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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 (enterotoxaemia), 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 oestrogen 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 in 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 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 contracted 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 30 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 southeast of Calicut. "Cunning 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 valleys 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 lapaidea 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 culu). 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 "steinithon" 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, serpentic 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 greenish 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 tawn 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 Anguda-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 elements 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 the privilege of studying the laterite in 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 of quartz and feldspar in the dikes. As late as 1930, the iron and manganese were usually found in the form of haematite, ilmenite, and magnetite, respectively. The oxidation of the haematite by the air produced ferric oxide, which, together with the iron oxide, formed the laterite mass.

As time went on, the authors showed that the laterite mass was composed of a large number of minerals, such as quartz, feldspar, mica, and chlorite. These minerals were further studied and their composition and structure were determined. The laterite mass was found to be composed of a mixture of primary and secondary minerals, with the primary minerals being the remnants of the original rocks and the secondary minerals being the products of weathering.

In the early 20th Century, the use of microscopes and other instruments allowed for a more detailed examination of the laterite mass. It was found that the laterite mass was composed of a mixture of primary and secondary minerals, with the primary minerals being the remnants of the original rocks and the secondary minerals being the products of weathering.

The laterite mass was found to be composed of a mixture of primary and secondary minerals, with the primary minerals being the remnants of the original rocks and the secondary minerals being the products of weathering. The secondary minerals were found to be composed of a mixture of iron oxide, aluminium oxide, and silica. The iron oxide was found to be concentrated in the form of haematite, ilmenite, and magnetite, respectively. The oxidation of the haematite by the air produced ferric oxide, which, together with the iron oxide, formed the laterite mass.
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 pisolitic 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 phenomenon of geological time 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 Kem-mangundi, 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>
<thead>
<tr>
<th>Table I</th>
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<tbody>
<tr>
<td>Laterite from Kemmangundi</td>
</tr>
<tr>
<td>Al₂O₃</td>
</tr>
<tr>
<td>Fe₂O₃</td>
</tr>
<tr>
<td>SiO₂</td>
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<tr>
<td>H₂O</td>
</tr>
<tr>
<td>CaO</td>
</tr>
<tr>
<td>MgO</td>
</tr>
<tr>
<td>TiO₂</td>
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</tbody>
</table>

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 Lamplough 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 adjectively.

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 100 feet; 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 200 feet.

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 1,000 feet 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 feet 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-quadrites 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 underlie much of the high level sand-plain country of the north-eastern and eastern wheat belt, the sandy soils of the elevated sand-plain 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 finely 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 rainwater falling on the surface above or higher up the slope. This is a purely concretionary laterite commonly styled "pisolithifer 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 pisolithifer 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

<table>
<thead>
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<th>Laterites from the Darling Range</th>
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<td>F₂O₃</td>
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<td>Cr₂O₃</td>
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Combined 100-00 100-43 100-15 100-50

Analyst: E.S.S.  F.S.S.  S.E.T.  R.T.P.
Date: 1901 1912 1947 1946

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 ilmenite.

Much of the limonite is probably goethite, but the presence of some lepidocrocite and magnhemite 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 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.

earlier slopes?

ferruginous crust

mottled zone

bleached zone

unaltered rock

Fig. 1.

This section has much to offer in enlightenment 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 kaolinitic clay.

The laterite has the typical composition of rocks of this group, using the term in the restricted 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 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
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 distinguishable from 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 relics 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 alkalies and alkaline 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 some of the structure from the dyke 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, quartzy 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 laterisation 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 oxides 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

| Thin grey sand, sandy loam, with limonitic concretions, laterite boulders, bare laterite masses. |
| Brown loam with dark purplish lumps or small round limonitic concretions. |
| Light brown, yellow or grey loam. |
| Brown loam, grey, reddish or light brown sandy loam or loamy sand over alluvium. |

Fig. 2(a). Unaltered granite, granitic gneiss, epidiorite, dolerite, meta-sediments, consolidated argillaceous sediments, etc.

As in Figure 2(a) above.

High level sandplains of grey and yellow sands and loamy sands with poorly to well developed illuvial horizon(s) of yellow to brown limonite-cemented argillaceous sandstone or concretions resembling laterite overlying more or less lithified argillaceous sands and sandy clays, and, rarely, conglomerate at base.

Granite, granitic gneiss, etc., weathered at contact with overlying sediments.

Fig. 2(b).

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.

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 sandplains. 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 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 surface, very similar to the "disintegration" type of nodule and apparently indistinguishable from them. In sandy loam soils 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 one 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 the Mineral Division outside office hours in order to carry out certain 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 Waltherius, 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*

Manuscript accepted—15th November, 1955

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 monzia and B. attenuata, Stirlingia latifolia, Hibbertia hypotricha, 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 dormancy in late summer. The moisture content of so 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 seasonal rains. Experiments to determine relative xerophytism have so far yielded inconclusive results owing to difficulties with water uptake by the cut-off leaves. Colateral studies on non-sclerophyllous shrubs which grow on the Perth coastal plain, indicate that a considerable degree of physiological diversity exists in the plants, 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, Erechtites hispidula maintained a high rate of transpiration in spring and in summer up to the time it died off.

