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THE  
PROCEEDINGS  
OF THE  
LINNEAN SOCIETY  
OF  
NEW SOUTH WALES

FOR THE YEAR

1941  
VOL. LXVI.

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WITH FOURTEEN PLATES.  
206 Text-figures.

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## ANNUAL GENERAL MEETING.

WEDNESDAY, 26th MARCH, 1941.

The Sixty-sixth Annual General Meeting was held in the Society's Rooms, Science House, Gloucester Street, Sydney, on Wednesday, 26th March, 1941.

Mr. R. H. Anderson, B.Sc.Agr., President, in the Chair.

The minutes of the preceding Annual General Meeting (27th March, 1940) were read and confirmed.

## PRESIDENTIAL ADDRESS.

The Sixty-sixth Annual General Meeting of this Society is being held at a time when the distractions of a world at war make it difficult to give due attention to ordinary activities. Nevertheless I have very much pleasure in recording for the Society a successful year in which its objects have been satisfactorily realized. We look forward with confidence to the coming year, being convinced in our minds that the knowledge we pursue has permanent worth in a world of changing values. Following the usual custom the first part of my address is devoted to a brief review of the Society's activities during the past year.

It was with very great regret that your Council accepted the resignation of Dr. A. B. Walkom from the position of Secretary of the Society. Dr. Walkom resigned on the 31st October, 1940, in order to take up the position of Director of the Australian Museum. He offered, however, to act as Honorary Secretary until 31st December, 1940, and this offer was gratefully accepted by your Council. Dr. Walkom has served our Society with distinction and efficiency since 1919, when he succeeded the late J. J. Fletcher as Secretary. He obtained the degree of B.Sc. at the University of Sydney in 1910, graduating with First Class Honours and the University Medal in Geology, and in 1918 was admitted to the degree of Doctor of Science, with Medal. He was Linnean Macleay Fellow of this Society in Geology for one year, resigning in 1913 to become Lecturer in Geology and Palaeontology at the University of Queensland, a position which he held until 1919, being President of the Royal Society of Queensland, 1918-19. While Secretary of the Society Dr. Walkom spent twelve months abroad as the holder of a Rockefeller Foundation Scholarship of the International Education Board. He was especially interested in the Mesozoic sediments of eastern Australia and is an outstanding authority on palaeobotany. Since 1926 he has been Honorary General Secretary of the Australian and New Zealand Association for the Advancement of Science, for several years Honorary Secretary of the Australian National Research Council, and also Editor-in-Chief of "Australian Science Abstracts". He was also Chairman, Honorary Secretary and Honorary Treasurer of the Science House Management Committee for a number of years. As Secretary of our Society Dr. Walkom has carried out his duties with tact and efficiency and has earned the respect and liking of every member. We thank him for his services and wish him every happiness in his new position, knowing that he will fill it with every distinction.

Your Council selected Dr. N. S. Noble as successor to Dr. Walkom and appointed him to the position of Secretary from 2nd January, 1941. Dr. Noble was formerly an entomologist in the New South Wales Department of Agriculture. He graduated as Bachelor of Science in Agriculture with First Class Honours in 1928 and was appointed Assistant Entomologist in the Department of Agriculture. In 1929 he was awarded a Walter and Eliza Hall Agricultural Research Fellowship. With this he proceeded to the University of London, undertaking there graduate study and research in entomology;

he also worked at the Stored Products Research Laboratory, Bucks., and spent twelve months at the University of California, where he obtained the degree of M.Sc. In 1932 he was awarded the Diploma of the Imperial College of Science, University of London. In May, 1938, he was admitted to the degree of Doctor of Science in Agriculture for a thesis on "Australian Parasitic and Phytophagous Chalcidoidea". The results of Dr. Noble's researches on a number of aspects of entomology have been published in thirty papers in various scientific journals. Dr. Noble has been the Business Manager of the Journal of the Australian Institute of Agricultural Science for the past four years.

Our Society has been singularly fortunate in the calibre of its past Secretaries, and I am quite certain that we have every reason to congratulate ourselves on our present choice. Your Council was thoroughly satisfied that Dr. Noble had the highest qualifications and we hope he will be happy in the services of the Society.

Since the last Annual Meeting the names of eleven members have been added to the list, two members and one Corresponding member have been lost by death, the names of four have been removed on account of arrears of subscription, and three have resigned.

Herbert James Carter, who died suddenly in Sydney on 16th April, 1940, when within a few days of completion of his eighty-second year, was born at Marlborough, Wilts., England, on 23rd April, 1858. He was educated at Aldenham School and Cambridge University, where he was a scholar of Jesus College. He was a mathematics master at the Sydney Grammar School from 1881 to 1901 and was Principal of Ascham Girls' School from then till 1914. He was President of this Society during 1925-26, and a member of Council from 1920 until 1939; also a Fellow of the Royal Entomological Society of London. For many years he was honorary entomologist to the Australian Museum. He was science editor of the *Australian Encyclopaedia*, published in 1926, and author of *Gulliver in the Bush*, in which he related many of his experiences in pursuit of his scientific work. He was especially interested in the Australian Coleoptera, particularly the families Tenebrionidae, Buprestidae, Cistelidae, and Dryopidae. In addition to descriptions of large numbers of new species, he paid particular attention to matters of synonymy, and published a number of check-lists of the families, and revisions of the Australian species of various genera. He did not shirk the drudgery of the work on synonymy, but often deplored the practice of some European colleagues who, on what he considered inadequate evidence, described large numbers of Australian species as new, and so added to the difficulties of Australian coleopterists. His papers appear in a number of scientific journals from 1905 onwards, chiefly these PROCEEDINGS, the Royal Zoological Society of New South Wales, and the Royal Society of South Australia. His last completed work, a short note on Dryopidae, was handed to Dr. Walkom only a few days before his death. His fine collection of Australian Coleoptera, including many types, has been given to the Division of Economic Entomology of the Council for Scientific and Industrial Research at Canberra. A charming personality, he left a host of friends in his scientific colleagues and in his former pupils, and our Society holds him in grateful and affectionate memory.

August Goerling, who died at Pinjarra, Western Australia, in January, 1941, had been a member of the Society since 1936. He was a keen student of natural history and a friend of the late H. J. Carter. He had made extensive collections of insects, being more especially interested in the Coleoptera.

William Mountier Bale, a Corresponding member of the Society since 1888, died on 4th October, 1940, at Kew, Victoria, at the age of eighty-nine years. He was an authority on the Hydrozoa and was a Fellow of the Royal Microscopical Society.

In November, 1940, Mr. A. F. Basset Hull tendered his resignation as a Councillor. Mr. Hull had been a member of the Council for about twenty-five years and his resignation was accepted with very great regret, it being resolved that there be placed on record in the minutes an expression of appreciation of his services to the Society.

In November, 1940, a letter was received from the Under-Secretary, Chief Secretary's Department, thanking the Council for suggestions in connection with the proposed amendment of the Birds and Animals Protection Act.

The proclamation protecting wild flowers and native plants was renewed for a further period of one year from 1st July, 1940, *Casuarina Cunninghamiana* (River Oak) having been added to the list of protected plants.

We offer congratulations to Professor J. P. Hill, who, during 1940, was awarded the Darwin Medal of the Royal Society of London; also to Dr. R. J. Noble, who was appointed N.S.W. Under-Secretary for Agriculture, and to Dr. H. G. Raggatt, who was appointed Geological Adviser to the Commonwealth Government in 1940.

The plant house for the Macleay Bacteriologist, the erection of which was made possible through the generosity of the Commonwealth Bank of Australia, Rural Bank of New South Wales, Bank of New South Wales and Commercial Banking Company of Sydney, Limited, was completed early in 1940. Mr. R. J. Swaby, B.Sc.Agr., the Biochemist assisting the Macleay Bacteriologist, resigned on 19th October, 1940, and Mr. R. C. Betty, B.Sc., who was selected to take his place, took up his duties on 1st February, 1941.

The year's work of the Society's research staff may be summarized thus:

Dr. H. L. Jensen, Macleay Bacteriologist to the Society, has carried out final experiments on the occurrence and distribution of free-living nitrogen-fixing bacteria in wheat soils and the results have been published in a paper written in collaboration with Mr. R. J. Swaby. This paper also includes experiments on the activity of anaerobic nitrogen-fixers (*Clostridium*) under soil conditions. The work on symbiosis between nitrogen-fixing and cellulose-decomposing organisms has been concluded. An introductory paper, dealing with the general aspects of the problem, was published in these PROCEEDINGS in December, 1940. A second paper, on the quantitative relationship between cellulose decomposition and nitrogen fixation under varying experimental conditions, has been submitted for publication in these PROCEEDINGS, and a third paper, dealing especially with anaerobic nitrogen-fixing bacteria, has been prepared. The results have shown consistently that nitrogen fixation on the basis of cellulosic materials, requires the co-operation of at least one partly or wholly anaerobic component in the association of organisms; this corroborates the results previously obtained in experiments with soils to which straw was added. A number of strains of root nodule bacteria from various clovers and medics have been studied. The bacteria from *Trifolium* spp. were found able to induce root nodule formation in plants at reactions far more acid than those from *Medicago* spp. No support has been found for the theory that molybdenum as a "trace element" stimulates nitrogen fixation in leguminous plants as it does in *Azotobacter*. Stimulation of plant growth by inoculation of the seed with *Azotobacter*, as claimed by many recent Russian investigators, has not been observed with certainty in leguminous pasture plants.

Miss Ilma Pidgeon, Linnean Macleay Fellow of the Society in Botany, has completed a paper on the "Ecology of the Central Coastal Area of New South Wales. iii", dealing with forest types on Hawkesbury Sandstone and Wianamatta Shales, and this has been submitted for publication in the PROCEEDINGS. This paper embodies several new technical features, including an attempt to represent the climatic tolerance of many species of *Eucalyptus*. It also contains a development of the author's views on the classification of vegetation. Miss Pidgeon has also prepared a report which has been submitted to the Council, and to the Council for Scientific and Industrial Research on the effects of different salts upon water loss from oranges. Experiments reveal that both uptake of water and water loss are affected by the hydrogen ion concentration of solutions in which the oranges are immersed, and that a desirable detergent should have a low pH value. The work has already provided information of value in the treatment of oranges for storage. Finally, work has been carried out on the developmental anatomy of orange rind.

Miss Valerie May, Linnean Macleay Fellow of the Society in Botany, has carried out experiments to determine the effect of different concentrations of a mineral nutrient on a plant's resistance to drought. In particular the effect of nitrogen has been studied. The effect of potassium and its interaction with nitrogen is also being examined. *Helianthus* has been used, as this plant is particularly suitable, for the technique employed, of analysing drought resistance by means of serial readings of a plant's height. In earlier

*Helianthus* experiments it was shown that plants given abundant nitrogen quickly exhausted their water supply and so suffered severely after a drought of only a fortnight, whereas smaller nitrogen-starved plants were more economical with their water supply and thrived after a drought lasting nearly four months. Further, in these two groups of plants there was no significant difference in the rate of loss of water per unit area. Thus the effect of the difference in concentration of nitrogen on the resistance of a plant to drought, might be only indirect, through plant size affecting the rapidity with which a given supply of water is exhausted. In a second *Helianthus* experiment, drought was measured in terms of the volume of water used rather than as the time during which no water was provided. The results will determine whether different concentrations of nitrogen and potassium affect the drought resistance of *Helianthus* other than by plant size and rate of use of water, both of which factors may be compensated for by root development in the field. Serial readings have been taken of leaf-area and water-use in addition to plant-height. A paper, "A Survey of the Mistletoe of New South Wales", will be published in the next Part of the PROCEEDINGS, while a second, to be published jointly with Professor E. Ashby, has been prepared for publication in the PROCEEDINGS. This paper gives some results of experiments on drought resistance.

Mr. John Allan Dulhunty, Linnean Macleay Fellow of the Society in Geology, has made considerable progress in the study of the stratigraphical arrangement of the torbanite deposits in the Upper Coal Measures of the Kamilaroi Basin. The general stratigraphy of the Western Coal Fields has been studied, and a stratigraphical framework has been obtained, which is now being used for the purpose of determining the various horizons occupied by the different torbanite deposits. Important developments have been made in connection with the classification of the different types of torbanite and associated materials, and the results obtained from the study of special physical and optical properties of torbanite, are being applied to field and laboratory problems. He has devised special apparatus for studies in the general microscopy of torbanite, and progress has been made in the investigation of micro-constitution and structure.

Miss Margaret Cumpston, Linnean Macleay Fellow of the Society in Zoology, resigned her Fellowship on 30th April, 1940, but before doing so, she prepared a paper which contains a summary of observations on the family Scarabaeidae with a bibliography of the literature of this important economic family of beetles.

Six applications for Linnean Macleay Fellowships were received in response to the Council's invitation of 25th September, 1940. I have pleasure in reminding you that the Council reappointed Miss Ilma M. Pidgeon and Mr. J. A. Dulhunty to Fellowships in Botany and Geology respectively for one year from 1st March, 1941, and appointed Mr. Mervyn E. Griffiths, M.Sc., and Dr. Germaine A. Joplin, B.Sc., to Linnean Macleay Fellowships in Physiology and Geology respectively for one year from 1st March, 1941.

Mr. Mervyn Edward Griffiths graduated in Science at the University of Sydney in 1937 with First Class Honours in Zoology. He carried out research in the School of Zoology, University of Sydney, for several years as holder of a Commonwealth Government Research Scholarship and was awarded the M.Sc. degree in 1938. In the same year he was awarded a Science Scholarship of the Royal Commissioners for the Exhibition of 1851, carrying out research at the Montreal Neurological Institute, the Biological Laboratories, Harvard University, the National Institute for Medical Research, London, and the Courtauld Institute of Biochemistry, London. Mr. Griffiths' researches, which have dealt particularly with glandular secretions, have been published in a number of papers in these PROCEEDINGS and several notes have also been published in *Nature*.

Dr. Germaine Anne Joplin graduated in Science at the University of Sydney in 1930, with First Class Honours in Geology and the University Medal, and was awarded the Deas-Thomson Scholarship in Geology for 1930, together with a Science Research Scholarship. In 1933, as holder of the Junior Fellowship of the International Federation of University Women, she carried out research at the University of Cambridge, for which she was awarded the Ph.D. degree. Since returning to Australia in 1935, Dr.

Joplin has been employed as acting-assistant lecturer in the Department of Geology, University of Sydney. She has carried out a number of geological investigations and the results of these researches have been published in British and Australian scientific journals.

During the coming year Miss Pidgeon proposes to complete the study of the anatomy and physiology of *Eucalyptus globulus* and also hopes to continue work on the statistical analysis of regenerating vegetation at Broken Hill. She also proposes to continue work on the physiology of water loss from oranges, and intends to complete her ecological studies of the central coastal area of New South Wales. Mr. J. A. Dulhunty will continue his investigation of the torbanite (oil shale) deposits of New South Wales. This will include a study of the environmental conditions of deposition and metamorphic evolution of the torbanite deposits and a microscopical study of the detailed structure of the gelosite and retinosite bodies in the torbanite. Mr. M. Griffiths intends to investigate the relationship of the secretions of the duodenum and the anterior lobe of the pituitary gland to carbohydrate metabolism with particular reference to diabetes mellitus. Dr. Germaine Joplin proposes to complete a petrological study of the Ordovician rocks at Cooma, investigating the relations between the igneous intrusions, the folding and the regional metamorphism. We wish them all a successful year's work.

The concluding part of Volume lxxv of the Society's PROCEEDINGS was issued in December. The complete volume (568 plus xl pages, seventeen plates, and 605 text-figures) contains thirty-four papers on various branches of Natural History. The volume was again larger than usual, as Council decided that the additional cost of publication of the Macleay Bacteriologist's extensive paper on the nitrogen economy of Australian wheat soils should be borne by the Income Account of the Bacteriology Fund. On account of rationing of paper, which began in the latter part of the year, it was decided to omit from the PROCEEDINGS the printed list of donations and exchanges, the list of members and the biological portion of the index. Moreover, the amount of words on the printed page was increased in Parts 5-6 by altering the length of the line from 28 ems to 30 ems, and the depth of the page from 43 to 48 ems.

Exchanges from scientific societies and institutions totalled 1,383 for the session, compared with 1,865, 1,860 and 1,833 for the three preceding years, this marked decline in the number of exchanges being due mainly to the war.

#### THE EFFECT OF SETTLEMENT UPON THE NEW SOUTH WALES FLORA.

In 1770, when Sir Joseph Banks made his first botanical collection in Botany Bay, he had an opportunity of studying a virgin flora which was apparently little affected by the few human inhabitants. With the arrival of the First Fleet in 1788, however, the first impact of the white man was made on the vegetation, and since that time the effects of settlement have produced many striking changes in the flora. It is probable, as indicated by Osborn (1928), that outside human interference with the indigenous flora does not necessarily date from comparatively recent years. It possibly goes back to a remote age, as early visitors to this continent were very likely to have brought plant seeds with them. But the influence of human voyagers prior to 1770 must have been very small, and it is only since the recent settlement by white men that any appreciable changes due to human interference have been made.

The effect on the flora in many districts has naturally been most marked and far reaching. It is, of course, true that many areas show little or no effects of settlement, and it is probably equally true that many of these areas will retain more or less indefinitely their distinctive flora quite uninfluenced by the activities of the white man. For, apart from natural reserves, there are many parts of New South Wales which are quite unsuited for settlement of any kind and sufficiently remote to be left undisturbed even in the midst of an expanding population. Such areas seem quite unsuitable for any likely utilization, and it is probable that they will always provide examples of natural flora uninfluenced by man.

Many parts of the Hawkesbury Sandstone areas seem to possess an uninviting barrenness which ensures a virgin flora. Parts of the Tablelands seem unlikely to be utilized for any purpose, and the arid country of the far west is, in many cases, unstocked

and likely to remain so. The Commonwealth Year Book for 1939 indicates that about 80% of New South Wales is unoccupied, the remainder being alienated, in the process of alienation, or held under leases or permits. It is probable, however, that at least some of the alienated land is little, if at all, affected by human settlement.

But the effect of settlement has had very striking results in many parts of the State and it is these which form the subject of this address.

When the white man came into this country he found land which, with a few exceptions, seemed singularly lacking in suitable food plants. He was compelled to clear away the forest and scrub cover to make way for his houses, roads and crops. He brought in domestic animals and made available suitable pasturage for them. In the pursuit of these activities he laid waste the native flora and introduced alien plants and animals, either intentionally or accidentally.

Broadly speaking, the effects of settlement on the flora can be studied under the following sections:

1. Effects of clearing land for roads, railways, towns, villages and homesteads.
2. Effects of clearing and utilizing land for crops.
3. Effects of utilizing land for pasture, including the introduction of domestic and other animals.
4. The effects of fires.
5. The introduction of insect and fungal pests.
6. The effect of usefulness to the white man upon subsequent distribution of individual plant species.

#### EFFECTS OF CLEARING LAND FOR ROADS, RAILWAYS, TOWNS, VILLAGES AND HOMESTEADS.

The actual areas cleared for such purposes are, of course, only small, but they are of importance in establishing centres from which the alien or introduced flora can become established. Many naturalized species have originated as escapes from garden cultivation, and some of our most troublesome weeds are ones which were formerly introduced as desirable garden subjects. *Echium plantagineum* (Paterson's Curse) was introduced into the Albury district as a garden plant about 1875. It escaped on to a travelling stock reserve and was subsequently distributed over a wide area. To-day it is firmly established in many parts of the State, being declared a noxious plant in over 50 shires and 40 municipalities. *Eichhornia speciosa* (Water Hyacinth) was introduced to the northern rivers as an attractive flowering plant. It was placed in Swan Creek on the Clarence River and found conditions so congenial that in two years it had taken possession of the creek. Subsequently pieces were taken and grown in other water-ways by people attracted by its ornamental character. In a few years it had grown so luxuriantly that it became a serious problem in northern rivers and streams.

*Hypericum perforatum* var. *angustifolium* (St. John's Wort) was also very probably first grown as a garden plant, but it soon escaped from cultivation and to-day it has been proclaimed noxious in a very large number of shires and municipalities. Although species of *Opuntia* were probably first brought to Australia as food plants for the cochineal insect, the true pest Pear was very probably introduced as a garden or hedge plant. The heavy infestation in the Scone district appears to have been started by Dr. Carlisle, who introduced it to his station garden in 1839, his manager subsequently planting it through the paddocks as a standby for stock during drought periods. So rapid was the spread of Prickly Pear from various centres that in 1925 some 60,000,000 acres were covered by it in Queensland and New South Wales. Since that time the area has been very much reduced by the activities of the larvae of the introduced moth *Cactoblastis cactorum*.

A fairly large proportion, however, of naturalized plants which have escaped from cultivation, shows little tendency to invade natural areas unless the way is prepared by considerable human interference. Many of them have little liking for straying beyond the artificial conditions created by man, and, although they have been recorded as naturalized for many years, cover only very small areas.

Alien plants are common along roadsides passing through natural country which is neither cultivated nor stocked, but there is usually very little evidence of them

spreading beyond a few yards from the road except at points which show signs of human interference.

When travelling along railway lines it is quite noticeable that the alien plants usually occur in a narrow fringe along the lines and do not invade to any appreciable extent the adjoining natural areas. It is also often noticed that the aliens are most conspicuous on moist better class soils on level ground and do not occur so frequently on dry soils on embankments. In some cases, of course, species like *Rubus fruticosus* (Blackberry) and *Lantana camara* invade adjoining areas, but even then their successful competition with the native flora is limited to certain areas.

A minor result of roads and rail lines being taken through densely covered country is the change in the composition of the flora along the fringe of the clearings due to the greater development of light-demanding or light-loving species.

Where roads or railways pass through cultivated or pastoral areas they are far more important as centres for the distribution of introductions. This is particularly the case where stock use the roads for travelling, as their fleeces or coats carry the seeds of plants from other districts. On country stock routes the vegetation has naturally undergone many changes, being subject to severe grazing, trampling and the deposition of dung. Stock travelling in trucks along railways spread the seeds of plants in dung or in other ways, railway embankments being often characterized by a flora very different to that of the surrounding country.

#### EFFECTS OF CLEARING AND UTILIZING LAND FOR CROPS.

The actual amount of land in New South Wales which has been under cultivation at one time or another is relatively small, the New South Wales Statistical Register for 1939 showing 7,044,038 acres as under cultivation, 3,199,626 under sown grasses, and 3,565,371 acres as land previously cropped, but not ploughed during the year.

These combined figures indicate that the total area which has been sown or cropped at any time is only about 7% of the total land area of the State. The area suitable for cultivation is estimated at between 15% and 16%.

Alien plants introduced on to such cultivated areas, however, spread to adjoining country to some extent, especially where the flora is disturbed by human interference other than direct cultural operations. The native flora on areas utilized for cultivation has, of course, very largely disappeared and been replaced by deliberate introductions such as food and forage plants, or by accidental introductions especially of those weeds which have shown particular ability for following the plough in most parts of the world.

At present there are some 546 species which have become naturalized in New South Wales, including 128 grasses. These come from many different countries, but the great majority are natives of Europe, Africa and North and South America. Countries having a somewhat similar climate naturally supply many of our introduced plants, so that regions round the Mediterranean, South Africa and South America are well represented. China and Japan contribute only six species, including one grass.

The family Gramineae contains the largest number of introduced species, many of which have been purposely brought here for their fodder value. The next most important family is the Compositae, which has supplied 75 species to our naturalized flora. Fifty species of Leguminosae have become established, including many useful fodder plants such as the various species of *Medicago* and *Trifolium*. Other families which are more or less strongly represented are the Cruciferae, Caryophyllaceae, Scrophulariaceae and Solanaceae.

These aliens, apart from those brought in as useful crop or forage plants, have been introduced in a number of ways. The principal source was impurities in seed imported for agricultural or pastoral purposes. For many years there was no check on such introductions, and a very large number of weeds and undesirable aliens must have become established in this way.

Breakwell (1918) gives an example of White Clover seed which contained 37,440 seeds of impurities to each pound. In 1908 the Federal Quarantine Act was passed which included an appendix forbidding the entry of certain plants. Gradually the

regulations enforcing this act were tightened so that at the present time seed impurities are not so likely a source of further introductions. As an example of seed impurities a fairly recent sample of perennial rye grass tested at the New South Wales Department of Agriculture showed approximately 12% of foreign seed, representing fourteen different species. The number of seed impurities per pound was estimated at 27,500. Some samples tested have shown impurities as high as 22%.

It is very likely that many plants have been introduced in fodder for stock during drought periods. Following such drought years and the importation of fodder from other countries, there has usually been local development of species new to this country. In some cases these have failed to retain their original hold, but in others they have found conditions to their liking and have become firmly established.

Quite a number of plants have been introduced in packing round goods, 35 species of plants being recorded in one occasion in the packing around some glass beakers. The ballast from ships emptied out on beaches or coastal land has been responsible for the entry of quite a number of aliens. Several interesting plants, for example, have been found at Stockton near areas where ballast had been discarded.

#### *Noxious Weeds.*

The naturalized flora has contributed most of our troublesome agricultural and pastoral weeds, the wide distribution of which has been helped by their rapidity of growth, great powers of reproduction, and the absence of natural enemies. During recent years *Chondrilla juncea* (Skeleton Weed) has proved particularly troublesome and has provided a serious problem in wheat-growing areas. Its rapid growth has been phenomenal since 1917 when it was first recorded, and to-day it covers many thousands of acres. Its wide distribution is due largely to its very efficient seed production and dispersal, its deep rhizomes, and its comparative unattractiveness to grazing animals. The most troublesome weeds contributed by alien floras include *Inula graveolens* (Stinkwort), *Lepidium draba* (Hoary Cress), *Hypericum perforatum* var. *angustifolium* (St. John's Wort), *Convolvulus arvensis* (Bindweed), *Rubus fruticosus* (Black-berry), *Xanthium spinosum* (Bathurst Burr), *Alternanthera echinata* (Khaki Weed), *Centaurea calcitrapa* (Star Thistle), *Echium plantagineum* (Paterson's Curse), *Lantana camara* and *Rosa rubiginosa* (Sweet Briar), but there are many others which have provided a serious problem for our landowners. In addition, some introductions, such as *Conium maculatum*, *Homeria collina*, *Salvia reflexa* and *Lamium amplexicaule*, are poisonous to stock and have been associated with stock losses.

Some of the naturalized species have become extremely widely distributed, but are not regarded as troublesome weeds, being usually quite easily controlled if desired. Included in this group are *Plantago lanceolata*, *Polygonum aviculare*, *Chenopodium album*, *Capsella bursa-pastoris*, *Euphorbia Peplus*, *Anagallis arvensis*, *Sonchus oleraceus*, *Malva parviflora*, *Amaranthus* spp., *Rumex* spp., *Medicago* spp., and *Trifolium* spp. These are mainly free-seeding, rapidly maturing annuals, which have a marked ability for adapting themselves to a wide range of soil and climatic conditions.

#### *Native Plants as Weeds.*

Although the aliens provide most of our weed problems yet some of the native species have found the new conditions created by man's interference quite favourable to their development. During recent years particularly, there has been a distinct tendency for native species to become rather troublesome to the farmer and pastoralist. *Bassia Birehii* (Galvanized Burr) has spread to a very considerable extent, especially in the north-west, and has been proclaimed a noxious plant throughout the State. Until about twenty-five years ago it was by no means common, but it gradually asserted itself in heavily stocked areas as its spiny nature renders it unattractive to stock. The spiny fruits adhere readily to wool and permit distribution over wide areas. After rain on overstocked land it often comes up in considerable quantity, and in some cases is even invading agricultural land. The closely related species *Bassia quinquecupis* has also become moderately troublesome, but is not regarded so seriously. It becomes detached from the ground, and is blown along by the wind, being one of the several

plants known as 'Roly-poly'. The dried plants are often piled up along fences making these more likely to be destroyed by fire by providing additional fuel.

*Solanum cinereum* (Narrawa Burr) is another spiny native plant which has been proclaimed noxious in quite a number of shires and municipalities. *Tribulus terrestris* (Caltrops) and *Emex australis* (Cat's Head) are further examples of native plants which have become troublesome chiefly because of their spiny fruits. Quite recently it was reported that *Eremocitrus glauca* was spreading in the Warren district on black soils as its rather prickly nature made it objectionable to stock, and it did not appear to be palatable in any way. *Carex longifolia*, one of the native sedges, has become fairly troublesome in pastures of the Illawarra and South Coast. It has harsh sharp-edged leaves which are avoided by stock. Fairly large tussocks are formed, occupying in some cases up to 25% of the paddocks. Abundant seed is produced during the summer months and the species is steadily increasing the area under its control. It appears possible that in some districts it will in time take possession of pastures or seriously diminish their value, especially on the poorer types of soil. Free-seeding shrubby species like *Cassinia arcuata* and *Olearia viscidula* often appear on cleared land and soon take possession. *Kunzea corifolia* and *Dodonaea triquetra* also tend to spread over cleared areas. *Sida rhombifolia* (Paddy's Lucerne) is another of the native plants which have prospered under the new conditions following settlement.

