56	1·44	4·40	6·49	5·99	4·42	2·56	1·51	0·56	0·38	28·89
Wet Days (No.)	2·2	1·8	5·6	9·1	13·6	19·3	22·0	16·8	15·0	11·1	6·9	5·6	129
Effectiveness (Est.)	0·3	0·5	0·6	1·9	7·1	11·9	11·2	7·9	4·6	2·5	0·9	0·5	49·5
Evapo-transpiration (Est.)	4·66	4·02	3·91	2·98	2·25	1·68	1·52	1·66	1·94	2·57	3·40	4·13	34·72

TABLE I.

Chemical Properties of Garden Island Soils

Profile No.*	Depth (ins.).	pH.	Percentage $CaCO_3$.	Percentage NaCl.	Percentage Total Soluble Salts.	Percentage Total Organic Carbon.	Percentage Total Nitrogen.	C/N.
1	A_0	7·4	23·5	0·012	0·09	26·8	1·46	18·4
	0– 2	7·9	59·2	0·008	0·06	13·6	0·58	23·4
	2– 9	8·2	75·5	0·008	0·04	2·9	0·19	15·2
	9–19	8·4	78·3	0·002	0·04	1·9	0·15	12·7
	19–32	8·4	82·9	0·006	0·04	1·9	0·08	23·8
2	A_0	7·2	41·7	0·010	0·09	21·8	0·94	23·2
	0– 9	8·3	76·8	0·006	0·04	3·5	0·18	19·5
	9–18	8·5	85·3	0·004	0·04	1·0	0·09	11·1
	18–30	8·6	88·7	0·006	0·03	0·6	0·03	20·0
3	0–4	8·3	85·5	0·002	0·04	3·6	0·19	25·3
	4–11	8·5	88·7	0·002	0·03	1·4	0·07	20·0
	11–29	8·6	90·0	0·002	0·02	1·2	n.d.	—
4	0– 8	8·2	69·8	0·010	0·05	4·6	0·40	11·5

* 1 Soil under *Acacia rostellifera* association.

2 Soil under *Callitris robusta* association.

3 Soil under *Melaleuca huegelii* association.

4 Shallow soil on limestone. Seasonal vegetation.

7.—Notes on the Geology of the Carnarvon (Northwest) Basin, Western Australia

By Curt Teichert*

Manuscript received—20th March, 1956.

Because of recent oil finds, the Carnarvon Basin, otherwise known as Northwest Basin, so named by A. Gibb Maitland in 1901, occupies a position of paramount importance among the major sedimentary basins in Australia. To exploit its possibilities detailed knowledge of its stratigraphy and structure is a necessity. The first comprehensive report on the geology of the Carnarvon Basin, since Raggatt's studies in 1936, has recently been published by Condon (1954) and the following comments on and corrections to this report are offered in an endeavour to clarify parts of the stratigraphy and to point out alternative structural interpretations.

Palaeontological Zoning

On p. 71, Condon lists a fossil assemblage from the Bulgadoo shale in which *Calceolispongia barrabiddiensis* and *C. acuminata* are included, together with *Pseudoschistoceras simile*. It should be noted that these two species of *Calceolispongia* are rather widely separated stratigraphically. *C. acuminata* is restricted to the top of the Bulgadoo Shale although its occurrence is probably slightly lower than indicated in a previous diagram (Teichert, 1949, pl. 26). *C. barrabiddiensis* occurs with *Pseudoschistoceras simile* in the Barrabiddy member (Teichert, 1952) of the Bulgadoo Shale, about 2,100 feet below the top of the formations. The two species of *Calceolispongia* characterize different palaeontological zones, which are at least 1,500 feet apart stratigraphically.

The most characteristic fossil of the Quinnanie Shale (p. 75-78) is *Hyperamminoides acicula* Parr which occurs in great quantities at the type locality and in all outcrop belts of the formation in the fault blocks to the east of Wandagee Hill. Everywhere these foraminifera can be washed in huge numbers out of the shales or their residual soils. Condon does not mention the occurrence of this fossil.