*Department of Botany, University of Western Australia

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 (± 10 feet in height) down to shrubs (± 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:—

A6  Sparse litter
A1  0in.- 3in.—Grey sand with little organic matter
A2  3in.- 8in.—Light grey sand—becoming leached
8in.-60in.—Highly leached white sand
B1  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) Weimann 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 absorption, 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, Bossaeae, 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 tested) 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**

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<th>Time (min.)</th>
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<td>2-6</td>
<td>2-7</td>
<td>2-8</td>
<td>2-9</td>
<td>2-10</td>
<td>2-2</td>
<td>2-4</td>
<td>2-1</td>
</tr>
</tbody>
</table>

16
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 occurred, 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. Rouschul, 1938)] as mg./sq. cm. 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 Piche 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) coiled the expression Sub-lethal Deficit for this and Rovigno (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 Rouschul (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 repeated 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 Rouschul’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 of simplicity, 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.

\[
\begin{array}{c}
\text{Sub-lethal Deficit} - \text{Dried out water content} \\
\times (\pm 5\% \text{ cells dead}) \\
\times 100
\end{array}
\]

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: ethylene glycol 9: ethylene glycol 1, isobutyl alcohol: 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 cyanophyilla and Conostephus pandium 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**

<table>
<thead>
<tr>
<th></th>
<th>Banksia menziesii</th>
<th>Banksia attenuata</th>
<th>Stirlingia latifolia</th>
<th>Hibbertia hypericoides</th>
<th>Bossiaea eriocarpa</th>
<th>Eucalyptus calophylla</th>
<th>Eucalyptus marginata</th>
<th>Hardenbergia comptoniana</th>
<th>Kennedya prostrata</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thick and cutinized epidermis</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>Cover of thick hairs on lower surface of leaf</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Depression of stomata</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Small inter-cellular spaces</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Well-developed mechanical tissue</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Bilateral structure of leaves</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Reduction in size of leaves</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>High number of stomates per unit area (sq. mm.)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
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</tr>
</tbody>
</table>

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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 shallowly. Eragrostis 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 ease 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 occurred 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 normal 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. Re-curving 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. Transpiration mg./g./min.
ST. Stomatal aperture

---. mg./sq. dm./min.
----- Light intensity
1. Daily march of transpiration in *Stirlingia latifolia*—mature leaves. University Station. (A) Early and late Spring, (B) Late Summer.

![Graph of transpiration for *Stirlingia latifolia*](image1)

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:—E₁ and TR₁
- Late Summer:—E₂ and TR₂
- Summer (after rainfall):—TR₃
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.

Bosilacea 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 Bosilacea 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 Bosilacea 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 surfaces 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, T2). 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 root 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 calcinus (soft-leaved xerophyte)

Phyllanthus is unusual in having quite thin and soft though small leaves and yet occurring as a character plant among the sclerophys. 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 isodecanoic-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 occurring 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 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**

<table>
<thead>
<tr>
<th></th>
<th>Spring</th>
<th>Early Summer</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>mg./g./min.</td>
<td>mg./cm.²/min.</td>
</tr>
<tr>
<td><em>Stirlingia latifolia</em></td>
<td>6.8</td>
<td>7.2</td>
</tr>
<tr>
<td>Young</td>
<td>12.6</td>
<td>19.3</td>
</tr>
<tr>
<td>Mature</td>
<td>4.3</td>
<td>4.9</td>
</tr>
<tr>
<td><em>Banksia attenuata</em></td>
<td>0.0</td>
<td>11.0</td>
</tr>
<tr>
<td>Young</td>
<td>2.0</td>
<td>7.0</td>
</tr>
<tr>
<td>Mature</td>
<td>4.9</td>
<td>13.8</td>
</tr>
</tbody>
</table>

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 Figures 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 increased 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 unhyt. 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**

<table>
<thead>
<tr>
<th>Soil Moisture and Soil Suction Force at 1-foot Depth</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Soil Moisture (%)</strong></td>
</tr>
<tr>
<td>-----------------------</td>
</tr>
</tbody>
</table>
| Sept. | Nov. | Dec. | Jan. | Feb. | 3-0 | 1-8 | 1-4 | 1-35 | 1-3 | 4-1 | 1-6 | 0-3 | \...
| Suction Force | 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 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.
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 Kennedia, 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 *Erechtites 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, *Erechtites 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 ruysa*. 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.