#### *Increase of Mistletoe.*

During recent years there has been a marked increase in the effects of Mistletoe in many districts. The problem is becoming quite a serious one, as many valuable trees are being killed by this parasite. In other cases trees are losing their vigour or are becoming mis-shapen. Most observers agree that the amount of infection is far greater than previously, but the reasons for this increase are by no means clear. It seems, however, that the problem is partly one resulting from the effects of settlement. The results of mistletoe infection are usually much more apparent on fairly open country than on closely timbered areas. Mistletoe is quite rare, for example, in rain-forest, and is essentially a light-loving plant. As the country is opened up infection is more common, possibly because of the greater light provided, or because the birds carrying seeds have fewer resting places. If there are fewer trees for the mistletoe bird on which to alight, the chances of an individual tree being infected must be increased. If this were so, however, the number of trees infected may not be actually increased although the effects of the parasite may be more noticeable. At all events the spread of Mistletoe does appear to be associated with the opening up of the country, and is probably one of the results of settlement.

Some observers also state that the increase in Mistletoe is due to the decrease in the numbers of koalas and opossums brought about by the demand for their skins. Evidence on this point, however, is contradictory, and it is by no means definite that koalas or opossums exercise any great effect in controlling Mistletoe. In some western districts, Mistletoe is relished by stock and is regarded as a useful standby during bad periods. One effect of settlement in this case might be the decreased quantity of Mistletoe in such districts, but no reliable observations are available on this point. In many parts of the State, however, the disturbance brought about by settlement has set up the problem of increasing parasitism of valuable trees and shrubs.

#### *Possibilities of Further Additions to the Naturalized Flora.*

No doubt the number of alien species established in New South Wales will increase from time to time, but the recording of new aliens is becoming far less frequent than formerly. The factors operating against the introduction of new species are the more rigid and efficient enforcement of legislation governing seed impurities and noxious plants, the less tolerant attitude of the landowner to aliens on his property, and the general effects of closer settlement.

The farmer and grazier no longer view with easy complacency the appearance of a new plant on their property. They tend to regard the strange plant as a potential trouble maker, and take steps to prevent its establishment. Of recent years the question of

noxious weeds has become a fairly acute one, and the farmer is far more concerned with the weed problem than formerly. In addition governmental authorities take the necessary steps to secure the eradication of any new arrival which has a bad record in other countries, or which is likely to prove troublesome in any way. For example, some years ago *Allium vineale* (Wild Garlic) made its appearance at Berridale on the Southern Tablelands. It is a fairly common weed in America, where it is troublesome in fields of small grain and in pastures, adding a garlic taint to wheat and dairy products. It has particularly efficient methods of reproduction, spreading from underground bulbs, aerial bulbils and seed. The aerial bulbils, being much the same shape and size as wheat grains, are difficult to separate from seed wheat and it therefore appeared to have serious potentialities as a noxious weed. Steps were accordingly taken to ensure its complete eradication, and warnings were issued to landowners to be on the outlook for it in other districts. The alien plant, recently arrived on our shores, does not experience so hearty a welcome as in former years.

Some recent introductions, however, have appeared to spread rather widely and rapidly. The Central American plant *Gomphrena dispersa* was first recorded in New South Wales only about five years ago, but since that time it has appeared in quite a number of localities, and is evidently increasing.

#### *Regeneration of Abandoned Land.*

Land once under cultivation but subsequently abandoned generally carries, at first, a high proportion of introduced species which, however, are often gradually replaced by the native ones. In other words, provided man's interference is withdrawn, the native species usually tend to dislodge the aliens. Hamilton (1919), in a study of salt marsh vegetation, describes an area at Cook's River where the land had been laid down in pasture. He found that the original vegetation was reappearing, and already some of the shrubby species had recaptured small areas and were driving back the introduced vegetation. Adamson and Osborn (1924) state that stringybark forests rather rapidly recapture cleared ground when this is abandoned. The forests developing on these cleared areas soon assume the same general features as the surrounding untouched portions, although certain species when once eliminated seem to have difficulty in returning. It was noted, however, that very few aliens survived.

Such reversion of abandoned land to the native flora seems to be quite the general rule, although in cases where the area is invaded by such vigorous competitors as Blackberry, Lantana and Prickly Pear the native plants have difficulty in re-establishing themselves.

#### THE EFFECTS OF UTILIZING LAND FOR PASTURES.

Probably the most far-reaching effect of settlement in New South Wales upon the indigenous flora was that produced by the introduction of animals, the grazing habits of which differed profoundly from those of the native fauna. With the white man came his sheep, cattle, horses, camels, foxes, and goats, all of which have become naturalized or live under conditions very closely approaching the wild state. One of the most important introductions, however, was the rabbit, which multiplied to such an extent that it soon became a major problem for the pastoralist.

The methods of grazing of these introduced animals were very different to those of the native marsupials. Osborn (1929) has pointed out that the damage done by kangaroos, even when they are numerous, is probably quite small. In observations at the Koonamore reserve he found that the marsupials did not graze closely, but merely pruned the grass tufts, leaving three or four inches of the leaf untouched. On the other hand, sheep and rabbits graze closely and the plants are frequently killed by heavy or sustained stocking.

Since settlement the number of stock in New South Wales has risen steadily. In 1939 there were approximately 49,000,000 sheep, 3,000,000 cattle and 548,000 horses. In some years the number of sheep has reached 53,000,000 and the effect on the native flora of supporting these animals has been enormous. Sheep tend to be very selective in their feeding, preferring low-growing fine plants. They relish the most tender shoots

and avoid as far as possible the coarser tall-growing species. Horses are even more selective, often concentrating on patches of the finer grasses until eaten out. Cattle, on the other hand, will consume the coarser grasses and herbage far more readily.

The rabbit, which became a pest after 1880, exercised a profound effect on the vegetation, being responsible for reducing the carrying capacity of the land to an alarming extent. Rabbits graze closely, and in addition, are most destructive of the perennial flora, including shrubs and trees. Woody plants, especially, find survival and regeneration difficult to accomplish in rabbit-infested country. They are often ring-barked, and many edible trees have been destroyed by rabbits eating the bark away from the trunk and even the lower branches. When reasonable amounts of feed are available rabbits exhibit certain selective habits, preferring some species to others. Peacock (1908) has pointed out that rabbits do not care for one of the White Everlastings (*Helipterum* sp.), and as a consequence this plant had taken possession of large areas.

#### *Effect of Stocking on Purely Natural Pastures.*

In the first place we might consider the effect of stocking on natural pastures which have not been sown, cultivated, or top-dressed in any way. Such pastures constitute the great bulk of land utilized by stock, particularly in the western division of the State. In many parts of New South Wales the native flora, although quite adequate for the needs of the indigenous animals, could not be expected to withstand the heavy demands of large numbers of close grazing animals. Osborn (1928) has pointed out that the indigenous grasses have not the underground renewal buds often associated with grasses on areas carrying a large herbivorous fauna. In addition, very few of the native plants produce rhizomes which would enable them to resist the effects of stocking. Some of our grasses, however, notably *Danthonia bipartita*, *Eragrostis eriopoda* and *Neurachne Mitchelliana*, have buds which appear to be better protected from grazing by the fact that they are very close to the ground or are situated just below soil level. In addition some protection to the buds seems to be given by woolly bracts. However, a fairly large proportion of our grasses and herbage plants appears more suitable for the sustenance of nomadic marsupials than the needs of modern, concentrated, stock-raising practices.

The temptation to exploit the pastoral wealth of the country soon led to an increase in the number of flocks and herds. The general tendency was for stock to eat out the more favoured species, resulting in a gradual alteration of the flora accompanied by a decrease in the carrying capacity of the country. In extreme cases practically the whole of the vegetation was destroyed. On most areas, however, the effects of stocking became apparent through the gradual disappearance of those species favoured by stock and which had limited powers of reproduction or little capacity for withstanding the effects of grazing. For example, it is generally recognized that *Themeda australis* will not stand much stocking and soon disappears from pastures. It is handicapped by the facts that it is relished by stock and has rather poor reproductive powers. The various species of *Danthonia* also tend to disappear under stocking. On the other hand species of *Aristida* and *Stipa* usually increase their numbers owing to comparative unpalatability and perhaps to their capacity for withstanding depleted soil fertility. *Chloris truncata* is another grass which is not so affected by stocking and which is usually one of the early colonizers of over-grazed land. This is probably due to its production of very abundant seed with high germination capacity, whereas many of the other grasses have rather poor seed production and low percentage of germination. *Tragus racemosus* is another species not so adversely affected by stocking.

In some paddocks after grazing *Eragrostis leptostachya* appears to be quite prominent, although a very palatable grass. It is probably aided by its habit of growth which is rather low and mat-like, and therefore better able to withstand certain types of stocking. In any case, it is apparent that some native species are better equipped than others to withstand grazing by introduced animals, and it is inevitable that such plants will become more prominent while others disappear.

The introduction of large numbers of animals also provides a vehicle for the wider distribution of those species producing burr-like fruits or seeds which can become attached to fleeces and coats. It is probable that the various species of *Calotis* have become more widely spread because of this factor, and possibly *Stipa* and *Aristida* species are favoured in the same way. Other native species adapted for distribution in the coats or fleeces of animals are *Tragus racemosus*, *Cenchrus pauciflorus*, *Acaena* spp., *Glycyrrhiza psoraleoides*, *Desmodium* spp., *Oncinocalyx Betchei*, *Bassia* spp. and *Daucus brachiatus*. Among the introduced plants might be mentioned *Medicago* spp., *Xanthium spinosum*, *Rumex* spp. and *Marrubium vulgare*.

Apart from actual grazing, heavy stocking may have the effect of loosening or pulverizing certain soils, resulting in drifting of the surface portion and exposure of the hard clay underneath. Suitable seed-beds are no longer available, and gradually the whole of the vegetation is destroyed, giving rise to the "scalded" plains of western areas. Clayey soils which are at all heavily stocked become hardened and offer very adverse habitats for regeneration of plants. Osborn, Wood and Paltridge (1935) found that the hard loam soils supporting *Kochia sedifolia* rapidly lost the surface mulch of fine soil under the combined influence of trampling by stock and of wind. This condition offered great obstacles to the establishment of any seedlings.

Broadly speaking, in New South Wales the effects of stocking on the native flora depend on the climatic and soil conditions of the area concerned and the nature of stocking. In many western portions of the State little or no clearing has been necessary. Such areas support two plant communities consisting of hardy perennial shrubs or trees and a large variety of annual herbs. The annual plants grow very quickly after rainfall, flowering and seeding in a very short time. Botanically this annual flora consists of a very wide range of species, most of which are eaten by stock during the short time they are available. But they are able to flower and mature seed in so short a time that stocking seldom results in wiping them out. The shrubs or small trees which constitute the permanent part of the vegetation consist largely of species of *Acacia*, *Myoporum*, *Eremophila*, *Casuarina*, *Atriplex*, *Bassia*, *Kochia*, *Geijera*, *Capparis*, *Owenia*, *Grevillea*, *Atalaya*, *Hakea*, *Apophyllum* and other genera. This flora provides the main reserve supply of fodder and is, unfortunately, often the most affected by continual stocking. Seedlings are destroyed and further growth is made difficult by continual trampling preventing the formation of suitable seed-beds. Rabbits destroy mature plants by ring-barking them, apart from eating seedling growth. It is therefore common to find very little development of seedlings and young growth of most woody shrubs and trees in areas subject to continuous stocking. Indeed, when travelling around New South Wales, one is impressed by the almost total absence of young trees or seedlings in most districts where settlement has taken place. The few trees left in many paddocks are becoming aged and unsuited for the provision of efficient shade and shelter. A great deal of planting will be necessary in many parts, although much could be done by encouraging natural regeneration through the exclusion of stock from selected portions.

Collins (1924) states that very few, if any, seedlings of Mulga were seen in a strip 300 miles in length in the far west of New South Wales, and that local observers asserted that crops of seedlings were very rare. On the other hand Nichols (1938) quotes Melville as showing evidence that stocking in Western Australia has probably little effect on Mulga regeneration, as young seedlings are distasteful to stock and are hardly ever touched. This is stated as probably due to the nature of the resinous secretions on the phyllodes and stems which vary according to the age of the plant, seasonal conditions, and the variety of the species. The tree is not considered edible until it reaches a height of about twelve feet. These are most interesting observations, but it is not certain how they are borne out by the behaviour of Mulga in New South Wales. It is a widely accepted opinion that Mulga seedlings are destroyed by stock, but more definite investigations are necessary on this point. Botanically, *Acacia aneura*, which is the most common species known as Mulga, is extremely variable, and it is quite possible that a number of very distinct varieties are involved. In different parts of

Australia the name Mulga is given to quite a number of distinct species of *Acacia*, and conflicting statements may therefore be due to the fact that reference is being made to entirely different species.

On western areas which are fairly heavily covered with trees or scrub some clearing is necessary. This is usually followed by good grass growth, but the tendency then is to overstock, resulting in the increased development of non-edible shrubs. The growth of these unpalatable species is also assisted by understocking of the rough growth in seasons of good rainfall. During recent years such species as *Cassia eremophila*, *Cassia artemesioides*, *Bertya Cunninghamii* and *Eremophila Mitchellii* have overrun some districts and are spreading from the poorer soils to better class ones. Carn (1938) states that on some areas there are 250 plants of *Cassia* spp. to the acre. Such growth of non-edible species has, of course, some value in preventing wind erosion.

In other parts of the State it is necessary to carry out a good deal of clearing in order to establish pastures. In many cases such clearing has been excessive, not even sufficient trees being left for shade and shelter. After clearing there is usually a considerable alteration in the ground flora due to the development of grasses and rosette plants. An apparently stable grassland community is produced which, however, is usually only maintained by grazing. If animals are excluded the tendency is for shrubs and young trees to reappear.

#### *Regeneration on Areas following Protection from Animals.*

It is frequently noted that areas fenced off from stock and rabbits show quite striking natural regeneration and a definite increase in the size, number and variety of plants and species constituting the ground flora. Provided stock are excluded, the natural flora has considerable recuperative powers, the marked improvement in the cover being due either to increased vigour and size of the original plants, or to the development of new plants. Fenced off areas in the neighbourhood of towns in western districts provide the botanist with the best opportunity of studying the natural flora, especially if he is in search of good specimens. Along many western rivers to which stock have access, for example, it is rare to see young plants of the River Gum, *Eucalyptus camaldulensis*, or of the River Oak, *Casuarina Cunninghamiana*. If such areas are fenced off, however, young seedlings soon make their appearance. Some western landowners have established small breakwinds or shelter belts by the simple expedient of fencing off strips, allowing regeneration to take place, and subsequently planting larger growing trees in the shelter provided by the naturally regenerated plants. An interesting example of regeneration following protection from grazing was that resulting from the efforts of the late Albert Morris in the Broken Hill district. Owing to the cutting of trees and larger shrubs for fuel and mining timber, and through the effects of very heavy stocking, the land in the neighbourhood of Broken Hill had become practically denuded of vegetation. Sand drift was common, and the difficulties in the way of planting trees seemed insuperable. Morris, however, was instrumental in having areas completely fenced off from stock, as he was convinced that the vegetation would "come back" if rested. The natural regeneration following on fencing justified his judgment, and he took advantage of the cover provided to plant out young trees. The experiment is only in the early stages, but it promises to yield far-reaching results which should be of great assistance in overcoming similar problems in other parts of the State.

In a statistical analysis of these areas Pidgeon and Ashby (1940) found that protection given by fencing over a period of less than two years increased the density of perennial plants on areas previously heavily grazed. There was also evidence that fencing increased perennials relatively more than annuals, both in variety and numbers. In some cases the number of annuals was found to be considerably lower in fenced than in unfenced areas, probably because of the greater competition offered by strong growing perennials. It was also observed that, in some cases, although the difference was very great in the amount of vegetation existing in fenced and unfenced parts, this was due to the increased growth of the individual plants rather than to an increase in numbers. Another interesting observation was that protection decreases the number of weeds or undesirable species while increasing the number of perennials, particularly of palatable

species. A great deal of work remains to be done before we know very much of the detailed effects of regeneration on areas following protection from animals, but we know enough to feel sure that this method of allowing natural regeneration to take place is one of the most promising ways of remedying, to some extent, the tremendous damage done to our natural pastures by continuous stocking. Protection from stock, although beneficial, is not sufficient as it is also necessary to exclude rabbits and to ensure their destruction within the area. At the Koonamore reserve the perennial flora was not restored after twelve years' protection from stock, and this result may have been due in part to the fact that, although the fencing was rabbit-proof, rabbits were common within the area and at times were numerous.

*Effects of Mineral Depletion and Lowering of Soil Fertility on Natural Pastures.*

Apart from the effects of grazing the composition of the flora may be altered by the results of mineral depletion and lowering of soil fertility. Although wool itself is relatively low in mineral constituents, yet its removal year after year involves a steady depletion of the mineral substances in the soil. A thousand pounds of unscoured wool is quoted by Wadham and Wood (1939) as containing 54 lb. of Nitrogen as  $N_2$ , 0.7 lb. of Phosphorus as  $P_2O_5$ , 56.2 lb. of Potassium as  $K_2O$ , 1.8 lb. of Calcium as  $CaO$ , 0.4 lb. of Magnesium as  $MgO$ , and 35.5 lb. of Sulphur. One whole sheep of 150 lb. live weight, however, contains 5.3 lb. of Phosphorus, so that, on properties from which sheep are sold, there is a much greater drain. The authors state that in southern Australia, where phosphate deficiency in soils is common, continuous grazing has almost certainly led to a depreciation in the type of herbage, due to the inability of many of the more valuable species to tolerate the low phosphatic status of the soil. A serious feature of phosphatic deficiency is the gradual disappearance of the more valuable natural grasses and their replacement by inferior species such as *Bothriochloa decipiens* or *Stipa* spp.

*Bothriochloa decipiens* (Red Grass) is an example of a species which has spread rapidly in some districts because of the effects of continuous grazing or cropping in reducing soil fertility. Moodie (1934) states that this grass has a wide range in New South Wales and is tolerant of extremely low fertility conditions. On better class soils it is not aggressive, but on poorer soils it soon becomes dominant and crowds out more valuable pasture plants. It grows fairly vigorously during spring and summer, and is eaten by stock, although they prefer other grasses if available. In good seasons, therefore, it is rejected by stock and produces large quantities of seed, which help it in the gradual elimination of other species. It provides fair summer pasturage but very little winter feed. Many pastures of this grass develop *Medicago* spp. and *Trifolium* spp. during winter, but eventually these disappear and an almost pure pasture of *Bothriochloa decipiens* is established which gives poor quality summer grazing, and which has a negligible winter carrying capacity. The pastoralist meets this problem by attempting to raise soil fertility through the use of superphosphate, and by sowing Subterranean Clover. After four or five years perennial grasses such as *Lolium perenne* (Rye grass), *Dactylis glomerata* (Cocksfoot) and *Phalaris tuberosa* can be established. The interesting point, however, is that on such areas the natural pastures have gradually been converted through the effects of stocking to an almost pure association of a comparatively unpalatable native grass. This necessitates treatment aimed at the establishment of introduced species. It is unlikely that any methods will be adopted which would have as an object the re-establishment of the better class native species formerly occupying the area.

It has been customary to divide pasture plants in New South Wales into two groups, namely, those demanding high fertility soils, and those which tolerate low fertility types. In the first group are species like *Lolium perenne*, *Trifolium* spp., *Phalaris tuberosa* and, to a less extent, *Paspalum dilatatum*, all of which have heavy carrying capacity. In the second group are *Sporobolus capensis*, *Chloris Gayana*, *Axonopus affinis* and most of the native species. These are not so suitable for heavy stocking. The opinion is often expressed that the low fertility tolerant plants, which usually give poor grazing, are succeeding in crowding out the better quality plants over large areas in the State. On many parts of the North Coast, for example, *Paspalum dilatatum* is finding it difficult

to compete against *Axonopus affinis*. Continuous grazing certainly does appear to lead to a regression in the type of vegetation owing to the inability of many of the better class species to tolerate phosphatic deficiency in the soils.

#### *Beneficial Effects of Stocking on Pastures.*

The effects of stocking in producing pasture deterioration are so obvious that the reverse side of the picture is often overlooked. In a few cases at least the presence of stock has a beneficial effect on pastures in certain respects. Blake (1938) draws attention to such improvement in typically ashy downs to the north of Barcaldene in Queensland. Areas which had been consistently and heavily stocked with sheep for several years carried a good stand of Mitchell grass and herbage, whereas adjoining land, which had been idle for many years, had very sparse vegetation. The loose nature of the soil is given as the probable reason. Continual trampling by stock compacts such soils, enabling them to hold moisture better, thus inducing better growth.

Osborn, Wood and Paltridge (1932), in a study of the growth and reaction to grazing of *Atriplex vesicarium*, one of the perennial saltbushes, at the Koonamore reserve, found that moderately heavily grazed areas showed no significant difference in the number of plants, but carried more healthy and vigorous plants. Grazing was observed to result in the mechanical removal of dead bushes, and to exercise a pruning of the live bushes, owing to the repeated removal of the terminal buds. Such pruning caused the development of lateral shoots and the formation of a more compact and vigorous bush. It was concluded that, under moderately heavy stocking, the health and vegetative vigour of the community was increased, and the area thus made more valuable for grazing. It was also observed that intermittent stocking was valuable in allowing seedlings to become established, and it was suggested that heavy intermittent stocking might be the most desirable type of stocking in saltbush country. On the other hand, lightly stocked saltbush country was found to be less healthy than moderately heavily stocked areas or even than completely unstocked country. This was attributed to the development of overcrowded communities, owing to the planting of seed by the hooves of sheep and the failure to remove old or dying plants by light trampling. On heavily overstocked areas, of course, the vegetation was completely destroyed.

In many parts of the State the trampling of sheep has been found useful as a fairly efficient and cheap method of covering grass or clover seed that has been broadcast.

#### *Effect of Pasture Improvement on the Vegetation.*

In the early days of settlement the natural grasses and herbage were relied upon to provide pasture. Improvements were made in the composition of the pasture by clearing and firing, but, as a general rule, no other methods were employed. Soon, however, the pastoralist, especially in districts of good rainfall, had to face the problem of replacing the natural vegetation with some more useful and productive type. In some cases, as for example on sandy coastal soils, the natural vegetation is poor, and the light soils are unable to support anything other than low-grade plants or weeds. In other districts continual stocking has reduced soil fertility and consequent carrying capacity. During recent years, therefore, there has developed a definite tendency to change from pure exploitation to a more intensive and intelligent utilization of the land. The sowing of introduced grasses and clovers is by no means new, as some areas have been sown with Perennial Rye, Cocksfoot, and clover for many years past.

The introduction of *Paspalum dilatatum*, which did so much to establish the dairying industry, was brought about as far back as 1883. It was not, however, until 1920 that declining fertility led to systematic investigations with fertilizers. It was found that the main requirement was to raise soil fertility in respect to both phosphates and nitrogen. Most New South Wales soils are deficient in phosphoric acid, and the use of superphosphate was found to produce quite striking improvements in many districts. Pastures fertilized with superphosphate were found to develop clovers to a marked extent, this in turn leading to nitrogen accretion and increased fertility. When the fertilizer is applied it is customary to sow seed of suitable grasses and fodder plants, so that the vegetation on these grasslands is undergoing considerable changes.

Moodie (1940) refers to the increase in the area of improved pastures, pointing out that there were only 19,314 acres of top-dressed pastures in 1927, but in 1938 this figure had increased to 875,730 acres. The top-dressing of pastures is not necessarily accompanied or preceded by cultivation. Only in a comparatively few cases is the area ploughed, but harrows or cultivators may be used to break the soil and cover the seed. All species recommended for sowing are introduced ones, and it is evident that there is in progress, in many parts of the State, a gradual conversion of natural grasslands to artificial pastures. In some districts and in certain sections of primary production there has always been a tendency to replace the natural vegetation entirely by introduced species. Wadham and Wood (1939) point out that it is approximately true that satisfactory dairying is seldom achieved in districts where native plants form the bulk of the vegetation. Dairying requires areas of fairly heavy rainfall, and these usually support dense growth of trees and shrubs. The natural herbage in such associations is generally scanty and usually consists of a few shade-loving species. When the ground is cleared, new plants suitable for pasture must be introduced, and these are almost always exotic species. In some dairying districts native grasses still form the bulk of the pasture, but with the increased popularity of the use of fertilizers such pastures will be gradually converted to introduced species. The native plants, generally, do not give the best returns on good soils where the rainfall is high, and therefore the effects of settlement in such districts will be ultimately to replace the natural vegetation with an exotic one.

In many parts of New South Wales, however, especially in the drier Western Division, there is no evidence to show that we can improve on the existing pastures by the introduction of alien plants. It is, of course, possible, that eventually some introduced plants will be found that will prove suitable for western districts, but the immediate prospect is that the native species will continue to provide the bulk of the vegetation.

McTaggart (1939) is of the opinion that plant introduction in Australia, as a whole, is restricted to a definite fringe belt, although in New South Wales this covers over half the State. There is, however, a substantial part of the State which is unlikely to be suitable for the establishment of exotic species.

Indeed it is generally true that native pastures throughout the State are not markedly invaded by introduced species, except where the soil has been disturbed or fertilized. There are, however, a few introduced plants which show ability for invading natural pastures. The various species of *Medicago* have spread very widely over the State, probably because their burry fruits are carried about by stock. They are so common and so firmly established that many landowners regard them as native plants. The several species of *Vulpia* also occur frequently in native pastures. These are free-seeding annuals which make rapid growth in early spring before the native grasses show much development. *Koeleria phleoides*, *Hordeum murinum* and *Briza* spp. are other aliens which are found widely throughout the State. In coastal areas *Paspalum dilatatum* has spread far beyond cultivation areas, although not so common on land which is not subject to man's influence in some way or another. *Axonopus affinis* spreads through the natural vegetation in North Coast districts, and the short-lived *Poa annua* makes its appearance under a wide range of conditions.

It might be concluded that the introduction of fodder plants and grasses and the wider use of fertilizers and grassland improvement methods have led to the replacement of the natural vegetation in many districts. The introduced plants in some cases have invaded the natural pastures, but on the other hand have not greatly altered their composition. Unless disturbed by cultivation or by the use of fertilizers, the natural pastures are likely to continue to consist very largely of native species.

#### THE EFFECTS OF FIRES.

Although naturally it is impossible to bring forward statistical proof it is reasonable to assume that, since settlement by the white man, bushfires have become far more frequent and widely distributed. Fires arising from natural causes have always existed but the great majority of fires are caused by human agency, either deliberately or through carelessness. No doubt the aborigines used fire when hunting game and it is probable

they fired grasslands in order to promote fresh young growth which would attract the animals they desired to hunt. It is possible that fire was used by them in a number of ways and at fairly regular intervals, but the extent of fires caused was probably small. Some evidence, however, has been brought forward to indicate that in some districts at least fires were common before the advent of the white man and may have actually decreased since his occupation. Howitt (1890) states that, in the Gippsland district of Victoria, country which was once open grassland was now covered with sapling growth of Eucalypts. The coming of the white man had resulted in the development of forests on grassland, and he attributed this to the less frequent occurrence of fires since settlement. The aborigines burnt off the grass either accidentally or intentionally each year preventing the seedling growth of trees. The white man excluded fire as far as possible, giving young tree growth opportunity to develop.

Domin (1911) formed the conclusion that some of the open forests of Queensland were not natural associations, but secondary ones changed mostly by bushfires started by aborigines. It is, therefore, difficult to estimate the extent and frequency of bushfires prior to settlement, but the general evidence points to the conclusion that, with possibly a few exceptions, fires have been far more frequent and extensive since the advent of the white man.