The measured section of the type Wandagee Formation (p. 79-80) gives an inadequate picture of the palaeontological zonation of this formation which has been carried out in great detail. It is impossible to repeat here the details which have been given elsewhere (Teichert, 1952). On p. 80 Condon mentions 66 feet of medium-hard grey quartz greywacke etc. from which he lists *Calceolispongia elegantula* and *C. multiformis*. These two crinoid species are excellent index fossils, but they do not occur together. *C. elegantula* is abundant in and very characteristic of the lowermost 80 feet of the Wandagee Formation (from which it is not listed by Condon); *C. multiformis* is restricted to beds 165-185 feet above the base of the formation. The position of the bed from which Condon lists these two species is at 102-162 feet above the base of the formation. It has been noted before (Teichert, 1949, p. 77, pl. 15 figs. 16-21) that some basal plates of *C. multiformis* resemble *C. elegantula*, but care should be taken in distinguishing the two species. This is always possible if comprehensive collections are available.

Stratigraphy

It is difficult from Condon's paper to obtain a clear picture of the relationships of the Norton and Nalbia Greywackes and the Baker Formation. Since I am personally responsible only for the Nalbia "Greywacke," I shall restrict my remarks to that formation. As it appears that Condon has had difficulties in tracing the formation outside the type section, 0.9 mile west of Quinnanie corner, the following notes on its distribution may be helpful: at the type section, the strike of the Nalbia Sandstone is N 20° W and it can be followed in this direction for approximately 1 mile until it is cut off by north-south striking fault. The same formation outcrops again in the next fault block to the west where its bottom crosses the south fence of Coolkilya Paddock 1,540 yards from the place where the top of the formation crosses the fence further east. This is on the east flank of the "Coolkilya syncline," the axis of which strikes N 10° W with a slight northerly plunge. The Nalbia Sandstone can be followed around the greater part of this syncline whose center is filled with rocks of the Coolkilya Formation. 450 yards south of the fence, in Woollies Paddock, the Nalbia Sandstone swings around the southern nose of the syncline. The northern part of the syncline is partly covered with dune sand. South of this sand area the total traceable outcrop belt of the Nalbia Sandstone is at least 4.5 miles long. There are also some outcrops of it to the north of the sand area and south of an important cross-fault, striking N 60° E, which cuts off the Coolkilya syncline on the north. All over this area the Nalbia Sandstone retains not

*Denver, Colorado.

Plate 1.—Oblique aerial view of the highly faulted area south of Minilya River in the vicinity of Wandagee Hill, taken fro
15,000 feet, looking due north. (West Aust. Trimet Run 207, 81 R). The Minilya River is seen in the upper part of pictur
a sand plain extends to the north of it. Drainage channel in middle of picture flows into Cundy Dam, drainage chann
in foreground into Mungadan Dam.

Indicated by back circles O:
1 Wandagee Homestead,
2 Mouribandy Dam,
3 Wandagee Wool Shed.

Indicated by △: Wandagee Hill Trig. Station.
Entire lines: formational boundaries.
Dashed lines: faults.
m—Mungadan Sandstone
c—Coolkilya Sanstone
n—Nalbia Sandstone
w—Wandagee Formation
q—Quinnanie Shale
d—Cundlego Sandstone
b—Bulgadoo Shale
G—Gypsum

Note that most faults in the Permian are broadly arcuate, the convex side of the arc facing west. These are th
east-dipping, normal antithetic faults. The fault in the west that separates Cretaceous from Permian rocks is a steeply west
dipping normal fault.

The syncline to the north of Wandagee Hill has been referred to as "Coolkilya syncline" in this and previous publications.

The cross-section Fig. 1 runs E-W almost exactly through the middle of the photograph. Alluvial formations are not
indicated.

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only its lithological characteristics, but also its palaeontological features with a rich *Schizodus-Oriocrassatella* assemblage in the lower part and abundant *Cleiothyridina* near the top.