---

**TABLE V**

**Soil Moisture at University Station, Late Summer**

<table>
<thead>
<tr>
<th>Depth of Soil Sample</th>
<th>Soil Moisture (%)</th>
<th>Suction Force (Atm.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 foot</td>
<td>1-5</td>
<td>50</td>
</tr>
<tr>
<td>4 feet</td>
<td>2-5</td>
<td>10</td>
</tr>
<tr>
<td>11 feet</td>
<td>4-0</td>
<td>Zero</td>
</tr>
</tbody>
</table>

---

**TABLE VI**

**Soil Moisture at Typical Maquis Areas**

<table>
<thead>
<tr>
<th>Species</th>
<th>Soil Moisture (%)</th>
<th>Suction Force (Atm.)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Eremophila scoparia</em></td>
<td>1.15 mg./sq.dm./min.</td>
<td></td>
</tr>
<tr>
<td><em>Casuarina lepidophloia</em></td>
<td>2.25 mg./sq.dm./min.</td>
<td></td>
</tr>
<tr>
<td><em>Acacia aneura</em></td>
<td>1.38 mg./sq.dm./min.</td>
<td></td>
</tr>
</tbody>
</table>

---

*Note:* The osmotic values for *Eremophila scoparia* and *Casuarina lepidophloia* are slightly higher than those for *Acacia aneura*. This may be due to the fact that *Eremophila scoparia* and *Casuarina lepidophloia* are more adapted to the arid conditions of inland South Australia, while *Acacia aneura* is more adapted to the more humid conditions of coastal South Australia.
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 Rouschel'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 *Bosostea* 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 *Banksea* 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 *Banksea* 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

I am indebted to Miss A. M. Baird for numerous discussions on the biology of sclerophylls in Western Australia and I also wish to gratefully acknowledge the help given by Miss J. Rayner in assisting in carrying out several of the experiments and in preparing the graphs for publication.

References


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

By Beryl I. Brewin

Manuscript accepted—17th May, 1955

A new sub-family Atapozonae 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 Eudoloma Cauilly, 1899, but the presence of a stalked brood pouch and of two median suckers in the tadpole clearly separate the genus.

Order Aplousobranchia Lahille, 1866
Family Clavelinidae Forbes and Hanley, 1848
Sub-Family Atapozonae, 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—Polyctorininae, Clavelininae and Holozonae. 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 specialised 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 tapers, 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, 2.3 cm. wide. Test light greenish brown, firm, with numerous irregularly-shaped test cells and containing also round brown “koitallen”—masses of foreign material. Zooids opening only on head region over which they are evenly and regularly distributed. Pharyngeal region salmon pink, abdominal 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 Sydnoecides 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 possession 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 spots 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 a more or less daily access to the life cycle of this ascidian will form a rewarding study.

References


Explanation of Lettering

- atrial lining.
- bp—brood pouch.
- em—cells of embryo.
- ifc—inner follicle cells.
- in—first portion of intestine.
- in’—second portion of intestine.
- oe—oesophagus.
- m—mantle wall.
- s—septum.
- sd—sperm duct.
- st—stomach.
- stbp—stalk of brood pouch.
- su—sucker.
- vp—vascular process.
- O—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 Crustacea (Protocallaniass 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 calcareous 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 13.5 × 18 mm. The lower end, probably a fracture plane, is flat (plate, 2d). Its outline is elliptical, measuring 19.2 × 21.2 mm., with an elliptical opening (5.5 × 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 edge 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 umb 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 occurrence 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”.

* University of Adelaide.
They resemble strikingly the uppermost peduncle plates of the new specimen. In \textit{Z. australis} the lower plates are described as “triangular, some acutely triangular and bowed outwards” (Withers 1935, p. 94). This similarity in shape between the lower latera of \textit{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 \textit{Z. concinna} (Morris) (Withers 1928, p. 106) is taken into consideration. Moreover, the valves in \textit{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 “\textit{Tetlima, Fusus} or \textit{Triton}, and \textit{Callianassa} or \textit{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 Crustacea 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 “\textit{Callianassa} or \textit{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 pebbelary body, probably chitinized 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.

\textit{Protocalianassa 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 ischiun 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 \textit{Callianassa}.

\textit{Measurements (in mm.)}

\begin{tabular}{|l|}
\hline
\textit{Length of abdomen (measured} \\
\textit{along dorsal curvature)} 37
\textit{Larger (right) first cheliped} \\
\textit{Length from base to tip of} \\
\textit{dactylus} 39
\textit{Length of propodus} 17
\textit{Height of propodus} 10
\textit{Length of dorsal edge of} \\
\textit{propodus} 12
\textit{Length of dactylus} 9
\textit{Length of carpus (dorsal)} 5
\textit{Length of merus} 8
\textit{Height of merus} 5
\textit{Length of ischiun} 5
\textit{Smaller (left) first perciopod} \\
\textit{Length of propodus} 11
\textit{Height of propodus} 5
\textit{Length of dorsal edge of pro-} \\
\textit{podus} 6
\textit{Length of dactylus} 7.5
\textit{Length of carpus (dorsal)} 4.5
\hline
\end{tabular}
Comparisons.—The new species is placed in the genus Protocallianassa Beurlen 1930, type species P. archlaci (H. Milne Edwards), which is distinguished by a linea thalassinae 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 Axilidae 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. urgoniicus Loretthe) 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 Glassner (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 occurrence of an Eocene fauna in the Perth Basin.

References

Explanation of Plate


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