Settlers have used fire freely in order to clear land for cultivation and for the improvement of pastures by promoting fresh young growth of grasses. Many people have become careless in its use, with the result that widespread and disastrous fires have been far more common in recent years. One has only to go back to the hot, dry summer of 1938-1939 for an example of bushfires which have devastated wide areas. Few bushlands, especially those close to settlement, do not show signs of frequent firing, and such fires must have an effect on the vegetation varying in extent according to severity and frequency. They are usually most severe on forested areas or dense scrubland as, apart from containing much inflammable material, these areas are not utilized by private landowners, who naturally are not so concerned about preventing fires or controlling them once they have started. In addition such areas are usually remote from densely settled areas, so that fires are often not observed until they have obtained a good start. Grass fires are not so common unless deliberately started and are more easy to control. The effects of fire, therefore, are more commonly observed on forest land, on areas carrying fairly dense shrubby growth, or on poor soil types such as the Hawkesbury Sandstone soils, which may support considerable natural growth, but which are not fertile enough for crop or pastoral utilization.

According to severity and frequency, fires may cause total destruction, partial destruction, or light burning. Total destruction of plant life on an area seldom, if ever, occurs, especially as the native flora has unusual powers of renascence. In such rare cases, however, where all or most of the vegetation is destroyed, restoration depends on invasion from adjoining areas. Thus species in the neighbourhood which produce wind-borne seed and which happen to be seeding at the time will have a big initial advantage in the colonizing of the denuded area. Some of the Compositae such as *Cassinea aculeata* and *Erechtites* species seem especially prolific on fired areas. However, there is always a certain amount of survival, and in many cases this is quite extensive, so that the association does not lose its identity. In other countries extensive fires appear to leave very few survivors of the original population, but it is characteristic of the Australian flora that the survival rate is high and that regeneration is rapid. Climax associations are seldom destroyed, and the effects of fire are less obvious than in other parts of the world. In many cases the plants forming the community, although considerably damaged by fire, establish themselves either by epicormic shoots or by shoots from root-stocks, ligno-tubers, or rhizomes. Many native species produce epicormic shoots, but the various species of *Eucalyptus* are most outstanding in this respect. The great majority of these produce suckers from trunks and branches very freely after fire, although a few do not. Jarrett and Petrie (1929) have pointed out that the big majority of trees in a *Eucalyptus regnans* Association were killed by fire, rarely producing new shoots. Regeneration was only possible through seed, and if the fires were frequent this would become impossible.

McLuckie and Petrie (1927) state that on the Kosciusko plateau the *Eucalyptus coriacea* Association did not possess the rapid renascence characteristic of other Eucalypt forests. After six years there was little evidence of shoots on the stems of *Eucalyptus coriacea* and *E. stellulata*, although shoots from the root-stock were common. In the most exposed situations no renascence was evident. It is often observed that *Eucalyptus oreades* and *E. nitens* find recovery difficult after fire. The ability to survive fires by Eucalypts appears to depend to some extent on the nature of the bark. Those species producing thick rough bark seem to insulate the cambium layer to some extent and are not so affected as the thinner smooth-barked species.

Apart from Eucalypts a number of other species produce epicormic shoots quite freely. Jarrett and Petrie (1929) quote *Senecio Bedfordii* as producing copious adventitious shoots on the stem, and also mention *Aster argophylla* and *Acacia melanoxyton*. Other species which come readily to mind are *Syncarpia laurifolia*, *Ceratopetalum gummi-ferum*, *Casuarina* spp. and *Banksia* spp. Even some of the more tender semi-brush type of trees found along water courses such as *Ceratopetalum apetalum*, *Tristania laurina* and *Eugenia Smithii*, have strong powers of regeneration provided the fires are not too severe.

Renascence after fire is also greatly helped by the production of ligno-tubers by many shrubs and the ability of many species to shoot from the root-stocks. Beadle (1940) points out that ligno-tubers are a peculiar feature of many Australian plants and are most common in the families Proteaceae and Myrtaceae. Plants having such tubers are seldom entirely destroyed by fire as they are often buried deeply enough in the soil to avoid excessively high temperatures. Species such as *Xylomelum pyriforme*, *Telopea speciosissima*, *Leptospermum* spp., *Banksia* spp., and mallee Eucalypts usually show strong powers of renascence from the root-stock after fire.

The possession of rhizomes is also of assistance in withstanding destruction by fire. Such rhizomes are often little affected by fires passing over the area and shoot strongly, especially after good rainfalls. *Pteridium aquilinum* is a common example of a species which strongly asserts itself on land which has been fired. Shoots coming from the rhizomes are often so dense that other species have some difficulty in establishing themselves although usually eventually successful. *Imperata cylindrica* var. *Koenigii* also exhibits good renascence owing to its possession of rhizomes. Jarrett and Petrie (1929) quote *Oxalis corniculata* and *Viola hederacea* as other examples.

Apart from rhizomes some species produce bulbs or other underground organs of propagation which help their regeneration after fire. This is particularly common in the Liliaceae, Orchidaceae and some of the Gramineae. One peculiar characteristic of some native ground orchids is that they flower far more freely after a fire has passed over the area. A well known example of this is *Lyperanthus nigricans*.

Plants not possessing any of these aids to regeneration, however, depend on fire-resistant seeds which are present in the soil or on the plants themselves. Thus regeneration is by no means confined to regrowth of surviving plants, but is often largely due to seedling development. Williams (1940) has stated that the regrowth after fire of swamp tea tree in the coastal areas at Dromana consisted almost entirely of seedlings as the damaged shrubs did not produce suckers. The fire-resistant qualities of the seed of many Australian plants is very well known, the most common examples being provided by the families Proteaceae, Myrtaceae, and Leguminosae. The seeds of *Acacia* have a very hard coat which protects the embryo from damage, and it is a common experience for seedling growth to be greatly stimulated by fire passing over the area. Many land-owners have been surprised to find a growth of *Acacia* on their land, following on grass or stubble fires. In some cases there has been no evidence of *Acacia* spp. in the district for many years, but the seed has lain dormant in the soil until turned up by the plough and subjected to fire. Growing plants of *Acacia* seldom recover after fire as they do not produce epicormic shoots or possess resurgent root-stocks, regeneration thus depending on seed. The hard, woody fruits of *Hakea* and other genera of the Proteaceae are admirably adapted for survival after fire. The seed is well protected from all but the hottest fires, but the heat is sufficient to perform the useful function of opening the fruits

and shedding the seeds. *Hakea pugioniformis*, for example, is often strongly in evidence on areas after fire. Species of this type possess a marked advantage over others. Actually fire by hastening the dehiscence of the fruits is a distinct aid to natural regeneration, especially as the ash and litter often provide a useful germinating bed. The seed of *Callitris* is also protected by the woody cone. Ability to survive fires, however, is not limited to those species with woody fruits as some plants with succulent fruits are quite fire-resistant, the seeds themselves having a good protective coat. Species of *Persoonia* provide examples of this. Beadle (1940) quotes figures showing that the number of seedlings which appear on a burned area far exceeds the number on an unburned area, particularly in moist communities, and he brings evidence indicating that the average bushfire does not kill the seeds of many species. He found that a temperature of 110°C. for four hours did not greatly reduce the percentage germination while a few seeds could withstand a temperature of 120°C. or even 130°C. for the same time.

In New South Wales, therefore, natural regeneration after fire is usually quite strong and the structure of the community may not be very greatly altered, especially if the percentage of species exhibiting strong powers of renaissance is very high. In most plant communities, however, there is a certain alteration and simplification because of the elimination of non-renascent types. These may become re-established by migration and the original community restored, but where fires are frequent a more or less permanent change may be brought about, as the interval between fires is not sufficiently long to allow higher phases to develop again. Pidgeon (1938) attributed the comparative paucity of species in some localities in the central coastal areas of New South Wales to the effects of repeated fires which resulted in the complete elimination of many species.

Even, however, where there is little apparent change in the composition of the community there is often considerable alteration in the condition of the individual plants, especially trees. Collectively the vegetation on areas which have regenerated after fire may appear quite good, but individually the trees are unsound, especially from a timber-producing point of view. After repeated firing many trees become hollow at the base and may blow over. Fire scars permit the entrance of timber-destroying fungi and insects, and the leading shoots are often destroyed, resulting in distorted growth. Sound straight growing trees become fewer and fewer.

The effects of frequent fires on the physical and other properties of the soil are imperfectly known as regards New South Wales soils, but the general effect is to reduce the amount of humus and to destroy the source of further humus by burning leaf litter. The soil tends to become hard and baked and does not provide good physical conditions for seedlings although the addition of ashes is helpful. Erosion may become more evident as surface run off is increased owing to the hardening of the soil. Useful micro-organisms may be destroyed. On hilly country the effects of forest fires may be especially harmful, as not only is the humus burnt away, but the ash may be washed away by rain. Unless the ash and leaf litter is restored to the soil the growth of trees and shrubs must result in impoverishment, especially in regard to the minor mineral constituents so necessary for plant growth. It might, however, be remembered that, in some parts of the world, soil burning is practised to obtain fertility. It is considered that firing produces a more friable seed bed and one which has been more or less efficiently sterilized. Beadle (1940) states that the Hawkesbury Sandstone soils are not affected to any great extent by fire. He supplies figures showing that fire does not appreciably alter the water-retaining capacity, loss on ignition, or pH value. But these figures show a definite, although slight, alteration in the physical properties of the soil, and it is likely that frequent firing would have an appreciable effect. The Hawkesbury Sandstone soils also, as a rule, have a lower percentage loss on ignition than other soils, and therefore may not be so affected by fire as other types.

An interesting result of fire in forest areas is the reduction of Mistletoe, as in many cases these parasites seem much more susceptible to fire injury than their hosts. After a fire has swept over an area it is quite common to notice how very few Mistletoes survive although the hosts make good recovery. Cleland (1940) records 36 dead Mistletoes on a tree of *Eucalyptus leucoxylon* which had recovered after a fire.

In summing up it might be stated that the more frequent and widely distributed fires following on settlement have caused some modifications of the flora in many districts. These changes, however, are not so great as in other parts of the world owing to the ability of the native species to survive after most fires, or to regenerate successfully from fire-resistant seeds. The effects of fire are rather imperfectly known and there is abundant opportunity for interesting investigational work. Apart from bush or forest fires there is room for detailed study on the use of fire on pastoral areas, especially as it affects yield, regeneration, soil conditions, and the structure of the plant community. Fire is used fairly commonly in some New South Wales pastures to burn off rank or old growth, the principal objects being to encourage fresh young growth, to provide more uniform grazing, and to permit the better distribution of stock. Little information, however, is available concerning the exact effect of firing on our pastures. It has been suggested that firing results in the elimination or reduction of *Medicago* species, as the seeds of these cannot survive the fairly great heat developed by some grass fires. In this respect fires may adversely affect grasslands. It is possible that in time they might greatly affect the botanical composition, but whether adversely or beneficially is not known.

Experience in other countries does not help us very much in estimating likely results. Bews (1918) found that continual burning on the eastern grasslands of South Africa had a very marked effect on the composition. *Anthistiria imberbis* was dominant before firing, but it was gradually replaced by other species, chiefly of *Aristida*. Experiments carried out by Hensel (1923) on Kansas pastures indicated that burnings were not injurious. It was found that burnings did not decrease the number of grass plants and that in the early part of the season there was considerably more grass growth after fire. He showed that both the mean maximum and mean minimum soil temperatures were higher on the burned pastures, and suggests that this might explain the earlier growth of grass. He found, however, that there was a change in the composition of the pastures, one result being a decrease in the number of sedges in the burned area. Australian pastures, however, offer an almost virgin field for this class of research work.

#### THE INTRODUCTION OF INSECT AND FUNGAL PESTS.

The native plants appear to have been little affected by the introduction of insect and fungal pests. These have caused considerable injury to the introduced flora, but there is little evidence of them having any noticeable effect on the indigenous plants. A number of introduced species of insects are known to infest some native plants but cause little injury.

*Ceroplastes destructor* (White Wax Scale) is found on quite a number of native plants, and the related species *Ceroplastes rubens* (Pink Wax Scale) is not uncommon. In addition a number of species of Coleoptera and Hemiptera, including Aphididae, occur on native plants, but they have little, if any, noticeable effect on the vegetation. None of the introduced fungal pests has any destructive effect on the natural flora, so that it seems correct to say that the native vegetation has remained unaffected to any appreciable extent by the fungal and insect pests introduced since settlement.

#### SPECIFIC USEFULNESS OF INDIGENOUS PLANTS AS A FACTOR IN SURVIVAL AND DISTRIBUTION.

From the early days of settlement the white man found that certain native species supplied some of his needs and were therefore much in demand. The first phase was undisguised exploitation of such plants without any consideration being given to the need for replacement. Early pioneers, for example, found certain timber-producing species most suitable for their requirements. In some cases species like *Cedrela australis* (Red Cedar) and *Araucaria Cunninghamii* (Hoop Pine) soon became comparatively rare except in the more inaccessible districts. As supplies became limited attention was given to the conservation of remaining supplies and the establishment of plantations. The general effect of settlement, therefore, was the gradual disappearance of certain species, but as the consequences of this were realized conservation and planting resulted.

The value of native shrubs and trees for feeding stock, especially during drought periods, was soon appreciated. Here again we notice a gradual disappearance of certain

species followed by conservation and later by an extension of their range and numbers. For example, *Brachychiton populneum* (Kurrajong) was soon valued as a very useful fodder and shelter tree. Many trees were sacrificed to ruthless lopping or even felling, but the pastoralist eventually realized that it was to his advantage to conserve supplies. Nowadays this species is widely planted in many parts of the State, and the present effect of settlement is to increase its numbers and to extend it beyond its natural range.

Species with horticultural value, or which are useful for shade and shelter purposes, have secured a wide distribution through planting. *Acacia Baileyana*, for example, had a very restricted natural distribution, being found only in one or two districts in the south-west of the State. Subsequently, however, it was widely cultivated in many parts of the State, and in quite a number of cases has started to spread naturally from the old planted trees. *Acacia podalyraefolia* is another wattle which has been cultivated widely because of its attractiveness, and which has become established in some districts. *Grevillea robusta* and *Melia azedarach* provide very interesting examples of native species which have extended their range through settlement, although in their case natural regeneration from artificially cultivated trees is seldom seen. Although limited in natural distribution to high rainfall areas of the North Coast and Queensland, where conditions are very favourable for tree growth, they have proved some of the hardiest species for planting in districts of comparatively low rainfall in western New South Wales. Their hardiness under conditions far removed from their natural range is surprising, but is probably due to the fact that they are most sensitive to adverse conditions during the very early part of their life, and, provided they survive this period, become quite hardy. As this sensitive stage is passed under favourable conditions in the nursery they are able to withstand the less favourable conditions met in later life. One effect of settlement therefore is to extend the range of useful species far beyond their natural habitat.

A similar interesting result of man's intrusion has been the exploitation of those species which appealed to him because of their floral beauty. Not prepared to admire them only in their natural setting, he felt urged to remove them to adorn his homes and his dwellings. The flower seller harvested his natural crops of native flowers, and all was well until even the unobservant noticed the gradual disappearance of species of *Boronia*, *Telopea*, *Eriostemon* and similarly attractive plants. The advent of motor transport extended the field of exploitation, public interest was stimulated, and eventually the legislature reacted with the Wild Flowers and Native Plants Protection Act. The result of this Act, although difficult to enforce because of inadequate policing facilities, has been to increase the number of plants of protected species in most districts. At least, if not more numerous, they are certainly more noticeable, and there appears to be adequate provision for regeneration. Thus the turn of the wheel passes again through exploitation to conservation.

#### DISCUSSION.

One hundred and fifty-three years of settlement have produced rather profound changes in the vegetation of New South Wales. The cultivation of crops and the introduction of exotic species have resulted, in some cases, in the complete or partial displacement of the native flora. The requirements of more concentrated grazing practices in districts of reasonably good rainfall have brought about a conversion of natural grasslands into pastures consisting almost entirely of introduced plants. But, in areas of low rainfall, the native vegetation still forms the most important part of the pastures and is likely to continue to do so. It seems true that the alien plant makes little headway against the indigenous species in most districts unless favoured by human interference.

Forest lands have been exploited and destroyed, and a forest policy has only begun to emerge from the disturbances created by pioneering settlement. As in the case of most newly settled countries, the utilization of land has been haphazard and based on a short-sighted policy of exploitation. To-day we find that in many districts carrying capacity appears to be declining owing to a deterioration in the grazing material. The results of erosion have become increasingly obvious, and other signs have pointed to the

unfavourable effects of a disturbed vegetation. But there are indications that we are attempting to do something towards a proper utilization of our land resources. It is becoming more widely realized that the future of Australia is largely dependent on a wise and proper use of her land, and that this in turn necessitates a far more comprehensive knowledge of our natural flora. It would, of course, be entirely wrong to say that the years since settlement have brought little progress in botanical knowledge. If this were said, a long line of brilliant and indefatigable botanists would turn in their graves with every justification. Considerable taxonomic research has been carried out on the New South Wales vegetation, and we know a great deal about its uses. But two things are necessary. We need to extend our knowledge, and we require that botanical workers, equipped with that knowledge, should play a far more important part in determining the forms of land utilization and in guiding the practices governing primary industries.

Systematic botany has a good record and has produced many able workers, but anyone familiar with the classification of our plants is only too painfully conscious of the many gaps in our knowledge. Ecological research can be said to have only commenced. We know little or nothing about various characteristics of our native species. Our knowledge of root habits, for example, is negligible. We have very few accurate details about reproductive methods and life histories of plants, and have little information concerning capacity to resist grazing. We are confused by variations in palatability in what is regarded as the one species. The erratic behaviour of supposed poisonous plants is a problem only lightly touched upon. In other words the study of our vegetation, in many respects, is only in the preliminary stages. Our knowledge of the results of past settlement indicates the necessity for making such study as complete as possible if land utilization is to have a proper basis. Because my interests lie largely in taxonomic botany, I would emphasize the necessity for a re-awakening of interest in that phase of botanical research, and would stress its importance in a close study of our vegetation. It is true that some workers in systematic botany have suffered from a lack of a proper appreciation of other botanical viewpoints, and have become "cribbed, cabined and confined" in the narrow fields of purely herbarium studies. We systematists have sometimes produced species which are merely fictions, useful in some respects, but lacking biological reality. Classification is now regarded as essentially team work, requiring not only the systematist, but the ecologist, geneticist and cytologist. Experimental taxonomy is being given increased attention and has great possibilities. The "new systematics" promise us a new heaven and a new earth in which the old-fashioned taxonomist must mend his ways. No doubt we are entering upon a new epoch of changed methods and concepts in classification, and most workers look forward to the future with anticipatory pleasure. At this point, however, my enthusiasm for the new order in systematic botany is checked by one or two practical doubts. I feel rather old fashioned when I admit a conviction that the classification and limitation of species will continue for a long time to be largely based on the classical method of comparative morphology. At all events that basis appears to be the most practical, even if it occasionally produces fictions. Knowing the difficulties involved in obtaining anything approaching completion in the classification of the New South Wales flora, even when based on easily observed morphological differences, I rather fear that classification based on biological team work is a thing of the dim and distant future. It is probable, however, that special groups of plants will receive such treatment. With the development of other branches of botany, especially those involving the stimulating use of experiment, taxonomy has been relegated to the background and given a lower status than it merits. But it seems to me that if we are to get anywhere with a proper study of our native plants we must first put our taxonomic house in order. There can be few developments without the preliminary work of the taxonomist, and we cannot deal with vegetation reliably or to the best advantage, unless we can first recognize the units of which it is composed. Ecological studies are, of course, extremely necessary and desirable. But in some cases the ecologist is inclined to underrate the importance of knowing his species. He often expresses the opinion that communities are more important than species, and that

ability to recognize all the species in a community is unnecessary in order to make a study of the vegetation. Certainly a limited knowledge of systematic botany does not preclude the student from attacking and solving many problems, but I cannot help feeling that the ecologist would be a far better ecologist if he had a thorough grip of the species involved. This of course implies close co-operation with the specialist in systematic botany, but there appears to be growing a rather regrettable tendency to underestimate the value of taxonomic knowledge. At times I am troubled by an unworthy suspicion that this represents a very human desire to belittle knowledge, the acquirement of which is considered too tedious. My emphasis on the importance of systematics in botanical research, apart from being probably unconvincing, may seem somewhat outside the subject of this address. But, if a study of the effects of settlement upon our vegetation has any lesson for us at all, it is to indicate clearly the necessity for a closer and more detailed examination of our native plants in all their aspects. In this taxonomy must play its fundamental part.

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Dr. G. A. Waterhouse, the Honorary Treasurer, presented the balance-sheets for the year ended 28th February, 1941, duly signed by the Auditor, Mr. S. J. Rayment, A.C.A. (Aust.); and he moved that they be received and adopted, which was carried unanimously.

No nominations of other candidates having been received, the Chairman declared the following elections for the ensuing session to be duly made:

*President:* A. B. Walkom, D.Sc.

*Members of Council:* E. C. Andrews, B.A., Ida A. Brown, D.Sc., W. R. Browne, D.Sc., Professor J. M. Holmes, B.Sc., Ph.D., F. H. Taylor, F.R.E.S., F.Z.S., A. B. Walkom, D.Sc.

*Auditor:* S. J. Rayment, A.C.A. (Aust.).

The retiring President, on behalf of members, then made a presentation to Dr. A. B. Walkom in appreciation of his long service with the Society as Secretary.

A cordial vote of thanks to the retiring President was carried by acclamation.

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# Linnean Society of New South Wales.

GENERAL ACCOUNT. Balance Sheet at 28th February, 1941.

## LIABILITIES.

	£	s.	d.	£	s.	d.
Capital: Amount received from Sir William Macleay during his lifetime . . . . .						
Further sum bequeathed by his Will . . . . .	20,000		0			0
Contingencies Reserve . . . . .	9,375		16			1
Accumulated Funds . . . . .	29,375		16			1
Commercial Banking Company of Sydney Ltd. . . . .	256		17			6
Suspense . . . . .	21		17			8
Current Liabilities . . . . .	278		15			2
	£29,654		11			3

## ASSETS.

	£	s.	d.	£	s.	d.
Fixed Assets—						
Australian Consolidated Loans, Bonds, at cost . . . . .			500			0
Metropolitan Water, Sewerage and Drainage Board, Debentures, at cost . . . . .			494			7
Rural Bank of N.S.W., Debentures, at cost . . . . .			386			0
Society's Freehold, at cost . . . . .			11,000			0
Science House (one-third share) . . . . .			14,650			0
Loans on Mortgage . . . . .			2,500			0
			29,530			7
Current Assets—						
Cash in hand . . . . .						10
Income Account . . . . .						114
			114			3
			£29,654			11

## INCOME ACCOUNT. Year Ended 28th February, 1941.

	£	s.	d.	£	s.	d.
To Balance from 1939-40 . . . . .	121		17			2
" Salaries . . . . .	855		16			8
" Printing Publications . . . . .	468		9			7
" Illustrations . . . . .	102		9			9
" Rates and Insurance . . . . .	570		19			4
" Postage . . . . .	304		10			6
" Petty Cash . . . . .	40		4			5
" Audit . . . . .	13		18			2
" Printing . . . . .	7		7			0
" Expenses . . . . .	22		15			8
" Attendance and Cleaning . . . . .	14		5			6
" Advertisements . . . . .	34		15			0
	12		19			8
	92		2			10
	£1,999		9			1
By Subscriptions: 1940/41 . . . . .						
Arrears . . . . .			154			7
In advance . . . . .			11			11
Associate . . . . .			12			5
			0			10
" Entrance Fees . . . . .						178
" Interest . . . . .						13
" Rent . . . . .						149
" Science House . . . . .						338
" Sales (including 60 copies of PROCEEDINGS purchased by Government of N.S.W.) . . . . .						275
" Fellowships Account (surplus income at 28th February, 1941, transferred) . . . . .						204
" Bank Expenses . . . . .						725
" Balance to 1941-42 . . . . .						114
			178			13
			13			13
			149			10
			338			0
			275			0
			204			2
			725			18
			114			3
			£1,999			9

## AUDITOR'S REPORT TO MEMBERS.

I have examined the books and vouchers of the Linnean Society for the year ended 28th February, 1941, and certify that the above Balance Sheet shows the true position of the state of the Society's affairs as shown by the books. Certificates of the investments have been produced.

S. J. RAYMENT, Chartered Accountant (Aust.),  
Auditor.

G. A. WATERHOUSE,  
Hon. Treasurer.

Sydney, 11th March, 1941.

4th March, 1941.

**LINNEAN MACLEAY FELLOWSHIPS ACCOUNT.**  
**BALANCE SHEET at 28th February, 1941.**

	£	s.	d.		£	s.	d.
<b>LIABILITIES.</b>				<b>ASSETS.</b>			
Accumulated Funds—				Fixed Assets—			
Amount bequeathed by Sir William Macleay	35,000	0	0	Australian Consolidated Loans, Bonds,	9,300	0	0
Surplus Income Capitalized	15,873	17	5	at cost	200	0	0
				War and Works Loan, at cost	9,500	0	0
				Metropolitan Water, Sewerage and			
				Drainage Board, Debentures, at			
				cost	1,005	0	0
				Rural Bank of N.S.W., Debentures			
				1943, at cost	1,310	16	8
				Rural Bank of N.S.W., Debentures			
				1949, at cost	477	10	0
				Loans on Mortgage	1,788	6	8
					38,218	14	5
					50,512	1	1
				Current Assets—			
				Commercial Banking Company of Sydney Ltd. . . . .	249	15	9
				Commonwealth Savings Bank . . . . .	112	0	7
					50,873	17	5
					£50,873	17	5

**INCOME ACCOUNT. Year Ended 28th February, 1941.**

	£	s.	d.
To Salaries of Linnean Macleay Fellows	1,266	13	4
" Capital Account	333	6	8
" General Account	725	18	10
	£2,325	18	10
By Interest	2,325	18	10
	£2,325	18	10

**AUDITOR'S REPORT TO MEMBERS.**

I have examined the books and vouchers of the Linnean Society for the year ended 28th February, 1941, and certify that the above Balance Sheet shows the true position of the state of the Society's affairs as shown by the books. Certificates of the investments have been produced.

S. J. RAYMENT, Chartered Accountant (Aust.),  
Auditor.

G. A. WATERHOUSE,  
Hon. Treasurer.

Sydney, 11th March, 1941. 4th March, 1941.

## BACTERIOLOGY ACCOUNT.

## BALANCE SHEET at 28th February, 1941.

LIABILITIES.		ASSETS.	
	£	s.	d.
Amount bequeathed by Sir William Macleay .. .. .	12,000	0	0
Accumulated Income Capitalized .. .. .	3,820	0	0
Accumulated Funds .. .. .	15,820	0	0
Income Account at 28th February, 1941 .. .. .	984	2	1
	<u>£16,804</u>	<u>2</u>	<u>1</u>
Fixed Assets—			
Australian Consolidated Loans, Bonds, at cost ..	15,820	0	0
Current Assets—			
Commercial Banking Company of Sydney Ltd. ..	222	12	5
Commonwealth Savings Bank .. .. .	755	9	8
Cash in hand .. .. .	6	0	0
	<u>£16,804</u>	<u>2</u>	<u>1</u>

## INCOME ACCOUNT. Year Ended 28th February, 1941.

	£	s.	d.
To Salaries .. .. .	849	7	1
" Plant House .. .. .	538	18	3
" Printing .. .. .	118	19	5
" Expenses .. .. .	11	4	11
" Petty Cash .. .. .	1	17	6
" Balance to 1941-42 .. .. .	984	2	1
	<u>£2,504</u>	<u>9</u>	<u>3</u>
By Balance from 1939-40 .. .. .	1,472	14	4
" Interest .. .. .	651	14	11
" Donations for assistant to Bacteriologist .. ..	400	0	0
	<u>£2,504</u>	<u>9</u>	<u>3</u>

## AUDITOR'S REPORT TO MEMBERS.

I have examined the books and vouchers of the Linnean Society for the year ended 28th February, 1941, and certify that the above Balance Sheet shows the true position of the state of the Society's affairs as shown by the books. Certificates of the investments have been produced.

S. J. RAYMENT, Chartered Accountant (Aust.),

Auditor.

G. A. WATERHOUSE,  
Hon. Treasurer.

Sydney, 11th March, 1941.

4th March, 1941.

## ABSTRACT OF PROCEEDINGS.

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### ORDINARY MONTHLY MEETING.

26th MARCH, 1941.

Dr. A. B. Walkom, President, in the Chair.

The Donations and Exchanges received since the previous Monthly Meeting (27th November, 1940), amounting to 16 Volumes, 319 Parts or Numbers, 15 Bulletins, 10 Reports and 16 Pamphlets, received from 102 Societies and Institutions and 3 private donors, were laid upon the table.