North of the Minilya River the Nalbia Sandstone outcrops in the syncline whose axis intersects the north bank of the river 650 yards north-east of Curdamuda Well. Outcrops of the Nalbia Sandstone, here unfossiliferous, are restricted to a narrow belt on the north side of the river.

Excellent outcrops of the Nalbia Sandstone are also found further south in Woollics Paddock. The belt of Nalbia Sandstone begins a little over 600 yards N 20° E of Wandagee Wool Shed where the beds strike 85°, dipping 30° S. The formation can be followed in a straight line along the strike for 1600 yards to a position just inside Dry Paddock where it is cut off by the major fault which runs along the west side of Wandagee Hill. In this outcrop belt both the lower pelecypod zone, and the upper *Cleiothyridina* zone are well developed.

Further south the characteristic pelecypod assemblage disappears but the *Cleiothyridina* zone is well recognizable around the nose of a little north-plunging anticline 1,600 yards south of Wandagee Wool Shed on the road to Mungadan Dam. This is close to the Cretaceous boundary fault and from here the Nalbia Sandstone can be followed first in a south-easterly direction, then swinging around the southern nose of the north-plunging syncline which lies west of Wandagee Hill.

East of Wandagee Hill, the Nalbia Sandstone becomes unfossiliferous, but retains its characteristic lithology. It occurs in two fault blocks which are separated by a curved east-dipping normal fault. The western-most of these blocks includes Wandagee Hill itself. The Nalbia Sandstone emerges from underneath a Pleistocene talus stream at a place 1,650 yards N 30° E of Wandagee Hill Trig. Station. It swings around Wandagee Hill in a wide, almost circular arc, and it is cut off by a fault 3,250 yards S 20° E of the same Trig. Station. About half way down the outcrop belt approaches to within 40 or 50 yards of the eastern boundary of Mungadan Paddock, but does not cross into Nalbia Paddock. The outcrop belt in Nalbia Paddock belongs to another fault block. On a bearing due east of Wandagee Hill Trig. Station, this belt lies at a distance of 2,900 yards from the latter and strikes about N 20° W, dipping west. To the north, the strike swings further west; to the south, it swings almost into a north-south direction. Total length of the outcrop belt is nearly 2 miles. On both ends, it terminates against the same curved fault which separates this block from the one to the west. On the whole, I should say that it would be difficult, if not impossible, in the closely faulted area east and north of Wandagee Hill, to map the Nalbia Sandstone from aerial photographs. Condon seems to have confused the Nalbia Sandstone with his "Norton Greywacke" and "Baker Formation." The type localities of these two formations are situated 30 to 40 miles from that of the Nalbia Sandstone and there is, as far as I know, no continuity of outcrops over the intervening area. Correlation between the northern Kennedy Range and the Wandagee area can only be established by means of close palaeontological control which has received little attention in Condon's report. Since Condon refers to a small outcrop area of the Norton Greywacke in the syncline north of the Minilya River " 9 miles west of Wandagee Homestead" (=650 yards north-east of Curdamuda Well, see above), there seems to be no question that in the Wandagee area he applied that name to the unfossiliferous or less fossiliferous facies of the Nalbia Sandstone.

This conclusion is also supported by his references to the heavy mineral work by Higgins and Carroll (1940). According to Condon, Higgins and Carroll's samples 1, 3 and 5 come from the Norton Greywacke. I collected these samples myself and to the best of my recollection, sample 3 comes from the Nalbia Sandstone, samples 1 and 5 come from somewhat higher beds, namely from the "*Fenestella* nodule beds" of the Coolkilya Formation. It should be remembered that Higgins and Carroll showed that there is no striking variation in heavy mineral amounts in the sequence below the "Wandagee Hill beds" (Mungadan Sandstone of present nomenclature) and that heavy minerals, therefore, offer little support in the correlation of these lower beds.

While it thus seems certain that "Norton Greywacke" is a synonym of the Nalbia Sandstone, perhaps including the lowest part of the Coolkilya Formation, it is more difficult to be sure which beds in the Wandagee area Condon correlates with the Baker Formation of the Kennedy Range. He says it overlies the "Norton Greywacke" which I have shown to be essentially identical with the Nalbia Sandstone. It would then seem that the Baker Formation corresponds to the lowest part of my Coolkilya Formation. However, this is characterized everywhere in the Wandagee area by light-grey weathering calcareous sandstone nodules with many specimens of *Fenestella*. Of these, there is no mention in Condon's report. In the Coolkilya syncline *Helicoprion*, together with *Propinacoceras*, *Paragastrioceras* and *Pseudogastrioceras*, was found just above the *Fenestella* nodule beds, but Condon (p. 87) refers the beds with these fossils to the Nalbia "Greywacke." Part of Condon's Nalbia "Greywacke" is thus older, part younger than the "Baker Formation." Apparently, there is something wrong with this correlation and further work is needed. If possible, this should be carried out mainly on the ground. If no continuity of outcrops can be established between the Kennedy Range and the Wandagee area, it would be better to apply a separate nomenclature to the two areas, unless correlations can be made beyond reasonable doubt.

On p. 97, Condon states that "the boundary between the Coolkilya Sandstone and the Mungadan Sandstone defined by Teichert (1952), is not a main lithological boundary" and he, therefore, proposes to revise the definition of these two formations. However, after reading his description of the upper part of the Coolkilya Sandstone in its type locality east of Wandagee Hill, I have little doubt that Condon's and my upper boundaries of this formation are the same. The top unit in Condon's section is "2 feet of hard red-brown ferruginous coarse-grained quartz greywacke, with interior and exterior moulds of spiriferids, pectenids and *Oriocrassatella*." There are actually two such red-brown horizons (which I had called "dark purple") only a few feet apart. The two can be followed all around the east side of Wandagee Hill and I chose them as markers for the top of the Coolkilya Sandstone (Teichert, 1952). In earlier papers (Teichert, 1949) this horizon had been called the top of the *"Linoproductus* beds of the Wandagee Series." There is thus no discrepancy between Condon's and my interpretation of the boundary between the Coolkilya "Greywacke" and the Mungadan Sandstone. Condon, however, omits to mention that the uppermost "red-brown" horizon with *Oriocrassatella* also marks the last occurrence of *Calceolispongia robusta*, an important index fossil of the Coolkilya Formation. Important members of the fauna of the latter are *Agathiceras*, *Pseudogastrioceras* and *Dictyoclostus*, all of which mark horizons in the upper part of the formation. On p. 94, Condon lists *Calceolispongia cf. rotundata* from the Mungadan Sandstone in a section in the Kennedy Range. That species, however, is restricted to the lower 165 feet of the Wandagee Formation, and, if correctly identified, suggests correlation of the beds in question with the Wandagee rather than the Coolkilya Formation.

Peculiarly, Condon has entirely omitted mention of the calcareous eolianites (or "coastal limestones") of Pleistocene, most probably Würm, age. These rocks are widespread along the coast north of Warroora as far as the vicinity of Cardabia Homestead. They are quite similar to the same formations well known elsewhere from Western Australia (see various joint and individual papers by Fairbridge and by Teichert) and their study is important for the interpretation of the late Quaternary history of the area. At Point Anderson, 6 miles south of Maud Landing, there are clearly two generations of eolianite, each topped by a travertinized layer which here takes the place of the rendzina soils developed between successive dune generations in more southerly latitudes (Fairbridge and Teichert, 1953). The fact that the earliest visible eolianite is now partly submerged, presents evidence for a comparatively recent rise in sea-level. From analogy with conditions in the south this rise should be post-Würm.