#### PAPERS READ.

1. Plant Ecology of the Bulli District. ii. Plant Communities of the Plateau and Scarp. By Consett Davis, M.Sc.
2. Plant Ecology of the Bulli District. iii. Plant Communities of the Coastal Slopes and Plain. By Consett Davis, M.Sc.
3. A Summary of certain Aspects of the Scarab Problem, and a Contribution to a Bibliography of the Family Scarabaeidae. By D. Margaret Cumpston, M.Sc.

### ORDINARY MONTHLY MEETING.

30th APRIL, 1941.

Dr. A. B. Walkom, President, in the Chair.

The President announced that the Council had elected Mr. E. C. Andrews, Mr. T. C. Roughley, Professor J. Macdonald Holmes and Mr. R. H. Anderson to be Vice-Presidents for the Session 1941-42.

The President also announced that the Council had elected Dr. G. A. Waterhouse to be Honorary Treasurer for the Session 1941-42.

The President, on behalf of members, expressed congratulations to Professor W. N. Benson on his election as a Fellow of the Royal Society of London.

The Donations and Exchanges received since the previous Monthly Meeting (26th March, 1941), amounting to 18 Volumes, 120 Parts or Numbers, 4 Bulletins, 3 Reports and 3 Pamphlets, received from 59 Societies and Institutions, were laid upon the table.

#### PAPERS READ.

1. Notes on Australian Diptera. xxxix. Family Chloropidae. Part iii. By John R. Malloch. (*Communicated by F. H. Taylor, F.R.E.S., F.Z.S.*)
2. A Survey of the Mistletoe of New South Wales. By Valerie May, M.Sc.
3. Studies on *Corticium rolfsii* (Sacc.) Curzi. By F. L. Milthorpe, B.Sc.Agr.

## PLANT ECOLOGY OF THE BULLI DISTRICT.

## PART II: PLANT COMMUNITIES OF THE PLATEAU AND SCARP.

By CONSETT DAVIS, M.Sc., Lecturer in Biology, New England University College.

(Plates i-ii; one Text-figure.)

[MS. received 9th February, 1940.\* Read 26th March, 1941.]

*Foreword.*

Unavoidably, a considerable period has elapsed between the appearance of Part i of this series (Davis, 1936) and the completion, for publication, of the remaining parts. During the interval, several important papers have appeared, dealing with the plant ecology of the New South Wales coastal region (Pidgeon, 1937, 1938; Fraser and Vickery, 1937, 1938, 1939; Osborn and Robertson, 1939). With reference to the classification of the *Eucalyptus* forest communities submitted in Part i, some further clarification is now necessary.

Pidgeon (1937) has advanced a classification of the *Eucalyptus* forests of the central coastal area of New South Wales, recognizing six associations in the entire region, with subordinate consociations, and giving much broader limits to the association unit than those adopted in Part i of this series. While it is freely admitted that this broader limitation for the association is in accordance with the application of North American workers, and that certain of the 'associations' listed in Part i of this series will in time take their place as 'consociations' within broad association limits, it is submitted that insufficient is known of the environmental, genetic and phylogenetic relations of the various *Eucalyptus* forest communities safely to dogmatize on the natural grouping of consociations at the present stage. If the association be regarded as generic, and the consociation as specific, the procedure adopted in Part i represents the erection of a number of monotypic genera, whereby, admittedly, natural relationships cannot be indicated; the alternative procedure, however, runs the risk of erecting genera including unrelated species.

The following table sets out the differences in the two classifications:

<i>Situation of Community.</i>	<i>Classification of Part i.</i>	<i>Classification of Pidgeon (1937).</i>
Hawkesbury Sandstone, little or no physiographic shelter.	<i>Eucalyptus Sieberiana</i> Association.	Mixed <i>Eucalyptus</i> Forest Association.
Do., moderate physiographic shelter.	<i>E. piperita</i> Association.	Do.
Do., good physiographic shelter.	<i>E. pilularis</i> Association.	Do.
Narrabeen Sandstone, little or no physiographic shelter.	<i>E. piperita</i> Association.	Do.
Do., moderate physiographic shelter; Chocolate Shale, little or no physiographic shelter.	<i>E. saligna</i> Association; <i>E. pilularis</i> Association (upper coastal slopes).	? <i>E. saligna-E. pilularis</i> Association.

\* Note added 23rd September, 1940.—An important paper on plant succession by Pidgeon (Proc. LINN. Soc. N.S.W., lxx, 221-249; issued 16th September, 1940) deals with the general aspects of the area of which the Bulli district forms merely a unit. Circumstances forbid the modification of the present two papers (Plant Ecology of the Bulli District. ii and iii) in the light of knowledge therein presented, or any discussion of points raised. Nevertheless, although much of the ground has been covered, it is still considered worth while to present these two papers in their original form, both as independent (though local and less complete) evidence of certain facts and as maintaining a somewhat different viewpoint on controversial issues.

<i>Situation of Community.</i>	<i>Classification of Part i.</i>	<i>Classification of Pidgeon (1937).</i>
Wianamatta Shale, little or no physiographic shelter.	<i>E. piperita</i> - <i>Angophora lanceolata</i> Association.	Mixed <i>Eucalyptus</i> Forest Association.
Upper Coal Measures (shales and sandstones), little or no physiographic shelter.	<i>E. pilularis</i> Association.	<i>E. saligna</i> - <i>E. pilularis</i> Association.
Upper Coal Measures (tuffaceous mudstone), little or no physiographic shelter.	Mixed <i>Eucalyptus</i> Forest. (a).	Mixed <i>Eucalyptus</i> Forest Association.
Recent Alluvial Soil, little or no physiographic shelter (climax of lagoon succession).	Mixed <i>Eucalyptus</i> Forest. (b).	Do.

The separation, in Part i, of the '*Eucalyptus piperita*-*Angophora lanceolata* Association' from the normal *E. piperita* Association is not justified, and the former is henceforth referred to as the *Angophora lanceolata* facies of the *Eucalyptus piperita* Association.

Pidgeon's grouping of the *Eucalyptus saligna* and *E. pilularis* communities as a single association is probably justified. In Part i the relationship was marked by referring to the communities as corresponding associations (p. 295). The tendency of *E. saligna* to predominate at the ecotone of the *E. pilularis* Association and the rain forest formation on the coastal slopes suggests that it requires better environmental conditions than *E. pilularis*. The distinction of the two associations is tentatively retained in this and subsequent parts for uniformity with the smaller sense of 'association' used throughout.

Pidgeon's separation of the *Eucalyptus pilularis* Community into two associations depending on soil origin (on Hawkesbury Sandstone, Mixed *Eucalyptus* Forest Association, pars; on richer soils, consociation of *E. saligna*-*E. pilularis* Association) seems to add to the complexity of the classification. The community on Hawkesbury Sandstone is closely similar to its manifestations elsewhere, both in the form and height of the dominant tree, and also in the presence of certain species of the lower strata (e.g., *Casuarina torulosa*, *Leucopogon lanceolatus*, *Pteridium aquilinum*, *Imperata cylindrica* var. *koenigii*, *Hardenbergia monophylla*) which are characteristic of the *E. pilularis* Community on Upper Coal Measures soils, but absent from poorer sandstone soils, such as in the *E. Sieberiana* Association. Even the soil properties are similar, due to the improvement of the water-retaining capacity of sandstone soils carrying *E. pilularis*, by humus accumulation, up to a point comparable with that of soils derived from less coarsely-grained rocks.

The *Eucalyptus Sieberiana* Association is a widespread and important unit, which scarcely appears in its typical form north of the Bulli district. It is extensively developed on soils derived from Devonian sandstones on the far south coast of New South Wales, particularly in the Eden district. It also occurs in Victoria and Tasmania, where it assumes the appearance of a wet sclerophyll forest, regarded by some workers as a distinct formation or sub-formation (Wood, 1937), although the distinction is arbitrary. North of the Bulli district other species (e.g., *E. gummifera*, *E. haemastoma*) occupy more important places on correspondingly poor soils, although *E. Sieberiana* extends north as far as the Hawkesbury River.

The separation of the communities dominated by *Eucalyptus piperita* from the *E. Sieberiana* Association appears to be justified, in order to emphasize the fact that *E. piperita* represents a definite grade higher than *E. Sieberiana* in soil requirements, just as *E. pilularis* represents a grade above *E. piperita*. This gradation tends to be obscured by grouping together under the one unit, as the Mixed *Eucalyptus* Forest Association of Pidgeon. It could be equally emphasized by calling the grades consociations (as allowed by Pidgeon, 1937, p. 335), but it would be difficult to group three such consociations into an association without harming other parts of the classification system, e.g., the recognition of the *E. pilularis* unit on all soil types, discussed above.

The classification of Part i is therefore retained throughout the series, with the exception of the *E. piperita-Angophora lanceolata* Association noted above. The classification has sufficient utility for the limited district here dealt with, although it would be difficult to apply it, even with logical extensions, throughout the entire sclerophyll formation of eastern Australia. This difficulty need not be met in the present series, which is purely local in nature; it is hoped that some synthesis of the different classifications will develop when the entire formation comes to be considered. It is further emphasized that the divergence from the classification of Pidgeon does not indicate a divergence in the observance of facts, but merely in opinion as to convenience of tabulation.

#### Nomenclature.

In general, the same procedure in taxonomic names is followed as in Part i, authors' names being appended to species only where the names given by Moore and Betche (1893) are not adhered to. For Pteridophytes the names given by Melvaine (1936) are used throughout, without authors. Many of the names used by Moore and Betche have now been superseded, but this work is nevertheless the only flora available to field workers. In a few cases the names used in Part i have been changed in this and subsequent parts for uniformity with the ecological papers mentioned above. The following are the changes:

*Eucalyptus gummifera* (Gaertn.) Hochr. (*E. corymbosa* of Part i); *Imperata cylindrica* Stapf. var. *koenigii* D. & S. (*I. arundinacea* of Part i); the generic name *Lomandra* is henceforth used in place of *Xerotes*. The name *Gymnoschoenus sphaerocephalus* (R.Br.) Hook. f., as used in Part i, is retained; this is apparently the correct name (see, e.g., Black, 1929, p. 91), although the species is listed by Moore and Betche as *Schoenus sphaerocephalus* Poir. (syn. *Mesomelaena sphaerocephala* Benth.), and by the Census (Maiden and Betche, 1916) as *Gymnoschoenus adustus* Nees.

#### METHODS.

(i). *Soil Analyses*.—A large number of soil samples were tested for various properties, and since the methods used, though constant throughout, were not the usual standard methods, they are detailed fully. The figures are strictly comparable *inter se*, but not necessarily with those given by other workers.

Except for pH and water content, all samples were passed through a sieve with circular holes of diameter 1 mm. The pH was determined by the quinhydrone method (gold electrode), standard procedure being adopted to eliminate the vitiation of the results for comparative purposes by drift. Soils were stirred with distilled water and quinhydrone, stood for 45 minutes, and again stirred. At the end of a further 15 minutes the E.M.F. was read without further stirring.

To estimate comparative water content the soils from a series were collected at the same time in sealed jars, and samples weighed as soon as possible. These were then dried at 90–100°C., the water content being calculated as a percentage of the dry weight.

The method of determining water-retaining capacity gives a higher reading than the methods usually adopted. Metal cylinders (height 2.5 cm.; diameter 5 cm.) with gauze bottoms were lined with filter-paper, cut to cover the bottom but to allow drainage at the periphery, since drainage through the filter-paper becomes impeded by clay particles. The lined cylinders were weighed dry ( $m_1$ ) and wet ( $m_2$ ). They were then filled with saturated soil, drained for 30 minutes, and weighed ( $m_3$ ). The whole was then dried to constant weight ( $m_4$ ) at 90–100°C. The water-retaining capacity is calculated

thus:  $\frac{m_3 - m_4 - (m_2 - m_1)}{m_4 - m_1} \cdot 100$ , representing a percentage of the dry weight. The usual

method of weighing soil dry, and allowing it to take up water, proved impracticable, as dry soils, especially sandy soils with high organic content, could not be caused to take up water without loss of part of the sample from the container. The high temperature of drying (90–100°C.) in the method used was essential from considerations of time; but it renders the final figure for water-retaining capacity high by including in it some water not available to plant roots.

Loss on ignition, of soils previously dried at 110°C., expressed as a percentage of the dry weight, gives a reasonably close approximation to the total organic content (humified and unhumified). Exceptions are soils of high clay content (especially Wianamatta Shale soils, and to a less extent soils from Chocolate Shale and some of the Upper Coal Measures), and the early stages of the sand-dune succession described in Part iii, where a fair proportion of calcium carbonate is present.

In representative samples the portion of the figures for loss on ignition, represented by humus, was estimated by determining the percentage of the original soil decomposed to gaseous and volatile substances by continued treatment with hot 6% hydrogen peroxide.

The chloride contents (listed in Part iii) were obtained by lixiviating a known weight of oven-dry soil with distilled water, and estimating the filtrate with standard silver nitrate. The chloride contents are expressed as a percentage weight of chlorine (chloride ion) per dry weight of soil. This figure is undoubtedly variable for any situation, due to seasonal factors of spray incidence and leaching. All the figures given refer to soils collected in July 1938, a period preceded by some time of low rainfall and little leaching. Figures for salinity of soil solution, as sodium chloride, grm. per litre (Lagatu and Sicard, 1911), depending on the water-content of the soil, may be calculated from the data of Table 4, Part iii. This factor, although it is at any one time a truer index of the conditions to which plant roots are subjected, must be exceedingly variable for any situation, due to seasonally varying soil moisture.

For all the above factors, soils of the A<sub>1</sub> horizon (1-4 inches), the zone of maximum utilization by plant roots, have been determined.

Percentage of water held at sticky-point and sand fraction were estimated for soils of varying origin. From these results the index of texture (Hardy, 1928) was calculated (percentage of water held at sticky-point less one-fifth percentage of sand). The samples used for this work were from the A<sub>2</sub> horizon, as in the A<sub>1</sub> horizon varying organic content would affect the water held at sticky-point; whereas the property, the investigation of which is here desired, is that of the original soil as conditioned by parent rock, and not the soil resulting from the interaction of vegetation with original soil.

The index of texture actually appears to be a less useful index of the soil with respect to vegetation than is the percentage of water held at sticky-point alone. The index of texture suffers further in that no distinction is made in its calculation between coarse and fine sand, both lowering the index of texture figure equally. Thus almost all the sand fraction of Hawkesbury Sandstone soils is coarse sand, and almost all that of Chocolate Shale soils is fine sand, the latter with a greater capacity to hold water in the estimation at sticky-point.

(ii). *Floristics*.—Only in the relatively homogeneous *Gymnoschoenus sphaerocephalus* Community (swamp subclimax on Hawkesbury Sandstone) were accurate quadrats undertaken. These took the form of metre-quadrats, each shoot of the rhizomatous vegetation being removed by shears and counted as one unit. This procedure was necessitated by the density of the vegetation (Pl. ii, C).

In the lower strata of the remaining communities, and in the tree stratum of the brush or rain-forest, rough counts of the numbers of each species in a series of areas were made. These areas were circles of 10 yard radius or, for brush trees, 20 yard radius. For each community, the number of individuals of each species was multiplied by the factor necessary to bring the commonest species to 100 units. The species were then graded into five classes: abundant (A), 100-41; common (C), 40-16; occasional (O), 15-6; rare (R), 5-3; and very rare (VR), 2 or less. These limits were chosen in consideration of the lack of complete domination by one species of the strata examined; it is clear that a species occurring in a ratio of 1:25 to the commonest species would not be rare, in the accepted sense, if the commonest species practically dominated the community; but in the communities examined co-dominance of a number of species was the rule.

Some modification of the results obtained was found necessary, due to the accumulation of additional data by inspection, without analysis, of certain areas not visited when the counts were made. This applies especially to the Hawkesbury Sandstone shrubs. The classes are therefore only approximate, but probably closer to the truth than a gradation by inspection alone could attain.

The proportion of the counts in which each species appeared gave some indication as to localization, and in the floristic lists species are tabulated as local (L) if this feature is particularly marked.

PLANT COMMUNITIES OF THE PLATEAU AND SCARP.

(1) *Hawkesbury Sandstone.*

(a). *Eucalyptus Sieberiana Association.*

This community (Pl. i, A and B), present in situations on the Hawkesbury Sandstone lacking physiographic shelter, is usually associated with fairly efficient drainage conditions, although the dominant occasionally approaches positions of fairly high water-table near the ecotone with swamp communities. Soils are typically of a depth greater than three feet, often much more, but in some places the association occurs on shallower soils, the dominant then being dwarfed and often malformed. These areas may be regarded as a stage in the lithosere, detailed later, immediately preceding the true climax.

Soil properties for certain typical parts of the association are given in Table 1. The texture of the soil originating from Hawkesbury Sandstone is coarse, although the weathering of local shale bands in this series gives a small but definite clay fraction in some places, and in particular gives the B horizon in most places the nature of a clay-sand. The following estimates were obtained for A<sub>2</sub> soils:

Water held at sticky-point 22-29%; sand fraction 96-97%; index of texture 3-10.

The uniformly low organic content is insufficient to counteract the coarseness of the soil, and the water-retaining capacity is low. The highest figure for water-retaining capacity (37%) represents a sample with higher clay-content than normal. Of the figures given for loss on ignition (2.3-3.5%), some 50% appears to represent humus. The soils are markedly acid, and appear to be poor in nutrient elements.

TABLE 1.  
*Properties of Soils on Hawkesbury Sandstone carrying Climax and Post-climax Communities.*

	W.R.C. (%).	Loss on Ignition (%).	pH.
<i>Eucalyptus Sieberiana</i> Association .. .. .	25	2.5	5.4
	29	3.2	4.9
	28	3.0	4.9
	29	2.9	5.2
	37	2.3	4.5
	33	3.5	4.9
<i>Eucalyptus piperita</i> Association.. .. .	43	7.3	5.2
	46	8.0	4.4
	49	8.7	4.6
	78	26.0	4.9
	83	30.0	4.7
	76	23.0	5.1
<i>Eucalyptus pilularis</i> Association .. .. .	80	23.0	5.0
	91	33.0	5.0
<i>Eucalyptus piperita</i> Association, near Brush Ecotone (Loddon Falls) .. .. .	113	49.0	4.6
Brush .. .. .	90	30.0	5.2
	120	35.0	5.2
	120	49.0	5.3
	130	48.0	5.0

Some indication of the range of the dominant has been given earlier. A consideration of its environment elsewhere suggests that neither poor drainage nor shallowness of soil is one of the limiting factors here preventing the development of species such as *Eucalyptus piperita* and *E. pilularis*. These factors are rather to be sought in the coarseness of the soil texture, and the resulting low water-retaining capacity in the absence of humus development.

Structurally the association is composed of a tree stratum typically 40-60 feet high, with discontinuous canopy. Low trees are relatively unimportant, *Banksia serrata* being common only in limited areas; some of the larger shrubs, however, fall within the microphanerophyte class. The shrub stratum is prominent and floristically diverse, though usually not continuous. The ground stratum seldom forms a complete cover, except in areas tending towards swamp conditions. The classification into life-forms is indicated in the floristic lists.

Floristically, the composition of the association is as follows:

- MM:\* A, *Eucalyptus Sieberiana* (dominant); O(LC), *E. gummifera*, *E. micrantha* Benth.; VR(L), *Casuarina suberosa*, *Acacia elata*.
- M: LC, *Banksia serrata* (Shrubs); C, *Leptospermum stellatum*, *L. flavescens*, *Banksia ericifolia*; O, *Hakea acicularis*; VR(L), *Kunzea corifolia*.
- N: A, *Grevillea oleoides*, *Hakea dactyloides*, *H. pugioniformis*, *Isopogon anemonifolius*, *Lambertia formosa*, *Persoonia lanceolata*, *P. salicina*, *Petrophila pulchella*, *Leptomeria acida*, *Olax stricta*, *Acacia discolor*, *A. juniperina*, *A. suaveolens*, *Aotus villosa*, *Bossiaea heterophylla*, *B. scolopendria*, *Dillwynia floribunda*, *Pultenaea elliptica*, *Ricinocarpus pinifolius*, *Pimelea linifolia*, *Leptospermum scoparium*, *Epacris microphylla*, *E. obtusifolia*, *Leucopogon juniperinus*, *L. microphyllus*, *Sprengelia incarnata*, *Dampiera stricta*; C, *Banksia spinulosa*, *Conospermum ellipticum*, *C. taxifolium*, *Grevillea sericea*, *G. punicea*, *Lomatia silaifolia*, *Acacia myrtifolia*, *Gompholobium latifolium*, *Comesperma ericinum*, *Baeckea crenulata*, *B. linifolia*, *Kunzea capitata*, *Trachymene linearis*, *Epacris paludosa*; O, *Symphonema paludosum*, *Xylomelum pyriforme*, *Daviesia ulicina*, *Gompholobium grandiflorum*, *Eriostemon Crowei*, *Phebalium diosmeum* Juss., *Dodonaea triquetra*, *Stackhousia viminea*, *Callistemon lanceolatus*, *Calythrix tetragona*, *Darwinia virgata*, *Leucopogon collinus*, *Woolisia pungens*, *Hemigenia purpurea*; R, *Banksia paludosa* R.Br., *Telopea speciosissima*, *Phyllota phyllicoides*, *Boronia pinnata*, *Lasiopetalum ferrugineum*, *Epacris longiflora*, *Leucopogon virgatus*, *Chloanthes Stoechadis*; VR, *Banksia aemula*, *Grevillea sphacelata*, *Cryptandra ericifolia*, *Melaleuca squamea*, *Leucopogon amplexicaulis*, *L. esquamatus*, *Dampiera Brownii*.
- Ch: A, *Lomandra obliqua* MacBride, *Patersonia glauca*; C, *Doryanthes excelsa*, *Mirbelia reticulata*, *Tetratheca ericifolia*, *Ampera spartioides*, *Hibbertia stricta*, *Stylidium graminifolium* Swartz; O, *Xanthorrhoea hastilis*, *Patersonia sericea*, *Conospermum tenuifolium*, *Grevillea capitellata*, *Darwinia taxifolia*, *Xanthosia pilosa*, *Opercularia ovata*, *Pomax umbellata*, *Lobelia dentata*; R, *Gompholobium minus*, *Hovea heterophylla*, *Hybanthus filiformis*, *Viola hederacea*, *Styphelia triflora*, *Goodenia heterophylla*; VR, *Kennedyia prostrata*, *Comesperma volubile*.
- H: A, *Haemodorum planifolium*, *Actinotus minor*; LC, *Selaginella uliginosa*; O, *Gahnia psittacorum*, *Lomandra longifolia* Labill., *L. filiformis* J. Britten; R, *Eragrostis Brownii*, *Stipa pubescens*, *Caustis flexuosa*, *Tricostularia paludosa* Benth., *Haemodorum teretifolium*; VR, *Entolasia marginata* Hughes, *Caustis pentandra*, *Stypandra caespitosa*, *Rubus fruticosus* (introd.).
- G: A, *Leptocarpus tenax*, *Lepyrodia scariosa*; O, *Thelymitra ixioideis*; VR, *Burchardia umbellata*, *Cryptostylis longifolia*, *Glossodia major*.
- E: O, *Cassytha paniculata*, *C. pubescens*; † VR, *Loranthus celastroides*. ‡

The above lists include some species (e.g., *Symphonema paludosum*, *Olax stricta*, *Baeckea* spp.) which are more characteristic of swampy areas, and others (e.g., *Leptocarpus tenax*, *Lepyrodia scariosa*) which occur in this association and in swamps in approximately equal frequencies. The frequency given above in all cases represents

\* Abbreviations for life-forms, frequency, and localization used throughout paper: MM, mega- and mesophanerophytes; M, microphanerophytes; N, nanophanerophytes; Ch, chamaephytes; H, hemicryptophytes; G, geophytes; HH, helo- and hydrophytes; S, stem-succulents; E, epiphytes. (Actually, no hydrophytes are present in the species listed under HH.) A, abundant; C, common; O, occasional; R, rare; VR, very rare; L, local or locally; LC, locally common (see METHODS, Floristics).

† Rooted hemiparasites, classed as "E", the nearest life-form.

‡ In these lists the species are arranged in order of families according to the classification of Engler and Prantl, and within each family, alphabetical.

that observed in the *Eucalyptus Sieberiana* Association, regardless of the frequency of the species elsewhere; it has been noted earlier that this association extends in some cases to rather poorly-drained soils.

Apart from minor environmental variations, such as in efficiency of drainage, with their resultant influences, e.g., on the proportion of swamp-tolerant species, the association is characterized by local variations, often striking, without apparent environmental cause. These variations are most marked in the shrub stratum; they may well be due to chance occurrences in seed dispersal, and to the extinction of some species in belts where bush-fires of preceding years have been most severe.

Two environmental variants were noted in Part i:

(1). On the eastern edge of the plateau, particularly north of Sublime Point, on the gradual slope running down towards the sandstone scarp (Fig. 1), the vegetation assumes an aspect slightly different from other parts of the plateau. Drainage conditions are good, so that species favoured by swampy conditions are absent. *Eucalyptus gummifera* increases in abundance, often becoming nearly as important as *E. Sieberiana*; both species are frequently stunted, as the soil is often very shallow. In most places the cover by the lower strata increases, often to 100%. Additional species found in this zone, but not elsewhere in the association, include:

N: *Xanthorrhoea arborea* R.Br., *Hakea saligna*, *Persoonia revoluta*, *Pultenaea daphnoides*, *Correa speciosa*, *Actinotus Helianthi*, *Dracophyllum secundum*, *Cassinia denticulata*, *Olearia elliptica* DC.

N (climbers): *Smilax glycyphylla*, *Billardiera scandens*.

Ch: *Dianella coerules*, *Halorrhagis teucrioides*, *Helichrysum scorpioides*.

G: *Lycopodium densum*, *Gleichenia flabellata*.

Certain species found elsewhere in the association increase in prominence; the following may be specified:

N: *Banksia spinulosa*, *Boronia pinnata*, *Phebalium diosmeum* Juss., *Lasiopetalum ferrugineum*, *Epacris longiflora*, *Chloanthes Stoechadis*.

Ch: *Xanthosia pilosa*, *Opercularia ovata*.

The factor inducing this variation seems to be the shelter from the west, which, while too slight to affect the trees, allows certain more mesophytic types to develop in the lower strata. The soil differs little, if at all, from that in other parts of the association. Certain species cannot be considered more mesophytic than those of other areas; such forms as *Xanthorrhoea arborea* and *Actinotus Helianthi*, occurring only at the very edge of the plateau, are to be considered rather as species limited to very dry, rocky habitats.

(2). The slopes facing west, in the more westerly parts of the area studied, are characterized by better drainage and lower rainfall than the flatter areas of the eastern parts of the plateau (cf. Part i). *Eucalyptus gummifera* increases in relative abundance; in the lower strata there are a decrease in percentage cover and a general absence of swamp-tolerant species.\*

The *Eucalyptus Sieberiana* Association is in general similar to much of the low forest on sandstone in the Sydney district, although its dominant fails to reach such development near Sydney either in size or frequency. The lower strata are somewhat poorer floristically than in corresponding situations near Sydney, and possess very few additional species (e.g., *Grevillea oleoides*).

(b). *Developments subject to Physiographic Shelter.*

With increasing physiographic shelter, Hawkesbury Sandstone soils carry successively higher types of vegetation, the sequence being *Eucalyptus piperita* Association-*E. pilularis* Association-Brush (sub-tropical rain-forest) (Pl. i, C, D, E respectively). The characteristics of the soils of this series are listed in Tables 1 and 2. The series is characterized by a successive rise in organic content of the soil, proportionally raising the water-retaining capacity, which appears to be the chief factor influencing the development of the first two associations. The addition of a higher

\* The occurrence of some well-developed trees of *Syncarpia laurifolia* Ten. near the Bulli Lookout, intermingled with *E. Sieberiana* in an otherwise normal part of the association, is absolutely unexplained. *Syncarpia* is a unit of a much higher vegetational community.

TABLE 2.  
*Hawkesbury Sandstone Soils on Transect with Increasing Shelter.*

	W.R.C. (%).	Loss on Ignition (%).	pH.	Water Content (%) (10.7.38).
<i>Eucalyptus Sieberiana</i> Association ..	37	2.3	4.5	1.9
<i>E. piperita</i> Association ... ..	46	8.0	4.4	8.2
<i>E. pilularis</i> Association .. .. .	80	23.0	5.0	12.9

proportion of humus\* to a soil of coarse texture raises the water-retaining capacity to the level of finer soils with less humus, such as carry these associations on the other geological series of the district.