Structure

Condon's discussion of the fault mechanics of the Carnarvon basin (pp. 135-138) is interesting, but his interpretation is not supported by the facts, at least not in those parts of the basin known to me. I shall restrict my discussion to Condon's section C-D on Plate 2, part of which is here reproduced as fig. 1A. The position of this section virtually coincides with that of one published by Clarke, Prider and Teichert (1944, p. 94) which was based on the present writer's at that time unpublished data, and to which Condon does not refer. In comparing such sections, and the interpretation they represent, it must be borne in mind that the faults themselves are rarely exposed. Their presence can be discovered by mapping, but their dips can, in most cases, only be inferred from general considerations. Condon believes that almost all faults in the Carnarvon basin are reversed or thrust faults and since (p. 138) he bases important economic conclusions on this interpretation, the matter is of more than theoretical interest. Condon himself records "a marked absence within the sediments of evidence of compression such as compressional joint systems, cleavage and drag-folds," but believes that this can be explained by assuming that "the stress which caused the faulting was carried mainly by the pre-Cambrian basement and that the faults in the sediments result from the faulting of the basement." Nevertheless, if there is upthrust in the basement, at least some of the usual manifestations of thrust-faulting should be discoverable in the sedimentary mantle here and there.

However, to say that evidence of compression is lacking is definitely an understatement, because wherever faulting is observed along the section here discussed, the evidence for tensional stresses is overwhelming. These are of three kinds: (1) abundance of calcitic veins as fillings of tension gashes everywhere near faults; (2) occurrence of wide tension rifts filled with secondary gypsum; and (3) the scattering of small blocks of sediments in random orientations along fault zones. The latter show no signs of crushing by compression such as one might expect along thrust-faults, but are simply blocks that have slumped into cracks opened up by faulting. Gypsum zones along faults are well developed and most easily observed in the following places: In Nalbia Paddock of Wandagee Station there is a gypsum belt whose southern end lies 2,250 yards almost due east of the Trig. Station on Wandagee Hill. From here it runs almost due north for about 1,500 yards, then swinging gradually into a more north-easterly direction. Its total length is over 1.5 miles and its greatest width at least 100 yards. The throw of this fault at the southern end of the gypsum belt is about 1,000 feet, decreasing towards the north. In 1940 and 1941, a large, widely visible eucalypt tree ("white gum" or "river gum") grew in the middle of this belt. If the tree is still there, the place should be easy to find.

Another narrower and longer gypsum belt is found in Dry and Coolkilya Paddocks on Wandagee Station. It crosses the fence between the two paddocks at 2,200 yards west of Quinnanie Corner, where it strikes almost due north and is about 50 feet wide. Southward it can be followed for about 0.5 mile until it disappears under alluvial cover. To the north, it extends at least 1.5 miles and marks a somewhat oblique fault along which first Coolkilya Formation, then Nalbia Sandstone, are cut off. To the west of the fault are flats underlain by Quinnanie Shale characterized by abundant *Hyperamminoides* (see above). The throw of the fault where it crosses the fence is approximately 1,200 feet.

These are two outstanding examples, but gypsum is found along fault zones elsewhere in the area.

Good surface evidence for east-dipping normal faults is found along the section line (Fig. 1) about halfway between Wandagee Hill and Williambury where, at Trig. Station K55 and to the east thereof, it intersects three fault

PLATE 2.—Oblique aerial view along east coast of Salt Lake (or "Salt Marsh"), taken from 15,000 feet, looking due south from point above upper part of lake. (West Australian Trimet Run 205, 66 R, 10). From lower left through centre of picture trends Chirrida anticline with 12-ft. terrace along its entire western flank. Note weakly incised consequent drainage on both flanks of anticline. The small, early Recent deltas on the terrace are not recognizable from this altitude, but the newer Recent deltas in front of the terrace are clearly visible.

Headland in upper right of picture is Sandy Bluff. The first river to the left (east) of it is the Minilya River; the next river is Barrabiddy Creek.

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blocks consisting of Callytharra Limestone and Wooramel Sandstone. These fault blocks form gently inclined west-sloping cuestas in which the hard Wooramel Sandstone has protected the softer Callytharra limestones and shales which form steep east-facing cliffs. At least near K 55 itself, and at the escarpment in the next block to the east, the faults (which are not exposed) must be situated quite close to the base of the escarpments. I have visited both localities several times and examined the rocks in detail. I am sure that there is no sign of upthrusting along these escarpments and that, as indeed one might expect, the cuestas owe their existence to a westward tilt of the fault blocks, along normal faults on both sides.