The rise in organic content seems to be associated chiefly with a high average moisture-content, a result of drainage conditions and weak insolation, depending on the physiography. It is not comparable with the rise of organic content under swampy conditions, to which are limited plants tolerant to low pH and poor root aeration. Apart from moisture-content, other factors inducing a high organic content in this series are decreased insolation and infrequency of bush-fires, both factors directly combating oxidation of soil humus. The infrequency of bush-fires is dependent on the relatively moist nature of the habitat and vegetation.

In no case studied could the full vegetational sequence be observed on a single transect. In the more gradual valleys south of Cataract Reservoir, *Eucalyptus Sieberiana* gives place to *E. piperita* (on the upper slopes) and *E. pilularis* (on the lower slopes and valley floor); shelter is throughout insufficient for brush, which however develops where erosion has led to the penetration of the Narrabeen beds at the bottom of some gullies. In the abrupt Hawkesbury Sandstone gorge at Loddon Falls, brush is developed at the lower levels; on the steep sides, *Eucalyptus piperita* occurs. *E. pilularis* does not

\* Humus accounts for approximately half of the loss-on-ignition figures of Tables 1 and 2.

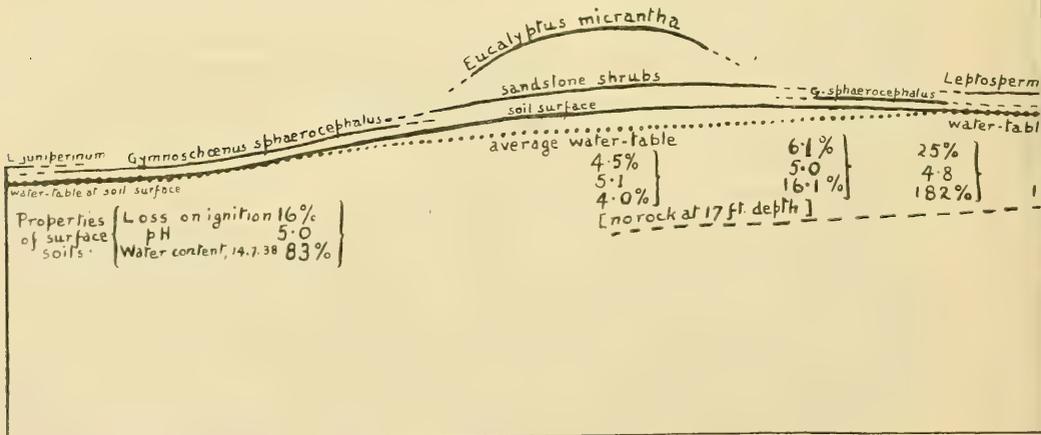


Fig. 1.—Section west of Hawkesbury Sandstone scarp, about half a mile north of ...  
average water-table

develop, the ecotone between the *Eucalyptus piperita* Association and the brush formation, where soil conditions are suitable for *E. pilularis*, is very narrow, due to the steepness of the slope. Brush is developed to a limited extent in several ravines in the Hawkesbury Sandstone scarp at the eastern limit of the plateau; *Eucalyptus piperita* and *E. pilularis* do not develop here as intermediates, the belt between *E. Sieberiana* (on the edge of the plateau) and the brush (in the floor of the ravine) constituting the rocky shoulders of the ravine, almost devoid of soil.

The limitation of brush to the lower parts of the Loddon Falls gorge and to the scarp ravines, together with a general consideration of brush development in the Bulli district as a whole, suggests that this formation is conditioned primarily by shelter from wind and sun, secondarily only by soil requirements. The assumption that *Eucalyptus piperita* and *E. pilularis* are conditioned by soil alone, and not by wind and sun, is based on the fact that their canopies are fully exposed in most situations studied on Hawkesbury Sandstone as on other soils.

Additional elements of the *Eucalyptus piperita* and *E. pilularis* Associations on the Hawkesbury Sandstone include the mesophanerophyte, *Casuarina torulosa* (second association only), and the microphanerophytes, *Hakea saligna*, *Persoonia linearis*, *Exocarpus cupressiformis*, *Acacia longifolia*, *A. mollissima* and *Elaeocarpus reticulatus*; the nanophanerophytes, *Trachymene Billardieri* and *Leucopogon lanceolatus*; the chamaephytes, *Hibbertia Billardieri* and *Hardenbergia monophylla*, and the geophyte *Pteridium aquilinum*. These are absent from the *E. Sieberiana* Association. There are also present species found in the *E. Sieberiana* Association only at the extreme east of the plateau (e.g., *Smilax glycyphylla*, *Pultenaea daphnoides*, *Halorrhagis teucroides* and *Cassinia denticulata*), and species of the normal *E. Sieberiana* Association (e.g., *Banksia spinulosa*, *Persoonia salicina*, *Lasiopetalum ferrugineum* and *Dodonaea triquetra*), sometimes increased in frequency compared to the *E. Sieberiana* Association (e.g., *Entolasia marginata* Hughes and *Viola hederacea*).

The high and low trees are characteristic of the *Eucalyptus piperita* and *E. pilularis* associations on other geological formations, the Eucalypts in some cases reaching nearly 100 feet in height. The lower strata include many of the same species as are found in these associations on other geological series, but are structurally different,

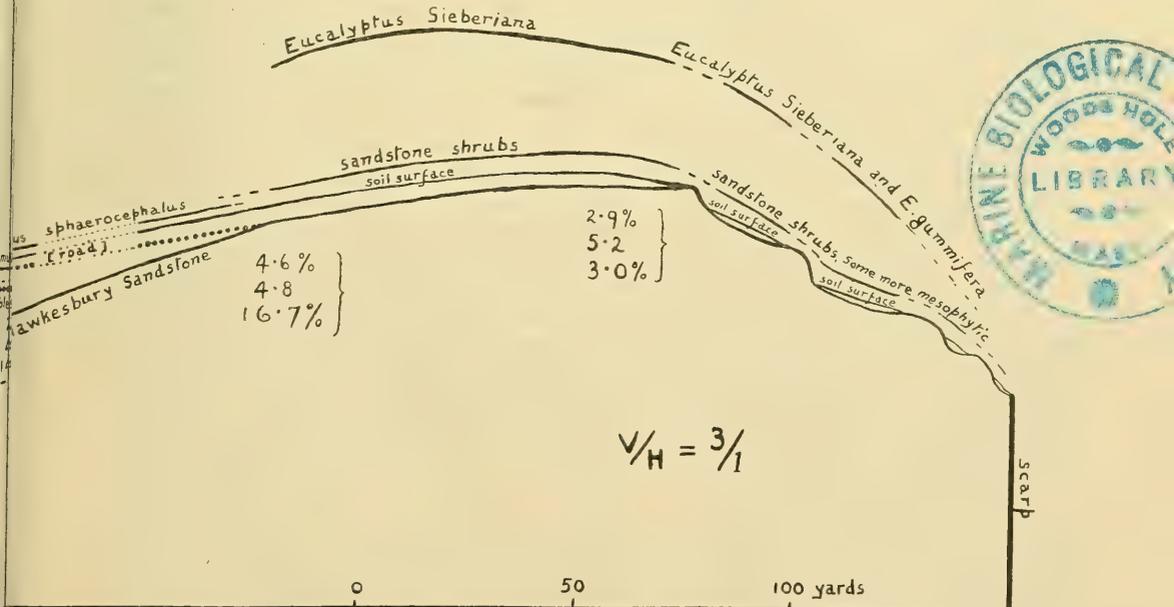


Fig. 1. Height and composition of vegetation, outline of soil surface, soil properties, and profile of rock surface.

especially in the lower percentage cover. This latter is partly due to the fact that Hawkesbury Sandstone situations carrying these associations (sloping valley sides) have a fairly high percentage of exposed rock.

Brush, as developed at Loddon Falls (Pl. i, E), has a structure more or less typical of this formation on other geological series (closed canopy, absence of shrubs, presence of a ground layer of ferns), but is very poor floristically:

- MM: *Doryphora Sassafras*, *Cryptocarya glaucescens*, *Callicoma serratifolia*, *Pittosporum undulatum*, *Eucryphia Moorei*, *Tristania laurina*.  
 M: *Drimys insipida* Druce, *Tristania nerifolia*.  
 Ch: *Todea barbara*.  
 H: *Adiantum diaphanum*, *Asplenium flabellifolium*.  
 E: *Davallia pyxidata*, *Pleopeltis diversifolia*, *Tmesipteris tannensis*.  
 (Epiphytes, also growing on rock surfaces.)

The only common tree amongst these, which is characteristically a brush type (as opposed to a member of the 'wet gully' or creek-edge flora), is *Doryphora Sassafras*. *Callicoma* and *Pittosporum*, though often occurring in true brush, also extend to the 'wet gully' flora, a brush-sclerophyll ecotone community, while the species of *Tristania* commonly occur beside rocky creeks, often with little shelter from wind and sun.

(c). *Lithoseres*.

It is impossible adequately to account for rock succession or zonation without first considering the past history and present course of the physiographic development of the area studied. The sandstone plateau, part of the Nepean Ramp, is an example of rejuvenated physiography, representing a late Tertiary peneplain raised by Pleistocene uplift.\* As such, its exposed rock surfaces are mostly manifestations of a highly immature topography. To this extent, the postclimax communities detailed in the preceding section may be considered expressions of a purely allogenic succession.

On the evidence of the physiographic facts cited above, zonations between bare rock and forest, except possibly in the case of certain of the moist lithoseres detailed later, are, on the average, retrogressive, though many simulate temporal succession, and in some cases exposure of a new rock surface by physiographic change (falls of rock, or scouring of soil into a relatively recently-formed gully) may be followed by colonization and true succession up to a certain stage, that is, up to a time when denuding factors once again come into play. In spite of general retrogression, it is convenient to regard the zonation stages from rock to forest as a lithosere, whilst remembering that allogenic factors prevent true succession to a climax under the average conditions of the area. The ultimate peneplanation of the area, in the processes of which plant life undoubtedly plays a part (e.g., in rock decomposition), is too distant to visualize in terms of the present flora.

Bare rock surfaces, leading by a vegetational zonation of xeric communities to forest, are to be found at the extreme easterly edge of the plateau, and also on its more dissected parts (e.g., west of Darkes' Forest, above Cataract Reservoir, and near Loddon Falls). Where the plateau abuts on the scarp, and on the gullies of these dissected regions, it exhibits bare rock at the edge, leading back to forest by a sequence of stages of vegetation, accompanied by an increase in soil depth. The plants nearest to the bare rock surface are most frequently xeric mosses, less frequently lichens, ferns (*Polypodium Billardieri*, *Cyclophorus serpens*) or orchids (*Dendrobium linguiforme*, *D. speciosum*). Next in linear sequence comes a zone of herbs and straggling shrubs (e.g., *Tillaea Sieberiana* Schultes, *Darwinia taxifolia*), leading to a community of typical sandstone shrubs (notably *Boronia pinnata*, *Actinotus Helianthi*, and certain Epacridaceae), and so to *Eucalyptus* forest, the trees being frequently stunted in the zone of shallower soil.

The floristics and soil changes of this sere have been fully detailed by Pidgeon (1938, pp. 4-15), and will receive no further consideration here. The situations listed above, where the plateau gives place to the easterly scarp or to dissecting gullies, are characterized by a soil becoming more shallow as the sudden fall in surface is approached. It should be obvious that westerly migration of the scarp, or further

\* Or uplift immediately preceding Pleistocene times.

dissection of the plateau by gullies (processes which are surely though gradually going on) can lead only to a decrease in size of the plateau, the communities of the plateau edge, which may be assumed to be more or less in equilibrium with the existing topography, being gradually forced backwards, whilst maintaining their present zonation. The immediate result of this process of erosion will be to denude of soil a greater percentage of rock than is exposed at present, although in some local instances conditions in newly-formed gullies will possibly be suitable for some of the postclimax communities dealt with in the preceding section.

Young trees of *Eucalyptus gummifera* have been noted on certain of the most easterly parts of the plateau, where shallow soil and bare rock form a mosaic of fairly level surface. Were it not for the westerly migration of the scarp, such a situation would almost certainly lead to the formation of the *Eucalyptus Sieberiana* Association. This development may be taking place in a few isolated cases, as the migration of the scarp is slow in terms of plant growth.

The rock exposures of the dissected areas (e.g., alternating ridges and gullies leading down to Cataract Reservoir) are more confused than those on the plateau edge, being usually represented by boulders projecting well above the soil surface. In such cases zonation is more abrupt and irregular than on the rock exposures of the more level areas of the plateau.

Zonation from rock to forest under wet, swampy conditions is characteristic of many parts of the plateau. In some cases at least, as where the rock exposure is surrounded by soil, deepening to carry forest vegetation, it seems probable that autogenic succession in time is proceeding. The succession is marked by an increase in soil depth and, in the later stages, a lowering of the water-table. Soil properties, illustrating this, and the decreasing organic content, are listed in Table 3. It should be noted that, although the water-content of the soil is here shown as successively decreasing, this does not apply under all weather conditions; in dry weather, the water-content of the soil of the first stage falls below that of the swamp stage.

TABLE 3.  
*Soil Properties for Moist Lithosere on Hawkesbury Sandstone.*

—	W.R.C. (%).	Loss on Ignition (%).	pH.	Water Content (%) (2.7.38.)
Wet Moss Stage .. .. .	73	17.0	4.9	71.0
“Hemicryptophyte Stage” .. ..	57	12.0	5.0	61.0
Local Swamp .. .. .	39	5.6	5.1	47.0
Local Swamp (with shrubs) .. ..	37	4.3	5.1	35.0
<i>Eucalyptus micrantha</i> Stage .. ..	32	3.1	5.4	14.0
<i>Eucalyptus Sieberiana</i> Association (climax)	25	2.5	5.4	4.4

The earliest stage of this moist lithosere (Pl. i, G) consists of mosses (unidentified), which are followed by the ‘hemicryptophyte stage’ (Pidgeon, l.c.), the most prominent species of which is *Lepyrodia scariosa*; the herbs *Drosera peltata*, *D. pygmaea*, *D. spathulata*, *Mitrasacme polymorpha* and *Utricularia lateriflora* are also common. This stage leads, by deepening of the soil, to the swamp stage, of the following floristic composition:

N: *A. Banksia latifolia*, *B. latifolia* var. *minor*, *Hakea pugioniformis*, *Epacris microphylla*, *Sprengelia incarnata*; C, *Symphyonema paludosum*, *Olax stricta*, *Viminaria denudata*, *Baeckea crenulata*, *B. linifolia*, *Leptospermum juniperinum* Sm.; O, *Grevillea oleoides*, *Persoonia salicina*, *Aotus villosa*, *Dillwynia floribunda*, *Callistemon lanceolatus*, *Leptospermum lanigerum*, *Melaleuca squarrosa*, *Epacris obtusifolia*, *E. paludosa*, *Dampiera stricta*; R, *Banksia paludosa* R.Br., *Hakea dactyloides*, *Isopogon anemonifolius*, *Lambertia formosa*, *Stackhousia viminea*;

VR, *Persoonia lanceolata*, *Petrophila pulchella*, *Pultenaea elliptica*, *Pimelea linifolia*, *Melaleuca thymifolia*, *Trachymene linearis*.

(Note: Some of the above shrubs, e.g., *Grevillea*, *Isopogon*, *Lambertia*, do not extend to the wettest parts of the swamps; most, however, are present under all conditions. The frequencies are for the average of a variety of local swamps.)

- Ch: A, *Bauera rubioides* (incl. var. *microphylla*), *Mitrasacme polymorpha*; C, *Drosera binata*, *D. spathulata*, *Euphrasia Brownii*, *Utricularia lateriflora*, *Goodenia bellidifolia*; O, *Drosera peltata*, *D. pygmaea*, *Boronia parviflora*, *Stylidium graminifolium* Swartz; R, *Hibbertia stricta*; VR, *Xanthorrhoea hastilis*, *Mitrasacme paludosa*, *Villarsia exaltata* F.v.M., *Utricularia dichotoma*.
- H: A, *Selaginella uliginosa*, *Gymnoschoenus sphaerocephalus*, *Hypolaena lateriflora* Benth., *Xanthorrhoea minor*; C, *Lindsaya linearis*, *Actinotus minor*; O, *Gahnia psittacorum*, *Tricostularia paludosa* Benth., *Xyris gracilis*, *Haemodorum planifolium*; VR, *Caustis flexuosa*, *Juncus planifolius*, *Haemodorum teretifolium*.
- HH: A, *Gleichenia dicarpa*, *Leptocarpus tenax*, *Leptrodia scariosa*, *Restio complanatus*, *Chorizandra sphaerocephala*, *Lepidosperma laterale*; LC, *Lycopodium laterale*; O, *Blandfordia nobilis*, *Sowerbaea juncea*; VR, *Burchardia umbellata*.  
(Note: All apparently cryptophytic species are classed as helophytes.)
- Th: O, *Halorrhagis micrantha*; R, *Centrolepis strigosa*.
- E: R, *Cassytha pubescens*.

The *Eucalyptus Sieberiana* Association, which may be regarded as the climax under these conditions, is reached only where drainage factors allow the lowering of the average water-table. *Eucalyptus micrantha* Benth. usually forms a definite ecotone between the swamp and the climax (Pl. i, H).

The parts of the swamp closer to the forest may be recognized as 'shrub swamp' (Pidgeon, l.c.); they are composed of the same species as are found in the swamp stage, with an increase in abundance of the shrubs found in the swamps, together with some shrubs less tolerant of a very high water-table. Even in the 'shrub-swamp', the shrub stratum is not nearly continuous; the ground stratum of both swamp and 'shrub-swamp' is continuous, the height of the vegetation being from 1-2 feet.

In one case, a young tree of *Eucalyptus micrantha* was noted in the 'shrub-swamp' stage, well beyond the limits of the older trees, indicating successional relationship in time.

(d). *Extensive Swamp or Moor Communities.*

On the relatively flat parts of the plateau, usually on deep soils (presumably part of the late Tertiary peneplain), extensive swamp or moor communities develop, sometimes up to 2-3 miles in extent. These swamps are particularly well developed immediately to the north and west of Sublime Point. The inhibition of tree development is due primarily to the high water-table; wherever the average water-table falls below 3-4 feet, *Eucalyptus Sieberiana*, or more often *E. micrantha* Benth., develops. This relationship is shown in Figure I, a section west of the scarp about half a mile north of Sublime Point. The soil properties of this large swamp, which may be termed the *Gymnoschoenus sphaerocephalus* Community (Pl. ii, A), are shown in Table 4. The soil is characterized by a high organic content (some 60% of the loss-on-ignition figure

TABLE 4.  
*Swamp Soils on Hawkesbury Sandstone.*

	W.R.C. (%)	Loss on Ignition (%)	pH.
<i>Gymnoschoenus sphaerocephalus</i> Community ..	81	21.0	4.8
	91	23.0	4.7
	120	25.0	4.8
Local Swamp .. .. .	58	16.0	5.0
Moor at Madden's Plains .. .. .	33	3.5	4.9
	39	4.2	4.8
	40	5.7	4.8
Shrub Swamps .. .. .	45	4.6	4.8
	46	6.1	5.0
	37	4.3	5.1

representing humus) and low pH. The plants of this community must tolerate a high water-table, with its resultant poor root aeration and high acidity. They are seldom subject to water shortage, although the surface soil to a depth of several inches occasionally becomes very dry in the higher parts of the community.

The floristics of this rather homogeneous community are set out below, the figures being those for eight quadrats each of one square metre. The numbers refer to each ascending shoot or cluster of vegetation; thus each ascending shoot of *Selaginella uliginosa* was taken as one unit, and each tussock of *Gymnoschoenus sphaerocephalus* is made up of from six to ten units, representing separate clusters of vegetation. Life forms are given for the vascular species, the seedlings of shrubs being classed as nanophanerophytes. Because of the density of the vegetation (Pl. ii, C), it was necessary to remove each shoot or plant with shears as it was counted.

Species.	Life-form.	Shoots per sq. metre for eight quadrats							
<i>Fossombronia</i> sp. . . . .	—	..	+	..	..	+	..	..	..
<i>Sphagnum</i> sp. . . . .	—	+	..	..	..	+	..	..	..
<i>Dichæta</i> sp. . . . .	—	..	+	..	..	+	..	..	..
<i>Lycopodium laterale</i> . . . . .	HH.	55	152	..	3	..	1	29	57
<i>Selaginella uliginosa</i> . . . . .	H.	117	227	126	187	73	129	98	167
<i>Schizæa bifida</i> . . . . .	HH.	..	1*	..	..	..	..	..	..
<i>Entolasia marginata</i> Hughes . . . . .	H.	..	..	..	9	..	..	..	..
<i>Chorizandra sphaerocephala</i> . . . . .	HH.	12	7	12	11	9	15	5	7
<i>Gymnoschoenus sphaerocephalus</i> . . . . .	H.	18	12	12	46	46	21	17	31
<i>Hypolaena lateriflora</i> Benth. . . . .	H.	49	23	47	69	108	121	31	37
<i>Lepidosperma Forsythii</i> Hamilt. . . . .	HH.	54	94	36	67	11	5	51	47
<i>Lepidosperma laterale</i> . . . . .	HH.	..	..	2	..	4	..	5	1
<i>Leptocarpus tenax</i> . . . . .	HH.	..	5	17	15	11	29	3	15
<i>Lepyrodia scariosa</i> . . . . .	HH.	7	5	30	..	1	27	5	13
<i>Restio complanatus</i> . . . . .	HH.	10	4	2	19	..	21	5	11
<i>Xyris gracilis</i> . . . . .	H.	..	5	7	35	5	21	..	6
<i>Xanthorrhoea minor</i> . . . . .	H.	..	..	6	1	8	..	5	7
<i>Banksia latifolia</i> var. <i>minor</i> . . . . .	N.	..	2†	..	..	..	..	1	..
<i>Hakea pugioniformis</i> . . . . .	N.	1†	..	1†	1†	1†	..	1	..
<i>Persoonia salicina</i> . . . . .	N.	..	..	1	..	..	..	..	..
<i>Drosera pygmaea</i> . . . . .	Ch.	..	..	..	..	3	..	..	2
<i>Viola hederacea</i> . . . . .	Ch.	..	..	..	3*	..	..	..	..
<i>Baeckea limifolia</i> . . . . .	N.	..	1†	..	..	..	..	..	..
<i>Epacris obtusifolia</i> . . . . .	N.	..	47†	..	..	2†	..	12†	..
<i>Mitrasacme polymorpha</i> . . . . .	Ch.	..	..	19	10	20	11	..	15
<i>Villarsia exaltata</i> F.v.M. . . . .	Ch.	3†	2†	1†	..	..	4†	..	..
<i>Utricularia lateriflora</i> . . . . .	Ch.	..	..	..	5	..	3	..	1
<i>Goodenia bellidifolia</i> . . . . .	Ch.	..	..	30†	3†	24†	2†	15†	5†

\* Weak plant. † Seedling. All apparently cryptophytic species are classed as helophytes.

From general inspection of other parts of this community, this table would appear to give a substantially correct picture of the floristics, except that *Banksia latifolia* (normal form) is as common as *B. latifolia* var. *minor*, and *Lepidosperma Forsythii* is generally less common than in the measured quadrats. In the lower parts of the swamp (Fig. 1), where the water-table is continuously at the surface, and where the water is usually moving in runnels or small creeks, *Leptospermum juniperinum* Sm. is developed in definite belts, sometimes with the addition of *Gahnia psittacorum*, rarely with a prominent belt of *Lepidosperma Forsythii*.

The community is exactly similar to the extensive 'Button-grass Plains' of Tasmania (especially important in western Tasmania and on the central plateau). The structure (tussocky vegetation 3-4 feet high, with smaller sedge-like vegetation and chamaephytic herbs at ground level, and occasional shrubs) is identical, and the most prominent species (*Gymnoschoenus sphaerocephalus*) is common to both. Many of the subsidiary species are common to both expressions of the community, though the Tasmanian development is, as would be expected, richer floristically, the present example being extra-limital.

Near the northern limit of the area studied, at Madden's Plains, equally extensive swamp-like tracts occur for two to three miles west of the scarp. The soil is here shallower than in the swamps immediately north of Sublime Point, rock level often being reached at 18 inches, and the conditions are throughout drier. The vegetation, which may be conveniently termed a 'moor', has more of the appearance of the 'shrub swamp' stage noted above (under wet lithosere). *Gymnoschoenus sphaerocephalus* is less, *Xanthorrhoea minor* more prominent, than in the swamps near Sublime Point. Shrubs are generally more abundant, those present in the Sublime Point swamps being increased in frequency, and others (e.g., *Melaleuca squarrosa*) added. In one sector, the Madden's Plains moor continues over a gentle rise to become continuous with the Sublime Point swamps immediately to the south.

The soils of the Madden's Plains moors are less subject to high water-table, and have a correspondingly lower organic content, although the pH is as low as in the Sublime Point swamps (Table 4).

These swamp and moor communities, both in the Bulli district and in Tasmania, are, surprisingly, very liable to fires. This is most likely in dry seasons, but even in rather damp weather a fire will 'run' through the *Gymnoschoenus sphaerocephalus* Community, each tussock of the dominant having always a basal residue of dead, combustible leaves. In the spring of 1935, almost the entire area of the swamps near Sublime Point, and parts of Madden's Plains, were swept by a fire which removed all the aerial parts of the vegetation. However, nearly all species of this community have hypogean parts which, buried in wet soil, survived the fire. The sedge-like types possess submerged or half-submerged rhizomes, while some of the shrubs have subterranean root-stocks capable of regeneration. Within three weeks from the time of the fire, the rhizomes had begun to send up new shoots (Pl. ii, D); in one year the community had regained its normal appearance, both in height and structure, and floristically. The only noticeable change was the unexplained decrease in abundance of *Lepidosperma Forsythii* Hamilton.

The value of cryptophytic and hemicryptophytic life-forms in swamp communities subject to fire is obvious; fire here replaces the unfavourable season, resistance to which formed the original criterion on which Raunkiaer based his life-form classification.

In the Bulli district, the high rainfall and relatively low saturation-deficit of the eastern parts of the plateau, where these swamp communities occur, probably assist in the retention of swamp conditions; other parts of the coastal range (e.g., the mountains behind Bateman's Bay), where similar conditions of rain and mist prevail, possess similar extensive swamps. The regeneration of the swamp communities, after fire, to their former level, indicates that the reduction of saturation-deficit at the soil surface, due to the dense tangle of vegetation characteristic of these communities, is relatively unimportant in maintaining the communities in their present state. After fire, the vegetation being removed, there is no delay in evaporation due to vegetational cover; nevertheless, this temporary removal of the vegetation has no effect in raising the shrub element of the subsequent vegetation, or in altering the community in any way towards a drier state.

In Tasmania, the reasons for the high water-table conditioning this community are more dependent on climate (rainfall, saturation-deficit), and less on drainage-inhibiting topography, than in the present case. The *Gymnoschoenus sphaerocephalus* Community is so widespread in Tasmania as almost to justify its recognition as a climax formation (high moor), although the presence of neighbouring formations (sclerophyll forest, temperate rain-forest) where drainage is more efficient renders such a classification doubtful. The general preponderance of forest communities in the Bulli district, however, leaves no doubt that the *Gymnoschoenus sphaerocephalus* Community should there be regarded as a subclimax, widespread in extent, controlled topographically by poor drainage conditions. Causes of the high water-table, which in many cases is higher than the slope of the ground would otherwise allow, are the clay horizon at 4 feet depth (probably formed by the weathering of shale bands in the Hawkesbury Sandstone when these soils were originally formed, rather than by vertical

movement of the clay fraction), and the presence in many places of soil furrows at right angles to the slope (Pl. ii, B), impeding water flow. These furrows alternate with parallel ridges carrying tussocky vegetation, distant from one to two yards, the variation in height between peak and trough of the soil surface being 4-12 inches. The furrows were particularly apparent in a visual survey of the area from the air. The troughs of these furrows have a relatively low percentage cover by vegetation. Their origin may possibly be sought in the burrowing activities of swamp crayfish,\* which are very common in this area; the troughs of the furrows are characterized by the presence of holes, the retreats of the crayfish. Once started, the maintenance of this system of furrows is not difficult to explain, the crayfish remaining in the moister and more congenial trough regions, the vegetation favouring the better-drained and less disturbed ridges. The initiation of the furrow system, with its surprising regularity, is more difficult to explain. It has not been observed in this community in Tasmania, where, however, crayfish of the same general habits are equally common.

In the swamps noted under 'wet lithoseres', the high water-table is usually due to the contour of the underlying rock; this does not apply in the Sublime Point swamps, where the soil is very deep (Fig. 1), and even at Madden's Plains, where the soil is shallower, the contour of the underlying rock is convex, and apparently would be ineffective in preventing lateral drainage.

Within the general area of the swamps, *Eucalyptus micrantha* Benth. develops wherever local conditions cause a lower water-table to occur (Pl. ii, E, F and G). These conditions are fulfilled in some cases by gentle hillocks or ridges, or above certain slight increases in the slope of the soil surface. Thus the *Eucalyptus micrantha* clump of Figure 1 (Pl. ii, F and G) is allowed by a relatively sudden, though still gentle, fall of the soil surface to the west of the clump (left in Figure 1) and to the north; the ground to the south of this clump carries the typical *Gymnoschoenus sphaerocephalus* Community, though it is on a slightly higher level than the clump. All such developments of *Eucalyptus micrantha* are bordered by a shrub zone (Pl. ii, F and G).

In the cases of two such clumps, younger trees of *E. micrantha* extend beyond the general outline. This would indicate a local forward succession, possibly caused by a fall in water-table following erosion of the soil below the clump, with a consequent increase in slope.

Throughout the swamp and moor communities, species of ants (*Myrmecia nigrocincta*, and others) form nests by raising dead leaves and sand grains onto the tussocky vegetation. Calcination of such nests leaves a residue of over 50% by weight. In the forest communities, especially at the ecotone of *E. micrantha* and swamp, these nests occur in considerable numbers, not raised, but on the surface of the drier soil. While this carriage of soil particles is discounted as a cause of local forward succession from swamp conditions, the effect of these ants in aerating the soil of swamp ecotone communities cannot be considered negligible.

On the rise between Madden's Plains and the Sublime Point swamps, in a typical moor community, young trees of *Eucalyptus gummifera* have developed during the last eight years (Pl. ii, H). The reason for this is unknown. It is very surprising to find this species apparently initiating a local succession to forest vegetation, instead of *E. Sieberiana* or *E. micrantha*, which are more tolerant of swamp conditions.

In conclusion, it may be stated that a general succession from these swamps and moors to forest can occur only when the drainage conditions are improved by a change in topography, by artificial drainage channels or by the gradual erosion of the plateau surface, e.g., further extension of the Loddon Falls gorge.

(c). *Vegetation of the Scarp.*

The vegetation of the scarp is efficiently sheltered from westerly winds, and from the sun after noon. Variations in the water-supply, from situations where the soil is continuously damp to those where it is usually very dry, account for the diversity of

\* *Euastacus hirsutus* (McCulloch).

species encountered. As a whole, the vegetation may be regarded as a retrograde lithosere, growing in unstable circumstances. In general, dynamic equilibrium obtains between the normal processes of autogenic succession and the retrograde influences of soil denudation and falling rock.

Drier areas consist of bare rock, partly covered by mats of *Cyclophorus serpens*, *Polypodium Billardieri* and *Dendrobium linguiforme*, with the nanophanerophytes, *Xanthorrhoea arborea* R.Br. and *Actinotus Helianthi*, developing where sufficient soil is formed. Moister areas consist of a mosaic of bare rock, liverworts and mosses, and, where sufficient soil is formed, the following species:

- N: (Shrubs, or trees less than six feet in height.) *Banksia ericifolia*, *Doryphora Sassafras*, *Callicoma serratifolia*, *Ceratopetalum apetalum*, *Pultenaea daphnoides*, *Cryptandra ericifolia*, *Pomaderris phillyroides*, *Backhousia myrtifolia*, *Leptospermum stellatum*, *Melaleuca hypericifolia*, *Tristania laurina*, *Dracophyllum secundum*, *Epacris coriacea*, *E. longiflora* and *Leucopogon lanceolatus*.
- Ch: *Todea barbara*, *Billardiera scandens*, *Viola hederacea*, *Halorrhagis teucroides*, *Xanthosia pilosa*, *X. tridentata*.
- H: *Blechnum capense*, *B. Patersoni*, *Gleichenia dicarpa*, *Gahnia psittacorum*, *Hypolaena lateriflora* Benth. (N.B. Hemicryptophytic under these conditions; some of the species are cryptophytic in deeper soils.)
- E: *Cassytha paniculata*.

The above species include some of the more mesophytic species of the *Eucalyptus Sieberiana* Association, some brush species, and a few swamp types restricted to seepage areas on the scarp.

### (2). Wianamatta Shale.

Vegetation at Darkes' Forest may be classed as the *Angophora lanceolata* facies of the *Eucalyptus piperita* Association (Pl. i, F). Structurally, it represents high forest (80-100 ft.), canopy subdiscontinuous, with a prominent low-tree stratum, an almost continuous shrub stratum, and a ground stratum, continuous only where the shrubs are least dense. Floristically, its composition is as follows:

- MM: A, *Angophora lanceolata*, *Eucalyptus piperita*; O, *Eucalyptus eugenioides*, *E. gummiifera*; R, *Eucalyptus micrantha* Benth., *E. Sieberiana*.
- M: C, *Acacia binervata*, *A. longifolia*; O, *Hakea saligna*, *Exocarpos cupressiformis*, *Rapanea variabilis* Mey.; R, *Acacia decurrens* var., *A. rubida*, *Leptospermum stellatum*.
- N: A, *Banksia ericifolia*, *B. spinulosa*, *Persoonia salicina*, *Acacia myrtifolia*; C, *Hakea pugioniformis*, *Lambertia formosa*, *Acacia discolor*, *Pultenaea daphnoides*, *Dampiera Brownii*; O, *Hakea dactyloides*, *Lomatia silaifolia*, *Persoonia ferruginea*, *P. lanceolata*, *Leptomeria acida*, *Pimelea linifolia*, *Epacris pulchella*, *Olearia ramulosa* Benth.; R, *Banksia paludosa* R.Br., *Lomatia ilicifolia*, *Leucopogon esquamatus*, *L. lanceolatus*, *Cassinia aurea*, *Olearia viscidula* Benth.
- N (climber): C, *Smilax glycyphylla*, *Kennedyia rubicunda*.
- Ch: C, *Doryanthes excelsa*, *Hibbertia Billardieri*, *Halorrhagis teucroides*; O, *Schoenus imberbis*, *Glycine clandestina*, *Viola hederacea*; R, *Patersonia glauca*.
- H: A, *Paspalum dilatatum* Poir. (introd.); C, *Culcita dubia*, *Blechnum cartilagineum*, *Lindsaya microphylla*, *Lomandra longifolia*, *Rubus fruticosus* (introd.).
- G: C, *Pteridium aquilinum*; R, *Pterostylis nutans*.
- Th: C, *Hypochaeris glabra* (introd.); O, *Poa annua* (introd.), *Gnaphalium purpureum*.
- E: C, *Loranthus celastroides*.

Soil properties for this community are given in Table 5. They give no indication why the community should appear to be a sandstone one, enriched by a few more mesophytic species, rather than a true shale community. The absence of such trees as *Eucalyptus pilularis* and *Syncarpia laurifolia* Ten., characteristic of the Wianamatta Shale in other districts, is inexplicable. Trees of *Eucalyptus globulus*, introduced in this area, flourish at Darkes' Forest.

### (3). Narrabeen Series.

In some areas between Bulli Lookout and Broker's Nose, the Hawkesbury Sandstone beds have been removed by erosion to expose the Narrabeen beds (Part i, Pl. xv). These latter consist of an upper layer of Chocolate Shale some 50 feet in depth, below which is a considerable thickness of rather fine-grained Narrabeen Sandstone. Erosion

TABLE 5.  
*Properties of Soils of Wianamatta and Narrabeen Series.*

	W.R.C. (%)	Loss on Ignition (%)*	pH.
Wianamatta Shale.			
<i>Eucalyptus piperita</i> Association ( <i>Angophora lanceolata</i> facies) .. .. .	91	28	5.0
	91	25	5.1
	97	24	5.5
Narrabeen Sandstone.			
<i>Eucalyptus piperita</i> Association, no physiographic shelter .. .. .	50	18	5.6
<i>Eucalyptus saligna</i> Association, partial physiographic shelter .. .. .	58	31	5.6
Chocolate Shale.			
<i>Eucalyptus saligna</i> Association, no physiographic shelter .. .. .	53	16	5.6
	60	14	6.3
	62	16	5.2
	71	16	5.2
	76	23	5.9
<i>Brush</i> , partial physiographic shelter ..	100	39	5.5
	130	36	5.3

\* Only a small fraction of this figure represents humus.

*A<sub>2</sub> Horizon.*

Derivation of Soil.	Water Held at Sticky-Point (%)	Sand Fraction (%)	Index of Texture.
Wianamatta Shale .. .. .	49.0	82	33
	50.1	83	33
	53.0	72	39
	55.0	70	41
Chocolate Shale .. .. .	46.4	94	28
	49.0	92	31
	50.7	89	33
Narrabeen Sandstone, relatively pure.. ..	30.0	93	11
Narrabeen Sandstone, contaminated with Chocolate Shale .. .. .	45.0	95	26
	46.7	95	28

of these beds is only incipient, and the Chocolate Shale weathers more rapidly than the underlying sandstone; under these circumstances, it is impossible to find a Narrabeen Sandstone soil uncontaminated with at least a small fraction of the shale soil. This, and the variation in slope and shelter, lead to some confusion in the arrangement of communities. It appears that on the least contaminated of the Narrabeen Sandstone soils, *Eucalyptus piperita* is dominant in unsheltered situations, with *E. eugenoides*, *E. gummifera*, *E. pilularis* and *E. saligna* of occasional occurrence, *E. paniculata* and *E. Sieberiana* rare. On the soils of the Chocolate Shale (except where physiographic shelter leads to the development of brush), and in moderately sheltered positions on the Narrabeen Sandstone, *Eucalyptus saligna* is dominant, with *E. pilularis* and *Syncarpia laurifolia* Ten. common, and *E. eugenoides*, *E. paniculata* and *E. piperita* rare. Introduced pine-trees (*Pinus radiata*) also occur in these communities.

The structure of these communities, which may be termed the *Eucalyptus piperita* and *E. saligna* associations respectively, is similar to the Darkes' Forest (Wianamatta Shale) community. Soil properties are shown in Table 5. The following represents a reasonably complete estimate of the floristics, most species being common to both associations:

MM: See above.

M: C, *Ezocarpus cupressiformis*, *Acacia longifolia*, *A. mollissima*; R, *Hakea saligna*.

- N: A, *Persoonia salicina*, *Idigofera australis*, *Pomaderris elliptica*, *Pimelea ligustrina*, *Prostanthera Sieberi* Benth.; C, *Banksia spinulosa*, *Persoonia ferruginea*, *P. lanceolata*, *Acacia discolor*, *A. suaveolens*; O, *Persoonia revoluta*, *Acacia myrtifolia*, *Zieria Smithii*, *Astrotricha floccosa*, *Cassinia longifolia*; R, *Persoonia linearis*, *Pultenaea daphnoides*, *Dodonaea triquetra*, *Lasiopetalum ferrugineum*, *Helichrysum diosmifolium*, *H. elatum*; VR, *Xylomelum pyriforme*, *Citriobatus multiflorus*, *Pultenaea flexilis*.
- Ch: C, *Hibbertia Billardieri*, *Halorrhagis teucrioides*; O, *Kennedya rubicunda*, *Viola hederacea*; R, *Billardiera scandens*, *Geranium pilosum*.
- H: LC, *Blechnum cartilagineum*, *Imperata cylindrica* var. *Koenigii*, *Paspalum dilatatum* Poir. (introd.), *Rubus fruticosus* (introd.); O, *Cynodon dactylon*; R, *Culcita dubia*, *Eragrostis Brownii*, *Stipa pubescens*.
- G: A, *Pteridium aquilinum*.
- Th: O, *Poa annua* (introd.), *Hypochoeris glabra* (introd.); R, *Gnaphalium luteoalbum*, *G. purpureum*.
- E: O, *Loranthus celastroides*, *Cassytha paniculata*; VR, *Cymbidium suave*.

In conditions of partial shelter from the west, brush develops on the Chocolate Shale; this formation occurs in efficient shelter on the Narrabeen Sandstone. It is structurally similar to the coastal brush to be described in the next part of this series. The only species present in the brush of the Narrabeen beds on the plateau area yet absent from the brush of the coastal slopes is the tree-fern, *Dicksonia antarctica*.

In parts of the *Eucalyptus saligna* Association (supra), where shelter is slightly too inefficient for true brush to develop, some species (e.g., *Livistona australis*, *Alsophila australis*) are added, giving the vegetation the nature of an ecotone community.

Around the borders of Cataract Reservoir (Pl. i, I), the vegetation shows a regular zonation conditioned by artificial raising of the water-table. *Myriophyllum propinquum* A. Cunn. is the chief representative of the floating stage; occasionally, fall in water level in the reservoir leaves this species on the drying mud surface, where it persists for a time as a land plant, usually forming red pigment. Near the upper limit of the water a hemicryptophytic zone occurs, with *Juncus pallidus*, *J. bufonius*, *Poa annua* (introd.), *Gratiola Peruviana* and, further back, *Imperata cylindrica* var. *Koenigii*. When expanses of mud are exposed below this zone by a fall in water level of long duration, therophytes temporarily colonize it (e.g., *Centipeda minima* A.Br. et Aschers, *Erigeron crispus* Pourret (introd.)). Behind the hemicryptophytic zone, the *Eucalyptus saligna* Association is present, shrubs of *Melaleuca squamea* and *Leptospermum flavescens* occupying an intermediate position where the high water-table inhibits tree development.

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EXPLANATION OF PLATES I-II.

Plate i.

- A.—*Eucalyptus Sieberiana* Association on Hawkesbury Sandstone, south of Cataract Reservoir.
- B.—*Eucalyptus Sieberiana* Association on Hawkesbury Sandstone, south of Sublime Point. The soil is rather shallow, and rock outcrops occur.
- C.—*Eucalyptus piperita* Association on Hawkesbury Sandstone, upper slopes of gully south of Cataract Reservoir.
- D.—*Eucalyptus ptilularis* Association on Hawkesbury Sandstone, lower slopes of gully south of Cataract Reservoir.
- E.—Depauperate brush (subtropical rain-forest formation) on Hawkesbury Sandstone, bottom of Loddon Falls Gorge.
- F.—*Eucalyptus piperita* Association (*Angophora lanceolata* facies) on Wianamatta Shale soil, Darke's Forest.
- G.—First stages of zonation from exposed Hawkesbury Sandstone rock under moist soil conditions (moist lithosere); mosses, and *Lepyrodia scariosa*. Near Loddon Falls.
- H.—Moist lithosere near Loddon Falls. Hawkesbury Sandstone outcrop in foreground, leading by moss and 'hemicyptophyte' stages to swamp and forest. Trees with pale trunks in middle distance are *Eucalyptus micrantha* Benth., passing to *Eucalyptus Sieberiana* Association in background.
- I.—Zonation beside Cataract Reservoir, Narrabeen Series.

Plate ii.

- A.—*Gymnoschoenus sphaerocephalus* Community north of Sublime Point.
- B.—Natural contour furrows in *Gymnoschoenus sphaerocephalus* Community north of Sublime Point. The position of the furrows is indicated by oblique lines of darker vegetation, corresponding to the wetter nature of the soil.
- C.—Metre quadrat in *Gymnoschoenus sphaerocephalus* Community, north of Sublime Point.
- D.—*Gymnoschoenus sphaerocephalus* Community north of Sublime Point, regenerating after a fire which had removed all aerial parts one month previously. *Gymnoschoenus sphaerocephalus* and *Xanthorrhoea minor* shooting from hypogean remains.
- E.—Clump of trees of *Eucalyptus micrantha* Benth. surrounded by *Gymnoschoenus sphaerocephalus* Community, south of Cataract Reservoir. Note young tree on left of clump.
- F, G.—Clump of young trees of *Eucalyptus micrantha* Benth. in *Gymnoschoenus sphaerocephalus* Community north of Sublime Point. The zone of shrubs outlying the trees corresponds to intermediate conditions of water-table (cf. Fig. 1).
- H.—*Gymnoschoenus sphaerocephalus* Community at Madden's Plains, with bushes and young trees of *Eucalyptus gummifera* developing.

APPENDIX.

Life-Form Spectra for Communities of Plateau.

	MM.	M.	N.	Ch.	H.	G.	HH.	Th.	S.	E.	No. of Species.
<i>Eucalyptus Sieberiana</i> Association ..	4	5	54	19	11	5	..	..	..	2	130
Swamp and Shrub Swamp (moist lithosere) .. .. .	..	..	43	22	18	..	13	3	..	1	74
<i>Gymnoschoenus sphaerocephalus</i> Community .. .. .	..	..	20	24	24	..	32	..	..	..	25
<i>Eucalyptus piperita</i> Association ( <i>Angophora lanceolata</i> facies) ..	12	14	42	12	10	3	..	5	..	2	59
<i>Eucalyptus saligna</i> and <i>E. piperita</i> Associations (Narrabeen Series)	15	7	41	10	13	2	..	7	..	5	59

## PLANT ECOLOGY OF THE BULLI DISTRICT.

## PART III: PLANT COMMUNITIES OF THE COASTAL SLOPES AND PLAIN.

By CONSETT DAVIS, M.Sc., Lecturer in Biology, New England University College.

(Plates iii-iv.)

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(1). *Eucalyptus pilularis* Association.

This community occupies soils of the Narrabeen Sandstone and Upper Coal Measures on the coastal slopes and plain where conditions are not favourable for the development of brush (subtropical rain-forest) or brush ecotone communities. One exception is the community occurring on soils derived from tuffaceous mudstone (Upper Coal Measures) at Towroddie (infra). Settlement has caused destruction or alteration of large areas of the *Eucalyptus pilularis* Association, much of the community as it exists at present representing second-growth timber of the dominant. Even where the high trees are untouched, the lower strata are often much altered by clearing and grazing, fire, and introduced plants. Areas from which the dominant has been entirely cleared have been omitted from the present study.

Structurally, the community (Pl. iv, A) comprises a high tree stratum of the dominant, together with *Eucalyptus paniculata* and *Syncarpia laurifolia* Ten., reaching over 150 feet in height in some cases; the canopy is never continuous. Mesophanerophytes (*Casuarina torulosa*, *Acacia binervata*) are moderately frequent on the slopes; microphanerophytes are seldom prominent. The shrub layer is rather sparse; the ground layer, chiefly hemicyptophytic, is almost continuous except on the driest ridges.

Soil properties (Table 1; for methods, see Part ii of this series) exhibit a wide range. The lowest figures for water-retaining capacity (30-36%) show no improvement over the Hawkesbury Sandstone soils of the plateau (cf. *Eucalyptus Sieberiana* Association, Part ii of this series), but the lower (e.g., B) horizons of the Upper Coal Measures soils show a marked increase in water-retaining capacity over the surface soils to which Table 1 applies.

TABLE 1.  
*Soil Properties for Eucalyptus Associations of Coastal Slopes and Plain.*

	W.R.C. (%).	Loss on Ignition (%)	pH.
<i>Eucalyptus pilularis</i> on soils of Upper Coal Measures (Shales and Sandstones) ..	30	2.8	6.2
	34	7.2	5.8
	36	10.0	5.5
	49	5.3	5.7
	49	9.2	5.5
	69	4.8	6.2
Mixed <i>Eucalyptus</i> Forest on tuffaceous mudstone soil, Upper Coal Measures .. ..	53	14.0	5.5
	88	18.0	5.2
	97	19.0	5.2
Mixed <i>Eucalyptus</i> Forest on recent alluvial soil (climax to subsaline lagoon succession) ..	63	13.0	6.3
	71	14.0	6.3
	83	18.0	6.1
	91	20.0	6.0

The following is a floristic estimate of the less disturbed parts of this association:

MM: A\* (dominant), *Eucalyptus pilularis*; C, *Casuarina torulosa* (slopes only), *Eucalyptus paniculata*, *Syncarpia laurifolia* Ten.; O (LC), *Acacia binervata*,

\* Abbreviations for life-form, frequency, and localization, as in Part ii of this series.

- Eucalyptus eugenioides* (plain only), *E. saligna* (brush ecotone dominant); VR, *Eucalyptus botryoides*.
- M: O, *Persoonia linearis*, *Leucopogon lanceolatus*, *Rapanea variabilis* Mey., *Notelaea longifolia*; R, *Elaeocarpus reticulatus*; VR, *Acacia mollissima*.
- N: A, *Acacia myrtifolia*, *A. suaveolens*; C, *Persoonia salicina*, *Indigofera australis*, *Oxylobium trilobatum*, *Pimelea ligustrina*, *Goodenia ovata*, *Helichrysum diosmifolium*, *Senecio dryadeus* Sieb.; O, *Zieria Smithii*, *Sida rhombifolia*, *Prostanthera Sieberi* Benth., *Helichrysum bracteatum* Willd., *H. elatum*, *Olearia ramulosa* Benth.; O (L), *Hakea pugioniformis*, *Citriobatus multiflorus*, *Leptospermum flavescens*, *Lantana camara* (introd.); R, *Pimelea limifolia*, *Cassinia denticulata*, *Olearia argophylla* F.v.M.; VR, *Phyllota phyllicoides*, *Pultenaea flexilis*.
- N (climbers): C, *Smilax glycyphylla*, *Clematis aristata*, *Billardiera scandens*; O, *Geitonoplesium cymosum*.
- Ch: A, *Hardenbergia monophylla*, *Hibbertia dentata*; C, *Viola hederacea*, *Plantago lanceolata* (introd.); O, *Dianella longifolia*, *D. revoluta*, *Glycine clandestina*, *Geranium pilosum*, *Hibbertia Billardieri*, *Halorrhagis teucroides*, *Astroloma humifusum*; R, *Dianella coerulea*, *Hypoxis hygrometrica*, *Tillaea Sieberiana* Schultes, *Bossiaea prostrata*; VR, *Desmodium varians*, *Plantago varia*.
- H: A, *Paspalum dilatatum* Poir. (introd.), *Rubus fruticosus* (introd.); C, *Doodia aspera*, *Cynodon dactylon*, *Eragrostis Brownii* (including var. *patens*), *Imperata cylindrica* var. *Koenigii*, *Carex paniculata*, *Lomandra longifolia* Labill.; LC, *Selaginella uliginosa*; O, *Themeda australis* Stapf., *Lomandra multiflora* Britt., *Oxalis corniculata*; O (L), *Adiantum aethiopicum*, *Asplenium flabellifolium*; R, *Blechnum cartilagineum*, *Calamagrostis quadrisetata* Spreng., *Oplismenus compositus*, *Poa caespitosa*; VR, *Stipa pubescens*, *Luzula campestris*, *Lomandra filiformis* J. Britten.
- G: A, *Pteridium aquilinum*; O, *Schelhammera undulata*, *Caladenia carnea*, *Dipodium punctatum*, *Pterostylis nutans*; O (L), *Burchardia umbellata*, *Microtis porrifolia*; R, *Tricoryne simplex*, *Caladenia alba*; VR, *Schizaea dichotoma*, *Calochilus campestris*, *Pterostylis ophioglossa*.
- E: C, *Loranthus celastroides*; O, *Cassytha paniculata*; VR, *Cassytha glabella*.
- Th: A, *Hypochoeris glabra* (introd.); C, *Wahlenbergia gracilis*, *Gnaphalium japonicum*, *Sonchus oleraceus* (introd.); O, *Poa annua* (introd.), *Phytolacca octandra* (introd.), *Anagallis arvensis* (introd.), *Erythraea australis*, *Solanum nigrum*, *Gnaphalium luteo-album*, *G. purpureum*, *Taraxacum officinale* Weber (introd.); R, *Stellaria flaccida*, *Erechthites arguta* DC.

On the wider parts of the coastal plain (e.g., near Corrimal) both *Syncarpia laurifolia* Ten. and *Eucalyptus eugenioides* assume a position of local dominance in a few cases. *Casuarina torulosa* is absent from these areas, being characteristic of the slopes. *Eucalyptus saligna* is not a typical member of this association, being rather the dominant of the brush ecotone community, which might almost be considered as part of the *Eucalyptus saligna* Association noted in Part ii of this series.

The absence of such trees as *Eucalyptus gummifera* and *E. Sieberiana* from the sclerophyll forests of the slopes and plain is somewhat surprising; it may be due to the higher pH of these areas (5.5-6.2, as opposed to 4.9-5.4 for soils carrying these species on the plateau), or to competition.

*Mixed Eucalyptus Forest.*

On the north side of Towroddie Creek a Mixed *Eucalyptus* Forest occurs on soils derived from a tuffaceous mudstone, a local representative of the Upper Coal Measures. Soils from this situation are finer in texture\* than is normal for the Upper Coal

\* Samples from the A<sub>2</sub> horizon of the mudstone soil and of other Upper Coal Measures soils have the following properties:

	Water Held at Sticky-Point (%).	Sand Fraction (%).	Index of Texture.
Mudstone	37.5	85	20
	38.0	84	21
Other Upper Coal Measures soils	19.0	88	2
	19.5	87	3
	25.9	95	7
	44.6	71	31
	45.0	70	31

Measures, but this does not adequately explain the difference between the vegetation and the normal *Eucalyptus pilularis* Association. The area is close to the sea, and only a slight distance above the level of a subsaline lagoon; however, on the south side of Towroddie Creek a pure stand of *Eucalyptus pilularis* is developed on soil derived from Upper Coal Measures shale, in an otherwise exactly comparable situation.

The trees of this mixed forest are lower than those of the *Eucalyptus pilularis* Association, and somewhat gnarled (Pl. iv, B), possibly as a result of sea-winds. Co-dominants are *Eucalyptus eugenioides*, *E. longifolia*, *E. paniculata* and *E. punctata*, with *E. botryoides* occurring occasionally. The lower strata, when undisturbed, resemble those of the *Eucalyptus pilularis* Association, including low trees of *Notelaea longifolia*, shrubs of *Acacia myrtifolia*, *Oxylobium trilobatum* and *Pimelea linifolia*, and a ground layer of *Pteridium aquilinum*, *Cynodon dactylon*, *Burchardia umbellata* and annuals such as *Hypochoeris glabra*, as its most important members. To these are added elements of the seres discussed below (e.g., *Leucopogon Richei* and *Hibbertia volubilis* from the psammosere, and *Gahnia psittacorum* from the subsaline hydrosere), and a few brush species (e.g., *Clerodendron tomentosum*).

The whole community agrees closely with the neighbouring Mixed *Eucalyptus* Forest occurring on recent alluvial soils, and interpreted as climax of the lagoon sere. This resemblance may possibly be explained by the assumption that the soil in the present case, though derived from the underlying rock, has in the recent past been partly flooded by lagoon waters, which have since been lowered by allogenic causes.

#### (2). Brush (Subtropical Rain Forest).

Brush is developed on soils derived from the Narrabeen Sandstone and Upper Coal Measures wherever sufficient shelter occurs, usually in situations with a copious supply of soil water. The formation occurs on the Chocolate Shale on the dissected parts of the plateau, tolerating on soils of this rock type either situations of efficient shelter, but low average soil moisture (e.g., immediately below the top of Bulli Pass), or situations with slight shelter from the west, but with a better supply of soil moisture (e.g., immediately west of the top of Bulli Pass; Davis, 1936, Pl. xv, J). Development of brush on Hawkesbury Sandstone soils is limited to areas of extreme shelter (cf. Part ii of this series).

Three main factors, then, enter into the conditioning of brush development.

(1) Physiographic shelter from dry (westerly) winds and, to a less extent, from insolation; (2) supply of soil moisture, dependent on drainage and evaporation; and (3) soil type as conditioned by parent rock. Factors (2) and (3) react together to some extent to govern the ultimate soil type, moisture supply governing humus formation, which, with the texture of the soil as formed from rock decomposition, determines the water-retaining capacity.

Considering these three variables, two facts seem clear: (i) Brush is able to develop in situations of decreasing shelter on soils of increasing fineness of texture; the series Hawkesbury Sandstone-Narrabeen Sandstone-Upper Coal Measures-Chocolate Shale seems to apply. The last-named soils have, it is true, a coarser texture than some of those of the Upper Coal Measures, yet there seems no doubt that they are the best soils of this district. Chemical as well as physical properties of the soils may explain this fact. (ii) Shelter from wind and sun seems more important than soil conditions in brush development. Thus, for the soils listed in Table 2, only low-grade brush (practically equivalent to the *Eucalyptus saligna* ecotone Community) develops on the last soil listed, which, with partial physiographic shelter, has better properties than the seventh soil listed, a dry, well-drained soil carrying highly-integrated brush in a position of extreme shelter. However, the fifth and sixth soil-samples listed, with excellent properties, carry highly-integrated brush with very slight shelter from the west.