Fig. 1B shows the structures which one would expect to find along the selected section if the hypothesis of thrust-faulting were correct. Although I am familiar with the detailed geology around all the faults shown in this section, I have never seen any field evidence suggesting structures of this kind. On the contrary, all the evidence, circumstantial and observational, supports the assumption of normal faults.

Fig. 1C shows how the structures can be interpreted as the result of normal faulting. There are some normal west dipping faults, the only major one probably in the Precambrian to the east. The dominating pattern is that of a set of antithetic, east-dipping adjustment faults (Teichert, 1948, 1952).

Antithetic faults were named and discussed by Cloos (1928), although they were well known before. They are due to rotational movements of fault blocks during which each block carries out a rotating movement around its centre of gravity. Such movements result from tension fracturing of sedimentary table lands, especially in wide flexure zones, if part of the sedimentary table is elevated. In such a situation, the stresses normally lead to formation of a small number of major faults which dip in the direction of the regional structural dip and are therefore called *homothetic* by Cloos, combined with a system of numerous faults which dip against the regional dip (hence, *antithetic*) and which assist in the release of tensional stresses. Such fault systems have been reproduced experimentally (Cloos, 1932) and they occur widely in nature (Cloos, 1936, pp. 226-269), particularly along continental margins (Cloos, 1939, p. 504). Generally the plane of the antithetic fault lies approximately at right angles to the plane of the beds of the respective fault block, or it may be slightly more gently inclined. In the faulted country between Wandagee Hill and Williambury, the prevailing dips of strata are between 20° and 25° west. The faults, separating the fault blocks, may therefore be expected to dip 65° to 70° east, but their dips may be as low as 50°. The entire fault pattern is due to uplift of the Precambrian basement in the east.

There is no good evidence to suggest where exactly the coast was situated during Devonian, Carboniferous and Permian time, except that it must have been well to the east of the present easternmost distribution of Palaeozoic rocks, that is, well inside of what is now the Western Australian Precambrian shield. In Palaeozoic times, the present shield margin formed part of the subsiding basement on which thick sedimentary series accumulated. In post-Palaeozoic times, the marginal sedimentation area was uplifted and its basement became part of the shield.

The overall regional rise of the Precambrian basement from the coast to the present edge of the Western Australian shield is of the order of 200 to 250 feet per mile. In other words, there is an overall seaward dip of the surface of the Precambrian of approximately 2°. The tensional stresses created by the uplift of the shield were released in the manner here suggested, by a few widely spaced west-dipping normal faults, and a system of numerous more closely spaced east-dipping antithetic faults.

The age of the main uplift which caused this structure pattern is pre-Cretaceous, because the Cretaceous transgresses over a faulted Palaeozoic basement. In places there has been some post-Cretaceous faulting, probably caused by continued uplift of the shield. The post-Cretaceous fault west of Wandagee Hill is a normal west-dipping fault which is possibly posthumous to a pre-Cretaceous antithetic east-dipping one. The possibility should be kept in mind that the pre-Cretaceous tensional fault pattern which is visible on the surface east of Wandagee Hill, continues westward below the infra-Cretaceous unconformity. This possibility has not been indicated on the sections Fig. 1A-C.

Discussing the oil possibilities of the Carnarvon Basin, Condon suggests that the thrust faults which he believes to exist in the basin "may provide adequate structural closure in some cases" (p. 154). Our interpretation affords no basis for such optimism. Antithetic tension faults will facilitate the escape of hydrocarbons. The search for oil in the Carnarvon basin must, therefore, be restricted to anticlinal structures and to structural and stratigraphic traps below the Cretaceous-Permian unconformity. It will be of the utmost practical importance to determine the exact age of the dislocations of the Palaeozoic rocks. The longer the interval between this tectonic episode and the Lower Cretaceous transgression, the greater the chances for Palaeozoic oil having escaped before it could be trapped.

Age of the Anticlinal Structures

In the western part of the basin occur a number of remarkable anticlines and domal structures all of which have been named and briefly described by Condon. He attributes their origin to upthrusts in the basement and for some of the major anticlines, such as Cape Range and Giralia, he states evidence for a two-stage uplift, both of which occurred after the deposition of the Miocene Trealla Limestone, and before the Pleistocene. Essentially then the formation of these, and by implication of all other anticlines is held to be epi-Miocene to Pliocene in age. While I find myself in basic agreement with these conclusions I believe that it is possible to demonstrate that the uplift of some anticlines took place later, or at least continued into post-Pliocene times.

Condon describes the occurrence of marine shell deposits in the vicinity of the Salt Lake to heights of 20-25 feet above present lake bottom. He does not, however, mention the presence of the remarkable terrace which is cut into

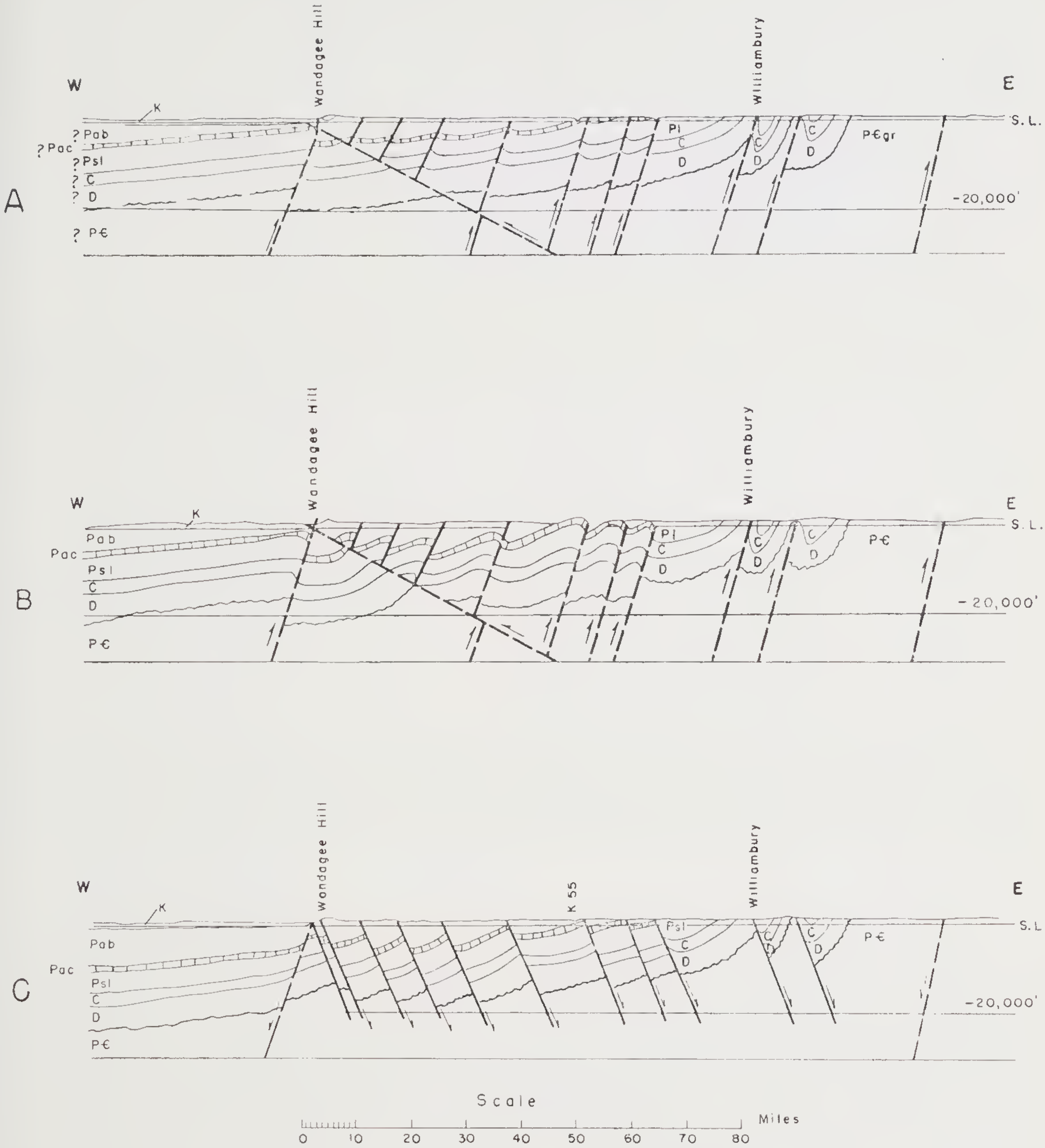

FIG. 1.—A, part of section C-D in Condon, 1954, Pl. 2. B, same section showing fictitious structures which would be in accordance with the interpretation of thrust-faulting, but which are not found in nature. C, same section showing interpretation of structures as an antithetic fault pattern. D Devonian, C Carboniferous, Psl Permian Lyons Group, Pac Permian Callytharra Limestone, Pab Permian Byro Group, K Cretaceous. Vertical scale approximately 2½ times horizontal scale.

the west flanks of the antielines on the east side of this generally dry lake. This terrace may be studied especially well along the entire west side of the Chirrida antieline (see Plate 2), where it lies at 11-12 feet above lake bottom level and is about 100 yards wide. It consists of loose deposits, partly shell layers, and partly sand. It is now ineised by the many consequent streamlets whieh run off the west flank of the antieline. These little streams have eut narrow small eanyons into the limestone roof of the antieline and at the mouth of each eanyon a small deltaic fan ean be seen to rest on the terraee. These are the deltas which were made by the eonsequent streamlets at the time when the sea covered the terrace. They consist of limestone rubble mixed with shells. After sea-level subsided the streamlets eut through the deltas and into the underlying terraee.