Brush develops on the upper coastal slopes, immediately below the scarp, except on several prominent ridges, where the *Eucalyptus pilularis* Association or *E. saligna* ecotone Community reaches the scarp. These upper slopes correspond to Narrabeen

Sandstone; Chocolate Shale exposures are very limited in extent on the slopes, except where the protecting Hawkesbury Sandstone cover has been entirely removed, as at the top of Bulli Pass. Soils of the upper slopes, at the level of the Narrabeen Sandstone, are contaminated with soil derived from overlying series, most markedly where erosion of the soft Chocolate Shale has been permitted by removal of the Hawkesbury Sandstone.

TABLE 2.  
*Properties of Soils carrying Brush (or Subtropical Rain Forest).*

	W.R.C. (%).	Loss on Ignition (%)*	pH.
Hawkesbury Sandstone, extreme shelter ..	90	30.0	5.2
	120	35.0	5.2
	120	49.0	5.3
	130	48.0	5.0
Chocolate Shale, partial shelter on plateau ..	100	39.0	5.5
	130	36.0	5.3
Easterly Slopes: soil derived chiefly from Chocolate Shale, very efficiently drained; extreme shelter.	60	21.0	5.8
	66	13.0	5.8
Easterly Slopes: soil derived from Narrabeen Sandstone mixed with talus from formations above; soil moisture high; shelter extreme to moderate.	200	38.0	6.9
Partial shelter; soil as above: Low-grade Brush.	61	9.4	5.9

\* From 20% to 60% of this figure represents humus.

On the lower slopes, brush is restricted to gullies and to the inner (western) side of the larger terraces. Depauperate brush occurs beyond these limits, and probably many parts of the coastal plain once carried a brush element, prior to disturbance following settlement. The alternation of brush, sclerophyll and ecotone communities has been studied in a belt-transect between the 200-ft. contour and the scarp at Coledale; true brush extended down to the inner side of a terrace a little above the 400-ft. contour; below this, ecotone communities were present on terraces, but sclerophyll forest characterized other parts of the ridge followed. In a transect at right angles to the above, between two ridges running down from the upper slopes to the sea, brush was developed only at the lowest point, ecotone vegetation on the ridge facing south (except at its summit), sclerophyll forest on the summits of both ridges and on all except the lowest part of the north-facing ridge.

The brush studied has the characteristic facies of this formation as found in other parts of the State, namely a variety of trees of medium height, mostly laurel-leaved, with continuous canopy; paucity of small trees in most cases, except the tree-fern *Alsophila australis*; almost complete absence of shrubs, and presence of a discontinuous ground layer composed chiefly of ferns. In addition, epiphytes and climbers are common.

Omitting high sclerophyllous trees which occasionally grow in the brush, penetrating the canopy (*Eucalyptus pilularis*, *E. saligna*, and more rarely *Syncarpia laurifolia* Ten., *Eucalyptus paniculata* and *E. quadrangulata* Deane and Maiden), and the elements characteristic of the brush-sclerophyll forest ecotone, but absent from the true brush, the floristics may be set out as follows:

MM: *A. Livistona australis*, *Ficus stephanocarpa* Warb., *Doryphora Sassafras*; C, *Ficus rubiginosa*, *Laportea gigas*, *Pennantia Cunninghamii*, *Cryptocarya glaucescens*, *Endiandra Sieberi*, *Callicoma serratifolia*, *Pittosporum undulatum*, *Ceratopetalum apetalum*, *Omalanthus populifolius*, *Sloanea australis*, *Eugenia Smithii*, *Trochocarpa laurina*, *Sideroxylon australe*, *Cargillia australis* R.Br.; O, *Archontophoenix Cunninghamiana* Wendl. et Drude, *Polyosma Cunninghamii*, *Schizomeria ovata*,

- Pittosporum revolutum*, *Claoxylon australe*, *Diploglottis Cunninghamii*, *Brachychiton acerifolius* F.v.M., *Eugenia myrtifolia*, *Panax Murrayi*, *Clerodendron tomentosum*; R, *Mollinedia macrophylla*, *Cryptocarya microneura*, *Tristania laurina*; VR, *Podocarpus elata*, *Pisonia Brunonianana*, *Quintinia Sieberi*, *Melia Azedarach*.
- MM (climbers): C, *Smilax australis*, *Clematis glycinoides*, *Sarcopetalum Harveyanum*, *Stephania hernandifolia*, *Palmeria scandens*, *Lyonsia straminea*, *Tecoma pandorana* Skeels, *Senecio mikanioides* Otto (introd.); O, *Piper hederaceum*, *Vitis hypoglauca*, *Lyonsia reticulata*; R, *Tylophora barbata*.
- M: A, *Alsophila australis*; C, *Panax sambucifolius*, *Psychotria lonicerioides*; O, *Drimys insipida* Druce, *Sambucus xanthocarpa*; R, *Croton Verreauxii*, *Phyllanthus Gastroemii*, *Backhousia myrtifolia*.
- M (climbers): C, *Eustrephus latifolius* R.Br., *Rubus parvifolius*; O, *Rubus Moluccanus*, R. Moorei; R, *Rubus rosifolius*, *Passiflora Herbertiana*, *Panax cephalobotrys*.
- N: A, *Lantana camara* (introd.) (chiefly in disturbed areas); O, *Citriobatus multiflorus*; R, *Abrophyllum ornans*.
- H: A, *Adiantum aethiopicum*, A. formosum, *Asplenium flabellifolium*, *Polystichum aculeatum*; C, *Blechnum capense*, B. Patersoni, *Pellaea falcata*; O, *Adiantum diaphanum*, *Dryopteris decomposita*, *Hypolepis tenuifolium*, *Sisyrrinchium paniculatum*; R, *Adiantum hispidulum*.
- G: A, *Gymnostachys anceps*; C, *Histiopteris incisa*, *Pteris umbrosa*.
- E: A, *Cyclophorus serpens*, *Pleopeltis diversifolia*, *Peperomia reflexa*, *Arthropteris tenella*, *Hymenophyllum tunbridgense*; C, *Polypodium Billardieri*; O, *Davallia pyxidata*, *Cymbidium suave*, *Sarcochilus falcatus*; R, *Asplenium nidus*, *Platyserium bifurcatum*; VR, *Tmesipteris tannensis*.

The ecotone between the brush and the *Eucalyptus pilularis* Association is dominated by *Eucalyptus saligna*, and contains the more tolerant of the species of the true brush (e.g., *Livistona australis*, *Omalanthus populifolius*, *Alsophila australis*, *Lantana camara*, *Rubus parvifolius*), together with certain species confined to the ecotone, and not extending into the true brush except in cleared spaces. The low trees, *Breynia oblongifolia*, *Eupomatia laurina*, *Synoum glandulosum* and *Rhodamnia trinervia*, fall in this category, and the higher *Acacia binervata*, which can stand drier conditions, is frequently prominent. The climbers, *Smilax glycyphylla* and *Eustrephus latifolius* R.Br., occur in this ecotone community, together with a ground layer including *Adiantum aethiopicum*, *Oplismenus compositus*, *Pollia cyanococca*, *Urtica incisa*, *Rubus fruticosus* (introd.), *Stellaria flaccida*, *Plectranthus parviflorus* and *Brunella vulgaris* L.

The present record of a sample of the Illawarra brush indicates that it is poorer floristically than the brush forests of northern New South Wales (cf. Fraser and Vickery, 1938). The list given is probably not complete, even for the area studied, but there can be no doubt that a number of species of this northern formation fail to reach as far south as the Bulli district. Some species (e.g., *Cedrela australis*) known to have occurred in the district in the past have not been met with; *Cedrela* may be extinct in the district (by reason of the demand for its timber), though specimens occur in the Gerringong area, a little to the south. Other brush species (e.g., *Pseudomorus Brunonianana*) have been found further to the south (Cambewarra Range), but have not yet been recorded near Bulli.

### (3). Sand-Dune Succession.

Consideration of sand-dune succession (psammosere), and the succession from subsaline lagoons (infra) must involve an account of recent movements of the strand-line. On a stable coast, both successions must ultimately reach a state of dynamic equilibrium between the upgrade tendencies of autogenic succession and the retrograde influences of wind action, marine erosion, and scouring by creeks. The district studied has no rivers discharging into the sea, so that the additional factor of the continual addition to the coast, of alluvium, may be neglected almost entirely.

It seems reasonably certain from other sources of information that the portion of coastline under consideration has been subjected, during the last 3,000 years, to a fall in sea-level of some 15 feet (see, e.g., Cotton, 1926). This has probably been gradual, extending over the whole period, and possibly continuing at the same rate, though evidence of this is lacking. In any event, this fall has converted shallow estuaries and bays into land-locked lagoons some feet above sea-level; on the outer side of these

lagoons are belts of dunes, possibly sand-bars of the former bays and estuaries. The lagoons reach the sea through breaks in these dunes, although difficulty of access to the sea usually maintains them at a level some feet above the sea; they are consequently not tidal or as saline as sea-water.

This slow allogenic action has given rise to new areas for plant colonization, and the vegetation of the dunes now appears to be reasonably stable, evidences of forward succession possibly referring to progress allowed by the more recent stages in the fall in sea-level. There is a certain amount of local retrogression, probably compensated by local succession in other sectors.

The zonation of the dune communities may thus be considered as a forward succession, probably brought to a standstill by the absence or extreme slowness of further change in the strand-line, and the inability of the pioneer stages of the vegetation to advance any further seaward (Pl. iii, C).

The sand-dune communities may be listed as follow:

(1). *Festuca litoralis*-*Spinifex hirsutus*-*Carex pumila* *Associes*.

This is the first community to develop, or, in terms of space, the most seaward. The first two species are of regular occurrence, *Carex pumila* being less common; it is questionable whether it deserves to rank in the naming of the associates, although, in certain dunes studied by the author in southern Tasmania, it and *Festuca* were equally important in this stage, while *Spinifex* was absent. The therophyte, *Cakile maritima*, occurs in and just below this community.

*Festuca* is a tussock-plant, and is most important in holding the sand against wind erosion on colonized areas, often remaining on sand hummocks when the surrounding sand at that level has been removed. *Spinifex*, with creeping stolons, is more important as a colonist of new areas, or areas which have been eroded. The rôles of these two species may therefore be regarded as passive and active respectively, in regard to soil stabilization (Pl. iii, A and C). On account of its greater mobility, *Spinifex* usually extends some distance beyond the seaward limit of *Festuca*.

(2). *Shrub-Dune*.

This community is dominated by shrubs of *Leptospermum laevigatum*, *Leucopogon Richei*, and *Acacia Sophorae* (Labill.) R.Br., with *Banksia integrifolia* in the shrub stage. The chamaephyte element (especially *Mesembryanthemum aequilaterale* and *Hibbertia volubilis*) occasionally forms a 'mat' stage extending seaward beyond the shrub line.

The shrub-dune represents the highest level of the dune area (Pl. iii, B), the ground behind it falling in level to the next stage (dune forest). The following is a floristic list for the shrub-dune:

- N: A, *Leptospermum laevigatum*, *Leucopogon Richei*; C, *Banksia integrifolia* (bush), *Acacia Sophorae* R.Br.; LC, *Lantana camara* (introd.); O, *Atriplex cinereum*, *Monotoca scoparia*, *Senecio lautus*; R, *Correa alba*.
- Ch: C, *Mesembryanthemum aequilaterale*, *Hibbertia volubilis*; O, *Commelina cyanea*, *Rhagodia hastata*, *Tetragonia expansa*, *Pelargonium australe*, *Calystegia Soldanella* R.Br.; R, *Rhagodia baccata* Moq.
- H: C, *Cynodon dactylon*; O, *Sporobolus virginicus*, *Scirpus nodosus*, *Dichondra repens*; R, *Imperata cylindrica* var. *Koenigii*, *Lomandra longifolia* Labill., *Oxalis corniculata*.
- G: O, *Pteridium aquilinum*.
- Th: O, *Sonchus oleraceus* (introd.), *Onopordon Acanthium* (introd.).

(3). *Eucalyptus botryoides*-*Banksia integrifolia* *Associes*.

On the inner slope leading down from the shrub-dune, and in sandy hollows still further from the sea, a forest dominated by *Banksia integrifolia* and *Eucalyptus botryoides*, usually some 40 feet in height, occurs. All elements of the shrub-dune stage occur in this forest, in approximately the same proportions. *Eucalyptus longifolia* and *Banksia serrata* occur rarely as low trees. Additional species include:

- M: *Pittosporum undulatum*, *Acacia linearis*, *Synoum glandulosum*, *Breynia oblongifolia*, *Cupaniopsis anacardioides* Radlk., *Clerodendron tomentosum*.
- M (climbers): *Lyonsia straminea*, *Tylophora barbata*.

N: *Sida rhombifolia* (occasionally chamaephytic), *Pimelea linifolia*, *Brachyloma daphnoides*.

N (climbers): *Geitonoplesium cymosum*, *Stephania hernandifolia*.

Ch: *Viola hederacea*, *Halorrhagis teucroides*.

H: *Themeda australis* Stapf., *Rubus fruticosus* (introd.).

E: *Cassytha paniculata*.

No climax Mixed *Eucalyptus* Forest occurs on dune soils in this area.

Retrograde factors adversely influencing the succession are marine erosion (action of waves during storms on the outer parts of the *Festuca-Spinifex-Carex* stage); wind erosion or blow-outs affecting chiefly the pioneer stage, where the soil is least efficiently stabilized, but sometimes affecting the higher stages, e.g., dune forest, after the intermediate stages have been removed (cf. Pl. iii, D); swamping of vegetation by drifting sand loosened by the preceding factor (affecting the dune forest community on the inner slope of the dunes, and noted to occur in many parts of the area); and erosion by the waters of lagoons, when they effect outflow to the sea (cf. Pl. iii, E). Opposed to these factors are the normal upgrade tendencies typical of any psammosere, namely, soil stabilization by vegetational cover, and improvement of the soil (especially with regard to water-retaining capacity) by the addition of organic remains. Proof of retrogression in some sectors is a matter of direct observation; proof of forward succession in other areas is deduced from examination of soil profiles with an auger, the soil of all stages passing, with increase in depth, to dune sand, by decrease of the percentage of organic matter.

Properties of surface soils in this psammosere are listed in Tables 3 and 3A. They indicate the increasing water-retaining capacity of the sere, due to accumulation of organic remains. Hydrogen peroxide tests indicate that the ratio of humus content to loss on ignition is 5-8% for the *Spinifex-Festuca-Carex* stage, 40% for the shrub-dune, 50% or a little over for the dune forest. Variations in chloride content, and in water-content (Table 3A) seem to be due to differences in drainage and leaching, the *Festuca* hummocks and the shrub-dune, on the dune crest, being efficiently drained and leached, part of the chloride leached from the latter passing to the dune forest soil on the inner slope. The soil of the dune forest, with its higher water-retaining capacity, would be less affected by percolation and leaching. Spray incidence is probably not greatly different in the various stages, but the lowest parts of the *Spinifex* zone occasionally come under the effect of waves. There is scarcely any significant change in pH throughout the sere, probably because of the buffering action of salts.

TABLE 3.  
*Soil Properties for Sand-Dune Succession.*

	W.R.C. (%).	Loss on Ignition (%).	pH.	Cl. (%).
Beach Sand .. .. .	22	3.2*	6.6	0.05
<i>Spinifex-Festuca</i> Associates .. .. .	24	0.6*	6.5	0.01
<i>Spinifex</i> .. .. .	24	0.5*	6.3	0.11
	25	1.9*	6.2	0.11
	25	2.8*	6.7	0.01
	27	3.3*	6.7	0.004
	27	4.0*	6.5	0.02
<i>Festuca</i> .. .. .	24	2.2*	6.5	0.005
	27	1.2*	6.8	0.002
Shrub-Dune .. .. .	28	2.6†	6.9	0.01
	29	2.2†	6.8	0.01
	31	0.9†	7.0	0.02
	32	1.2†	6.9	0.02
<i>Eucalyptus botryoides-Banksia integrifolia</i>	30	4.0	6.3	0.02
Associates .. .. .	32	2.9	6.6	0.02
	36	4.2	6.6	0.02
	50	5.5	6.1	0.03
Climax .. .. .		Does not develop		

TABLE 3A.  
Soil Properties on Transect at North Towroddie.

—	W.R.C. (%)	Loss on Ignition (%)	pH.	Cl. (%)	Water Content (%) (14.7.38).
<i>Spinifex</i> .. .. .	27	4.0*	6.5	0.03	3.3
<i>Festuca</i> (hummock) ..	24	2.2*	6.5	0.01	2.8
Shrub-dune .. .. .	29	2.2†	6.8	0.01	0.7
Dune Forest .. .. .	30	4.0	6.3	0.02	2.9

\* Almost entirely due to calcium carbonate.

† Largely due to calcium carbonate.

(4). *Subsaline Lagoon Succession.*

This is a typical subsaline hydrosere, proceeding at the borders of the coastal lagoons whose formation by falling sea-level has been noted above. In general, forward succession in time seems to prevail, the allogenic causes of lagoon formation being too recent for any final equilibrium yet to have been reached. Retrogression by scouring is slight, and confined to the outer side of bends in the narrower parts of the lagoons, and especially at the lagoon mouths, where the outflow, though discontinuous, may sometimes be rapid (e.g., immediately following the breaking of the sand-bar obstruction after a period when outflow has been cut off).

In general, the lagoon borders are flat, and in some cases rise rather gradually to drier ground with alluvial soil carrying Mixed *Eucalyptus* Forest, regarded as the climax of the sere. The immediate cause of the succession is the raising of soil level by alluvium and plant remains, probably aided by fall in lagoon level;\* the resultant fall in water-table relative to the soil surface allows a lowering of humus content (Table 4). The pH falls, as the buffering by lagoon waters decreases, to a minimum in the *Eucalyptus robusta* Associates, and rises again as the conditions become finally drier. Soil properties are listed in Table 4; over 50%, sometimes almost 100%, of the figures for loss on ignition represent humus. The properties of the first stage (*Phragmites*) are not listed, being atypical of this stage in other districts (infra); the properties for the *Cladium junceum* stage are bracketed, as this community is absent from the lagoon (Towroddie Lagoon) where the other samples, representing a transect, were collected. The sample for the *Cladium junceum* stage represents part of the community beside Bellambi Lagoon, where the salinity and water-level were temporarily in a different state from Towroddie Lagoon at the time of sampling.

The stages may be listed as follow:

TABLE 4.  
Soil Properties for Subsaline Lagoon Succession.

—	W.R.C. (%)	Loss on Ignition (%)	pH.	Cl. (%)	Water Content (%) (4.7.38).
<i>Juncus maritimus</i> Associates ..	170	59	6.0	3.4	400
<i>Cladium junceum</i> Associates ..	(140)	(48)	(5.2)	(1.9)	(120)
<i>Casuarina glauca</i> Associates ..	140	50	4.6	2.8	220
<i>Eucalyptus robusta</i> Associates ..	140	47	3.4	0.45	33
Mixed <i>Eucalyptus</i> Forest (Climax) ..	63-91	13-20	6.0-6.3	0.05-0.08	4-7
<i>Melaleuca</i> Communities:					
<i>M. ericifolia</i> , close to lagoon margin.	87	18	6.1	0.32	120
<i>Melaleuca</i> spp., several feet above level of lagoon ..	39	6.9	5.7	0.02	12
	35	8.8	5.8	0.12	12

\* Over a long period of time. The outlet system causes a considerable fluctuation in lagoon level from season to season, but this fluctuation cancels out as a cause of succession.

(1). *Phragmites communis* Associates.

The half-submerged species *Phragmites communis* Trin. is not well developed in the lagoons studied, nor are the submerged or floating stages (*Zostera nana*, *Ruppia maritima*, and filamentous algae such as *Cladophora*). The factor limiting the greater development of *Phragmites* appears to be the high and often rapidly-changing salinity. The species becomes more prominent in the upper waters of these lagoons, but here the neighbouring vegetation has been so much altered by clearing that a full study was unprofitable. In these upper reaches, where the salinity is low, *Triglochin procera*, *Alisma Plantago* and *Villarsia exaltata* F.v.M. occur occasionally, growing half-submerged.

In the parts of Towroddie and Bellambi Lagoons where the succeeding stages (cf. Table 4) were most fully studied, there are local sparse stands of *Phragmites communis*; the soil (submerged) has here a low organic content and a pH approximating to the lagoon water. It includes a high proportion of intrusive dune sand. In other regions, the soil of the *Phragmites communis* Associates has typically a very high organic content, the pH approximating to that of the surrounding water, usually high.

(2). *Juncus maritimus* Associates.

*Juncus maritimus* is well developed around the margins of the lagoons studied (Pl. iv, C). The soil of this stage is always water-logged, though covered with surface water only when the lagoon level is abnormally high. The organic content is high; humus content lowers the pH below that of lagoon water. The chloride content is usually high.

(3). *Cladium junceum* Associates.

On the flatter parts of lagoon margins, a definite belt of *Cladium junceum* R.Br. develops behind the *Juncus maritimus* Associates. The soil has a lower water-content, organic content, and pH than the preceding stage.

The following herbaceous species occur among the dominants of stages (2) and (3), and occasionally on parts of the lagoon margin lacking *Cladium* and *Juncus*: *Salicornia australis*, *Spergularia rubra*, *Apium prostratum*, *Hydrocotyle vulgaris*, *Samolus repens*, *Dichondra repens*, *Wilsonia Backhousei*, *Lobelia anceps*, *Selliera radicans*, *Cotula coronopifolia*, *C. reptans*.

At the lagoon mouths, on flats of dune sand flooded by lagoon water, over which sea-water occasionally gains entry to the lagoons during rough weather, several of these species (e.g., *Apium prostratum*, *Hydrocotyle vulgaris*) often become temporarily established in what may be considered an intermediate between psammosere and hydrosere.

(4). *Casuarina glauca* Associates.

With decreasing water-content, soils of the lagoon margin carry a low forest of *Casuarina glauca*. Surface soils of this community are periodically, deeper soils continuously, water-logged. The pH, chloride content and organic content are slightly lower than in the preceding stages.

In addition to the dominant, *Casuarina glauca*, and the orchid, *Dendrobium teretifolium*, epiphytic on it, this stage possesses a ground layer of *Juncus maritimus* or *Cladium junceum*, together with some of the herbs of the preceding stages (e.g., *Selliera radicans*).

(5). *Eucalyptus robusta* Associates.

On drier soils, with somewhat reduced organic and chloride content, and with the lowest pH of the sere, a forest of *Eucalyptus robusta* develops, the trees being typically 40-50 feet in height. In typical parts of this stage, the ground layer is composed almost entirely of *Gahnia psittacorum*; occasionally, species relict from a previous stage (e.g., *Cladium junceum*) occur. In the dried parts of this associates, which may be regarded as an ecotone community, species of the climax community or of the *Melaleuca* Community (infra) enter.

(6). *Climax.*

With increasing efficiency of soil drainage, Mixed *Eucalyptus* Forest occurs. There is usually a rather abrupt rise in ground level of two feet or more between the preceding stage and this forest, which is interpreted as the climax. There seems little doubt, however, that the soil is alluvial, and has been a swamp soil in the past. The facts may be explained by a rather sudden fall in lagoon level at some past time, instead of a gradual increase in soil level by the accumulation of soil and plant remains. The occurrence of trees characteristic of damper stages (*Eucalyptus robusta*, *Melaleuca linariifolia*) at certain points within this forest does not appear to represent individual relics of an earlier stage as such; the time since the suggested fall in lagoon level would probably far exceed the life of any such tree. These trees may be regarded as relict species (not individuals), persisting where local conditions of drainage have remained in the earlier state.

The commonest trees of this forest are *Eucalyptus longifolia* and *E. punctata*; *E. botryoides*, *E. paniculata*, *E. eugenioides* and *E. pilularis* are also frequent. *E. robusta* occurs locally in damper situations, e.g., in slight depressions. The trees are rather widely spaced, and usually only some 50 feet in height. Old trees of *Melaleuca linariifolia*, up to 30 feet in height, are scattered throughout the forest. The lower layers are strongly suggestive of the mixed forest on tuffaceous mudstone discussed earlier. They include species of the normal *Eucalyptus pilularis* Association, species of the earlier stages of the lagoon sere, brush or brush ecotone species, and, much more rarely, dune forest species.

The lower strata have been too much altered by clearing to justify an estimate of the frequency of component species. Below is a list of species classified under life-forms, and exclusive of the trees mentioned above:

M: *Pittosporum undulatum*, *Breynia oblongifolia*, *Notelaea longifolia*, *Clerodendron tomentosum*.

M (climber): *Lyonsia straminea*.

N: *Persoonia linearis*, *P. salicina*, *Acacia juniperina*, *A. myrtifolia*, *A. suaveolens*, *Oxylobium trilobatum*, *Sida rhombifolia*, *Pimelea linifolia*, *Callistemon linearis*, *Leptospermum laevigatum*, *Melaleuca nodosa*, *Leucopogon Richei*, *Lantana camara* (introd.).

N (climbers): *Geitonoplesium cymosum*, *Stephania hernandifolia*.

Ch: *Viola hederacea*, *Halorrhagis teucroides*, *Plantago lanceolata* (introd.).

H: *Cynodon dactylon*, *Eragrostis Brownii*, *Paspalum dilatatum* Poir. (introd.), *Sporobolus virginicus*, *Carex paniculata*, *Gahnia psittacorum*, *Juncus prismatocarpus*, *Rubus fruticosus* (introd.), *Oxalis corniculata*, *Dichondra repens*.

G: *Pteridium aquilinum*, *Cladium junceum*, *Burchardia umbellata*.

E: *Loranthus celastroides*, *Cassytha paniculata*.

S: *Opuntia inermis* P.DC. (introd.).

Th: *Solanum nigrum*, *Wahlenbergia gracilis*, *Hypochoeris glabra* (introd.), *Onopordon Acanthium* (introd.).

Soils of this climax forest have a greatly decreased water, chloride and organic content compared with the preceding stage. The pH is higher, due to drier conditions. The water-retaining capacity is moderately high.

In addition to the above communities, another, which may be termed the *Melaleuca* Community, is associated with the subsaline hydrosere. The species usually occur as a closed shrub thicket, sometimes due to regeneration after clearing. The following species frequently occur: *Melaleuca linariifolia*, *M. ericifolia*, *M. nodosa*, *Callistemon linearis*, while *M. styphelioides* and *M. thymifolia* are rare. The first species listed is fairly common as a low tree.

The *Melaleuca* Community may be regarded as a stage (alternative rather than regular) in the lagoon succession, immediately preceding the climax. It is found chiefly on flats subject to periodic flooding by rain-water, seldom on soils influenced by the more saline lagoon water.

*Salinity of Soil Solution:* The following figures, calculated on chloride and water contents of soils on July 4, 1938, indicate the salinity of the soil solution for that date:

*Juncus maritimus* Associates, 14°/∞; *Casuarina glauca* Associates, 21°/∞; *Eucalyptus robusta* Associates, 22°/∞; climax, 19–21°/∞.

It is apparent that compensation for decreased chloride content, by decreased moisture content, maintains the salinity of the soil solution fairly constant throughout the sere under these conditions; following wet weather, the discrepancy between the stages would increase. On this date, the salinity of Towroddie Lagoon, on the borders of which the above samples were collected, was 17°/∞. At this time, Bellambi Lagoon (near mouth) had a salinity of 26°/∞ (sea-water 35°/∞), and the *Cladium junceum* Associates, beside this part of Bellambi Lagoon, 26°/∞ also.

The salinities of soil solutions for the *Melaleuca* communities listed in Table 4 are 4.3°/∞, 2.7°/∞ and 16.2°/∞ respectively. At the same time, part of this community was found bordering an isolated pool well above lagoon level; the salinity of this pool, whose water impregnated the soil of the *Melaleuca* Community, was only 1.2°/∞.

(5). *Sea-Cliff Vegetation.*

Zonation of communities on sea-cliffs in this region does not represent an autogenic succession any more than does the mosaic of developmental stages found on the Hawkesbury Sandstone scarp (Part ii of this series). Under present conditions, marine erosion renders any change retrogressive; however, any further fall in relative sea-level would probably promote conditions suitable for forward succession.

Two subclimax zones, dominated by herbs and shrubs respectively, lead back to the *Eucalyptus pilularis* Association. The first extends from a little above the extreme high-tide level to some 20–25 feet; the shrub community extends thence to the *Eucalyptus pilularis* Association, the distance varying from place to place, and being governed by the extent of unstable soil conditions on the cliff face and summit.