At the north end of the Salt Lake, around the mouth of the Lyndon River, there is a river terrace, 12 feet above the river flat, whieh eonsists of red, brown, and partly gypseous sand. This terraee is partieularly well developed east of the Lyndon River where it is up to half a mile wide. It is in the same position, hence most probably of the same age as the terraee along the west side of Chirrida antieline.

What is the age of the terraee and its superimposed deltas? The height of 11-12 feet above lake bottom as well as the remarkable persisteney of the feature immediately suggest eorrelation with the 10-ft. beneh which has been so widely recognized in the southwestern part of Western Australia (see Teichert, 1947, 1950; Fairbridge, 1950; Fairbridge and Teiehert, 1953; and other papers by the same authors) and the age of which is regarded as early Reeent. This dating is supported by the youthful appearance of the terrace and its deltas. The small size of the latter would suggest that they represent a comparatively short span of time.

The position of the terrace poses some interesting problems. Condon stated (p. 125) that the present lake bottom is very elose to ordinary high tide level, but more reeent surveys by Ray Geophysies (Aust.) Pty. (kindly supplied by W.A. Petroleum Pty. Ltd. through eourtesy of Professor R. T. Prider) have shown that along the Chirrida anticline the level of the lake bottom lies approximately 2 feet below mean sea-level. The tides along the coast near Carnarvon are somewhat variable, but spring range is about 4 feet (Hodgkin, 1957). The lake bottom along its eastern coast is therefore now situated at about low water springs. The surface of the terrace along the west side of Chirrida anticline must have been formed somewhere between low water and mean sea-level and it is thus apparent that little if any movement of this anticline has occurred since the mid-Recent drop of sea-level, that is during the last 3,000 or 4,000 years. Conditions along other antielines might well be different. The study of features attributable to Late Quaternary sea-level movements, partieularly the 10-ft. beneh, may well be helpful in the analysis of young movements in this eoastal belt. Where its present level deviates appreciably from 10 ft. above Low Water it could be dedueed with great confidenee that very young movements have taken plaee. In the ease of Chirrida antieline the small amount of erosion which took plaee prior to and during the formation of the 12-ft. terrace seems to indieate a very young age of this struetural feature whieh, I think, must have eome into existence during the Pleistoeene. There has apparently been no measurable movement sinee early Reeent time.

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