TABLE 5.  
*Soil Properties for Sea-Cliff Communities.*

	W.R.C. (%)	Loss on Ignition (%)	pH.	Cl. (%)
Herb Zone (10–15 ft. above sea-level) ..	25	2.7	6.4	0.14
	27	3.9	7.4	0.01
	37	5.0	6.9	0.07
	37	6.2	7.2	0.02
Lowest part of Shrub Zone (25 ft. above sea-level).	59	7.7	7.0	0.10
Shrub Zone (30–50 ft. above sea-level) ..	45	20.0	6.6	0.09
	53	12.0	6.9	0.04
	60	14.0	5.3	0.13
	82	16.0	6.3	0.40

Properties of soils of these subclimax communities are listed in Table 5. The soils are derived from rocks of the Upper Coal Measures, and are usually, clayey, the lower samples with a greater or lesser admixture of beach sand. Chloride content appears to be governed by local factors of spray incidence and leaching, rather than by the height directly. The pH is usually high, probably because of the salts derived from sea spray. The limiting factor in shrub and tree development seems to be depth and stability of soil, rather than water-retaining capacity, humus or chloride content, pH, or wind exposure.

The herb zone contains the following species:

Ch: *A. Apium prostratum*, *Samolus repens*, *Lobelia anceps*; C, *Pelargonium australe*, *Plantago lanceolata* (introd.), *P. varia*; O (LC), *Scaevola calendulacea* Druce,\* *Cotula coronopifolia*; O, *Tetragonia expansa*; R, *Rhagodia nutans*.

H: C, *Scirpus nodosus*, *Lomandra longifolia* Labill.; O, *Stenotaphrum secundatum* Kuntze (introd.).

Th: C, *Hypochoeris glabra* (introd.), *Sonchus oleraceus* (introd.); O, *Rumex crispus* (introd.), *Inula graveolens* (introd.); R, *Sonchus asper* Hill (introd.).

\* Incorrectly listed in Part I as *Scaevola hispida*.

The species of the shrub zone which reaches the lowest level is *Westringia rosmariniformis*. Members of the herb zone which extend to the shrub zone are *Plantago* spp., *Scirpus nodosus*, *Lomandra longifolia*, *Stenotaphrum secundatum*, and all the therophytes listed above. In addition, the following species occur in the shrub zone (Pl. iv, D):

- N: A, *Casuarina glauca* (bush; Pl. iv, E), *Banksia integrifolia* (bush), *Acacia myrtifolia*, *Leptospermum laevigatum*, *Westringia rosmariniformis*; C, *Pomaderris ferruginea* Sieb., *Lantana camara* (introd.); O, *Acacia suaveolens*, *Pultenaea retusa*, *Eucalyptus paniculata* (bush), *Melaleuca hypericifolia*, *Leucopogon Richei*; R, *Hakea pugioniformis*, *Persoonia salicina* (small-leaved variation), *Acacia juniperina*, *Oxylobium trilobatum*, *Zieria Smithii*, *Sida rhombifolia*, *Brachyloma daphnoides*; VR, *Pittosporum undulatum* (bush), *Breynia oblongifolia* (bush), *Phyllanthus Ferdinandi*, *Cupaniopsis anacardioides* Radlk. (bush), *Goodenia ovata*, *Olearia ramulosa* Benth.
- N (climbers): A, *Kennedyia rubicunda*; C, *Smilax glycyphylla*, *Hardenbergia monophylla*; O, *Clematis aristata*, *Billardiera scandens*; VR, *Stephania hernandifolia*, *Tylophora barbata*.
- Ch: C, *Mesembryanthemum aequilaterale*, *Hibbertia Billardieri*, *H. volubilis*; O, *Commelina cyanea*, *Dianella revoluta*, *Glycine clandestina*, *Halorrhagis teucrioides*; R, *Scirpus cernuus* Vahl., *Bossiaea prostrata*; VR, *Desmodium varians*.
- H: A, *Paspalum dilatatum* Poir. (introd.), *Rubus fruticosus* (introd.); C, *Themeda australis* Stapf., *Dichondra repens*; O(LC), *Gleichenia speluncæ* R.Br.; R, *Cyperus polystachyus*, *Scirpus prolifer*, *Ocalis corniculata*; VR, *Adiantum aethiopicum*.
- G: O, *Pteridium aquilinum*; R, *Lepidosperma laterale*, *Schoenus melanostachys*, *Tricoryne simplex*.
- Th: O, *Phytolacca octandra* L. (introd.), *Taraxacum officinale* Weber (introd.); R, *Briza maxima* L. (introd.); *Poranthera microphylla*, *Anagallis arvensis* (introd.), *Polymeria calycina*, *Erythraea australis*, *Galium australe*, *Sherardia arvensis* (introd.), *Aster squamatus* (introd.), *Bidens pilosus*, *Onopordon Acanthium* (introd.), *Sonchus megalocarpus* J. M. Black (introd.).
- E: O(LC), *Cassytha paniculata*.

The above list testifies in itself to the diversity of habitats at this level on the sea-cliffs. The species include normal units of the *Eucalyptus pilularis* Association (e.g., *Eucalyptus paniculata*, *Kennedyia rubicunda*, *Oxylobium trilobatum*); brush types confined to relatively moist and sheltered parts of the cliffs (*Pittosporum undulatum*, *Tylophora barbata*, *Stephania hernandifolia*, *Adiantum aethiopicum*); swamp types confined to local soaks (*Cyperus melanostachys*, *Lepidosperma laterale*, *Scirpus prolifer*); and members of the coastal psammosere (*Banksia integrifolia*, *Leptospermum laevigatum*, *Mesembryanthemum aequilaterale*) and lagoon succession (*Apium prostratum*, *Lobelia anceps*, *Cotula coronopifolia*).

The sea-cliff vegetation bears some resemblance to the vegetation of the Five Islands (Davis, Day and Waterhouse, 1938). Of the Five Islands species, some 50% are represented on the sea-cliffs studied, and some 70% on the sea-cliffs, dunes and lagoon sere taken together.

The development of the *Eucalyptus pilularis* Association, on cliff tops with deeper and more stable soil, represents an increase in the height of *Banksia integrifolia* and *Eucalyptus paniculata*, and addition of *E. pilularis* and *Syncarpia laurifolia* Ten. *Banksia integrifolia* does not extend inland more than some 50 yards in this region; some species of the lower strata of the sea-cliff vegetation (e.g., *Leptospermum laevigatum*) are even more closely restricted to the immediate vicinity of the sea. *Casuarina glauca*, which occurs as stunted bushes in the shrub zone on the cliffs, very seldom reaches tree status; as soon as conditions become suitable for tree development, some factor (probably competition) excludes this species.

*Note:* In this and the preceding part (Davis, 1941), species have been classified into life-forms as closely as possible. Strict classification is often difficult because of the lack of a definitely unfavourable season (cf. Part i, Climate). Some species are listed as of different life-form in different communities; thus a cryptophyte is classed as G in a dry community, HH where it extends into a swamp community; or a typical cryptophyte, if growing in a situation of restricted soil depth (e.g., on the Hawkesbury Sandstone scarp) becomes a hemicryptophyte. Climbers have been referred to the class of phanerophytes whose height they reach most typically in the community concerned;

in some cases, a climbing plant is classed as a chamaephyte if it occurs in a certain community typically as a straggling plant less than one foot in height. In the case of phanerophytes (including climbers), if any doubt exists as to which height-class a species most characteristically falls into, in the community concerned, it is classed in the upper of the two possible classes. The rooted hemiparasite *Cassytha* is classed throughout as an epiphyte.

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EXPLANATION OF PLATES III-IV.

Plate iii.

A.—Pioneer stages of the psammosere at Towroddie. *Festuca litoralis* holds the sand in hummocks where the surrounding sand has been removed by wind action; stolons of *Spinifex hirsutus* colonize the sand at the new level.

B.—Psammosere at Towroddie: *Spinifex hirsutus* and tussocks of *Festuca litoralis* to the left; shrub stage on crest of dune; dune forest (lower strata cleared) on inshore slope.

C.—Pioneer stages of psammosere (*Spinifex*, *Festuca*) in equilibrium with marine erosion at the extreme limit of wave action, Towroddie Beach. Shrub dune in background, blow-out area almost devoid of vegetation in left middle-distance.

D.—Dune forest and shrubs on residual hillock at Bellambi, the surrounding area having been denuded by wind action. The foreground consists of pioneer dune plants, soil and vegetation being slightly atypical of this stage, due to occasional flooding by lagoon water.

E.—Panorama of mouth of Bellambi Lagoon, north bank. Both hydrosere and psammosere are affected by scouring caused by occasional rapid outflow of pent-up lagoon waters.

Plate iv.

A.—*Eucalyptus pilularis* Association near Austinmer.

B.—Mixed *Eucalyptus* Forest on tuffaceous mudstone, north of Towroddie Creek. The lower strata have been altered by clearing.

C.—Early stages of lagoon succession, Towroddie: *Juncus maritimus* Associates backed by *Casuarina glauca* Associates. Open waters of lagoon on extreme right; *Phragmites communis* Associates scarcely developed.

D.—Sea-cliff at North Austinmer, with shrub zone on upper parts.

E.—Shrub zone on sea-cliff, South Austinmer: Stunted form of *Casuarina glauca*. The camera case is 8 inches high.

APPENDIX.

*Life-Form Spectra for Communities of Coastal Slopes and Plain.*

	MM.	M.	N.	Ch.	H.	G.	HH.	Th.	S.	E.	No. of Species.
<i>Eucalyptus pilularis</i> Association	7	6	26 (22+4)	15	19	11	..	13	..	3	109
Brush (excluding purely ecotone species).	53 (41+12)	15 (8+7)	3	..	13	3	..	..	..	13	96
Climax to Lagoon Sere (Mixed <i>Eucalyptus</i> Forest).	14	10 (3+2)	30 (26+4)	6	20	6	..	8	2	4	50

Conventional lettering for life-forms.

Where classes MM, M and/or N are represented by climbers in addition to other forms, the percentages of climbers are also indicated (second of two numbers in brackets below percentage of total).

A SUMMARY OF CERTAIN ASPECTS OF THE SCARAB PROBLEM, AND A CONTRIBUTION TO A BIBLIOGRAPHY OF THE FAMILY SCARABAEIDAE.

By D. MARGARET CUMPSTON, M.Sc.\*

[Read 26th March, 1941.]

During the last two years the writer has carried out certain investigations on the larvae of Australian species of the family Scarabaeidae. It is thought that a summary of certain aspects of the problem, together with a bibliography of the literature consulted during the work, may be of future use. In an appendix two bibliographical lists have been included; the first deals with work done overseas, and is subdivided into morphological, physiological, ecological and miscellaneous sections, together with some papers on breeding and rearing technique; the second, dealing with Australian economic species, is listed under the host plants. The first list includes only relatively few publications out of the mass of literature dealing with this group, and is published in the hope that it may save part, at least, of the preliminary reading necessary in starting any problem. The second list is not entirely complete, but does cover most of the species known to be injurious.

A SUMMARY OF CERTAIN ASPECTS OF CONDITIONS AFFECTING SCARABAEIDAE OF ECONOMIC IMPORTANCE.

The eggs are laid some inches below the soil surface, in spring and early summer, being usually deposited in clusters in cavities made by the female. The larvae work their way upwards after hatching, and feed at varying depths below the soil surface. Feeding generally takes place at night: the larvae may approach the surface sufficiently close to disturb it. There are three instars: the total life-cycle ranges from three or four months to three years (in some North American Scarabaeidae). Feeding takes place all through the summer. During the winter the larvae are found at greater depths, enclosed in small cells moulded by pressure of the body on the surrounding soil particles. This cell may also be formed at any time when the larva is not feeding. The depth to which the larvae descend depends on the climate, the size of the larva and the ease of penetration.

The following spring, the larvae work their way up again and feed on the young roots. In young plants the roots are cut off right to the stem, all new rootlets devoured, and the plant may even be pulled entirely under the surface as the larva feeds. It is at this time that the damage is most apparent, becoming manifest as areas of stunted growth and dead plants. Plants are always more affected where conditions are adverse to vigorous growth, but these conditions usually also render the soil habitat more unfavourable for larval development. Where growth is strong, the plants may outgrow the grub attack; this is an important factor in limiting larval damage. In those species with a two-year life-cycle the damage is greater and extends over a more prolonged period, the larvae passing two winters in a dormant state. The damage even with the heaviest grub population is not very apparent until the final instar.

When the larva is fully grown it again burrows downwards. Ritcher (1939) states that the depth of pupation varies with the species and the type of soil; he concludes that soil factors may affect the pupation levels, but do not alter the relative positions of the various species, and also that differences in latitude seem to have little effect on the depth at which a given species pupates. The larva enters the prepupal state when it sheds the rectal contents, which are used as a plaster in the formation of the ovoid pupal cell. This plaster ensures a fairly firm and impermeable structure. The prepupa has a creamy-white appearance, and just prior to pupation is incapable of any movement but a restricted jerking of the abdomen. The pupa is of the exarate type. The adult requires several days after emergence before it hardens and assumes the proper colouration: until then it does not leave the pupal cell. The adults usually first emerge

\* This paper was prepared when the writer held a Linnean Macleay Fellowship in Zoology.

in early spring or summer (notable exceptions are *Metanastes vulgivagus* and *Heteronychus sanctae-helenae*, which emerge towards the end of summer and hibernate in the adult form), and may have a life-time of two to three months, during which period they lay numerous egg-batches.

The beetles of this family are both diurnal and nocturnal; during their quiescent periods they congregate under rubbish on the ground, or beneath the soil surface. During feeding or copulation periods they appear in swarms. In the main, they attack foliage, many confining themselves to native vegetation, but some attack vines and orchard trees, doing considerable damage. *Anodontonyx noxius* (*A. tetricus*) is found in the field in the afternoon; the adults have never been observed to feed above ground, emerging apparently to copulate (McCarthy, 1928). On the other hand, *Anoplognathus* species are to be seen swarming over Eucalypts during the day and completely stripping the young trees: copulation in these species also takes place above ground. *Sericesthis pruinosa* is a crepuscular species (Froggatt, 1919); the majority of the Dynastinae are nocturnal.

Oviposition preferences and mating habits vary. The females of *Anodontonyx noxius* show a decided preference for freshly turned soil when they return after copulation. Soil worked some weeks prior to the appearance of the beetles, or land free from natural growth is more attractive than stubble or grassed land (McCarthy, 1928). *Heteronychus sanctae-helenae* lays its eggs chiefly in low-lying paspalum land (*Agric. Gaz. N.S.W.*, 1936), *Aphodius tasmaniae* is attracted particularly to areas rich in sheep dung (Swan, 1934). *Lepidiota caudata* prefers buildings, trees, charred stumps, etc., on which to mate, and mating females fall to the ground, burrow in and oviposit. Eggs are not normally laid in land which is fallowed at the time of flight (Smith, 1936). Mating habits and oviposition preferences are of importance because they enable prediction of the degree of larval concentration in various areas.

The spread of any species of scarab is erratic, depending mainly upon the movements of the adults. These, although capable of sustained flight, do not often use this capacity, and there is no marked migration. The larval damage is usually scattered, present in one part of a district and absent from others; in one paddock, while surrounding ones are barely damaged. Larvae move freely in a vertical direction in sympathy with changes in moisture levels during the year; their outward horizontal movement may be limited, although opinion is divided upon this point. Smith (1936) states that the areas of damaged pasture gradually extend owing to the lateral migration of the larvae, until each area may cover an acre or more, and several may merge before larval development is completed. Illingworth and Dodd (1921) on the other hand state that normally there is little lateral movement of the grubs in the soil. The apparent advance of the larvae across the fields is marked by the yellowing of the cane-tops. This is explained by relative infestation: the parts of the field nearest the feeding and mating trees are more heavily infested. *Aphodius tasmaniae* larvae do migrate, digging new burrows as they move outwards (Swan, 1934). Experiments on larval migration have been carried out in Germany (Schwerdtfeger, 1939). The larvae of *Melolontha melolontha*, during the vegetation period, move mainly horizontally from root to root. The rate at which the larvae migrated in summer was dependent on temperature, the size of the larvae, and the structure of the soil: it is calculated that in nature a larva covers an average total distance of about five to six and a half feet, with a maximum of about ten to fifteen feet. The spread of infestation by larval migration is therefore negligible in forests, but is of greater importance in gardens. According to this author, the vertical migration is comparatively slight, the average movement being between approximately five and nine inches in summer, and fourteen and twenty-three inches in winter. Larvae of *Popillia japonica* (Hawley, 1934 and 1935) under greenhouse conditions have moved horizontal distances as great as seven feet, which is as far as the bins used in the tests would permit. There was considerable individual variation in the distances travelled, but the tendency to move about is much more evident in fallow ground than in grass sod. Under natural conditions the distance travelled is not nearly as great, since the larvae change the direction of their movement at frequent intervals.

The larval habits of the various species are in general similar. *Aphodius tasmaniae*, as already mentioned, differs in the construction of vertical tunnels in the soil. The larvae have fairly decided food preferences, according to Hayes (1929), who collected extensively through North America.

It is generally considered that scarab larvae feed both on living roots and on humus. It does not seem definitely known whether the larvae feed on living roots in preference to the humus in the soil, or whether humus is their primary food, roots being attacked only when there is a deficiency of organic matter in the soil. It is stated that *Heteronychus sanctae-helenae* larvae feed chiefly on decaying organic matter (*Agric. Gaz. N.S.W.*, 1936) and also that larvae of *Anodontonyx noxius* (*A. tetricus*) live in the early stages on roots of weeds and grasses as well as on humus, although they can subsist entirely on the latter (McCarthy, 1928). Illingworth and Dodd (1921) stated that larvae of sugar-cane beetles normally depend upon humus for their food, adducing various observed facts in support of their statement. The only experimental rearing of larvae was done by Fox and Ludwig in America (1937); they found that it was possible to rear larvae of the Japanese beetle from egg to adult on decayed vegetable matter alone, although in such instances development was somewhat retarded as compared with that of larvae also supplied with other food, such as grains of wheat. They later (1938) published the results of a lengthy series of experiments on the same species (*Popillia japonica*) in an attempt to find the medium which would be most satisfactory for rearing purposes: from these experiments some interesting conclusions have been reached. The media used were various kinds of decayed plant matter, soil, living and dead wheat, and yeast. It was found that the only medium which was satisfactory when used alone was *Andropogon* "mould", and it was inferred that the same may be true for "moulds" derived from Gramineae (grasses) in general, and especially from the more succulent forms such as the common pasture and lawn grasses. If this is so, it seems that living roots are not essential for larval growth under natural conditions. Soil plus *Andropogon* "mould" gave the maximum survival for the entire larval period. The improvement in survival attending the addition of wheat to the various media appears to bear an inverse relation to the taxonomic affinities of the plant furnishing the "mould" to the grasses. It appears from this that larvae under lawns and pastures would be able to survive without attacking the plant roots, but for the inadequate supply of disintegrated plant matter where the population is dense. Smith (1936), in dealing with *Lepidiota caudata* on the Atherton Tableland, states that although the humus content of the soil in grub-infested districts is generally good, the activity of the pest shows no parallel with the several available humus determinations, deducing therefore that the humus content can hardly be a controlling factor in larval distribution.

The larvae have quite a definite effect upon the soil and vegetation, apart from actual attack, the magnitude of the effect being directly proportional to the numbers of the larvae. There is the mechanical effect of disturbance by continual movement of the larvae through the soil (the soil may become very friable and dry through freer circulation of air, thus greatly affecting shallow root systems, part of which will have already been destroyed), and the chemical and physical effect of ingestion of quantities of soil from which the humus is removed in transit. Where the larval population is high, the soil may assume "pellet" characteristics. Where *Aphodius* larvae occur in numbers so much soil may be thrown out of the burrows that the soil surface is covered by a loose mulch nearly one inch in depth. The regeneration of pasture already destroyed by the feeding activities of the grubs may be prevented, resulting in bare patches. Smith (1936) showed that the white grub population in pastures induced alterations in soil capillarity, indicating a marked disturbance in the moisture-holding capacity of the soil.

The prolonged subterranean existence of a scarab renders the conditions prevailing in its soil habitat of extreme importance. The egg, larval and pupal stages are all spent in the soil: these comprise the major part of the life-history, rated as high as 98% of the total life-cycle. Also adults have in most species less of a terrestrial than a subterranean existence. For instance, the introduced species *Heteronychus sanctae-helenae* normally spends several months underground during winter, while conditions may force imagines of other species to remain in their pupal cells for more or less protracted

periods. This occurs when the soil is dry and packed hard so that it is impossible for them to force their way out. In such a case the adult mortality is high. When the earth becomes sufficiently moist the emerging swarms will be formed of a mixture of recently transformed and older adults. The incidence and duration of the flight period and the intensity of the flight are thus subject to marked fluctuations. Smith (1936) states that in Queensland spring rainfall is directly correlated with the seasonal importance of the pest species *Lepidiota caudata*, since beetle emergence depends entirely upon a prior soaking of the soil. It is interesting to notice, as he points out, that seasons which the farmer would consider favourable for dairying, i.e., seasons which are characterized by good spring rains, are equally favourable to the pest, liberating swarms of adults. A susceptible belt is much better served by a rainfall which limits the beetle emergence.

Eggs cannot withstand desiccation. For *Melolontha melolontha* L. (Schuch, 1938) it has been shown that the eggs require a marked degree of moisture in their environment, and develop normally only when in direct contact with a moist substratum permitting access of air. If saturated air was the only source from which the eggs could absorb moisture, there was an increase in mortality and the newly hatched larvae were much shrivelled and notably lighter in weight than normal ones. On the other hand, eggs kept under water were gradually killed, presumably because of interference with their gaseous metabolism.

The cell constructed by the larva is its protective device: by its construction the larva is able to ensure a microclimate which is to a certain extent under its own control. There are certain conditions under which it is unable to form a cell—if the ground is too hard, or so saturated that the hole becomes filled with water—in which case the larva usually succumbs after a number of days. Fidler (1936) deals with the physical factors of the soil microclimate, and the relation between these and the behaviour of the larvae inhabiting it. The larvae used were those of the species *Serica brunnea*. The most important factors are shown to be soil temperature and soil moisture. He showed that there is a distinct relation between the water-content of the soil and the concentration of the body fluid of the larva. In the larval cell the larva can raise the humidity a small amount per cent. by evaporation, without dangerous loss of body fluid. In winter the temperature near the surface of the soil may reach a point below that which the insect can tolerate. The larva is able to evade this by migration downwards, where it is subjected to lack of oxygen and food, both retarding metabolism. He showed, however, that they can exist under practically anaerobic conditions at low temperatures. For *Melolontha melolontha* (Schwerdtfeger, 1939a) it has been shown that the larvae in the early instars became inactive at about 43°F. This relatively high point of inactivity would prevent larvae in position in the ground for hibernation from moving to a greater depth to escape increasing cold. This appears to be the reason for their normally hibernating at a depth of 19–24 inches, at which the lethal temperature is hardly ever reached. On the other hand, larvae of *Serica brunnea*, if stimulated by adverse conditions, are capable of movement to the optimum level even if the temperature is only a few degrees above their fatal zone (Fidler, 1936).

In autumn the limiting factor seems to be excess of soil moisture in the presence of relatively high temperatures: this is inclined to be fatal in itself, but is also favourable for a biotic factor in the larval ecology—development of fungoid and bacterial diseases. In summer larvae may suffer from lack of moisture. This also has the indirect effect of removing the food supply of the larva at a time when high temperatures have induced rapid metabolism (Fidler, 1936). Larvae of *Melolontha melolontha* are very resistant to variations in soil moisture, but if the absolute water content of the upper soil fall below 3% they move downwards, possibly because of the difficulty of moving in dry earth (Schwerdtfeger, 1939). Temperature changes at hibernation depths are much smaller than those at the surface; they decrease with increase in depth. The temperature of the surface soil is less affected by that of the air when there is a covering of vegetation. Larvae therefore would not undergo rapid fluctuations in temperature. There is a main temperature inversion in spring and autumn (Mail, 1930), when the deeper soil ceases to lose and gain heat respectively. McColloch and Hayes (1923) showed that whenever this change took place the larvae moved either up or

down. Sweetman (1931) considers that the length of the life cycle is dependent upon the physical ecological factors.

Smith deals with the chemical factors of the soil habitat (acidity and humus values), and white grub distribution in relation to these. The acidity of soils in the grub-infested areas is uniformly high. On the Atherton Tableland the northern and north-western boundaries have been fairly stable for some time. This may be due to change in soil type with change of pH values from acid to alkaline. In areas subject to heavy rainfall soils will tend to become more and more acid through leaching, and the areas liable to grub infestation will become greater. Smith takes a critical pH value as 5.5, below which possible infestation is inferred. Following on removal of bases by leaching, is deterioration of physical characters from good crumb structure to single grain structure. *Lepidiota laevis* is restricted to definitely alkaline areas. In some parts of the world definite correlations have been established between soil texture and grub-susceptibility.

#### *Australian Economic Species.*

The majority of the damage is caused by the root-feeding larvae (with the outstanding exception of the two species, *Metanastes vulgivagus* and *Heteronychus sanctae-helenae*, in which the boring habits of the adults are directly responsible for weakening or death of the plants); the adults as a rule feed on the foliage of native plants, but there may be localized and sporadic outbreaks, in which vines and orchard trees are damaged (e.g., *Diphucephala colaspoides*). Larval Scarabaeidae infest a large variety of plants, ranging from grass lands, lawns and field crops, to strawberries, Eucalypts, and young nursery trees, maize, sugar-cane and vegetables. The actual economic status of the family in Australia is at present indefinitely known. Larvae infesting the Queensland cane-fields present a serious problem; heavy damage to pastures occurs in Queensland (on the Atherton Tableland, where pasture deterioration due to scarabs is a serious matter); in New South Wales on the Dorrigo and Southern Tablelands and in coastal districts, in South Australia and in Victoria. The only introduced pest species is *Heteronychus sanctae-helenae*: the rest of the species which have become pests are indigenous. In many cases the first outbreaks have been of comparatively recent occurrence. Clearing of native scrub and coarse grass not only removed the natural source of food, but replacement by fine cultivated grasses, cereal crops, etc., has often created conditions favourable for survival, with abundant food.

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## APPENDIX.

## I. LITERATURE ON OVERSEAS WORK.

(a). *Miscellaneous.*

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## 2. LITERATURE ON AUSTRALIAN ECONOMIC SPECIES.\*

- a. Sugar-cane. *Queensland*.  
Fully 50 species of Scarabaeidae have been recorded from cane-fields. Of these the following are accounted major pests:  
*Lepidoderma albobirtum* Waterh., *Pseudoholophylla furfuracea* Burm., *Lepidiota frenchi* Blkb., *Lepidiota trichosterna* Lea, *Lepidiota caudata* Blkb., *Anoplognathus boisduvali* Boisd., *Dasygnathus australis-dejeani* Macl.  
Slightly injurious species are:  
*Anomala australasiae* Blkb., *Isodon puncticollis* Macl., *Cacachroa decorticata* Macl., *Lepidiota consobrina* Gir., *Lepidiota grata* Blkb., *Lepidiota rothei* Blkb.  
The information published on sugar-cane pest species is to be found in the *Queensland Agricultural Journal* (frequently under the heading "Cane Pest Combat and Control"), and in the Reports and Bulletins of the Division of Entomology of the Queensland Bureau of Sugar Experiment Stations.
- b. Maize and Sugar-cane. *Queensland and New South Wales*.  
*Metanastes vulgivagus* Olliff (*Pentodon australis* Blkb.). *Qd. Agric. J.*, 1924-1930—on sugar-cane.  
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\* This literature has been grouped under the plants attacked and also under the specific insect concerned. Papers are not listed alphabetically, but according to the year of publication.

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- c. Maize, Sugar-cane, Vegetable Crops, Banana, Grass Areas. *New South Wales*.  
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Arrow, G. J., 1932.—A Few New Species of *Melolonthine* Coleoptera. *Ann. and Mag. N. Hist.*, Ser. 10, ix, 189-197. (Concerning erroneous identification of *A. tetricus*.)
- c. Strawberry, Grasses, Eucalypts, Orchard Trees. *New South Wales*.  
*Anoplognathus analis*.  
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- g. Lucerne, Strawberry, Pastures, Cereal Crops, Sugar-cane. *Victoria, S. Australia, Queensland*.  
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## NOTES ON AUSTRALIAN DIPTERA. XXXIX.

FAMILY CHLOROPIDAE, Part iii.\*

By JOHN R. MALLOCH.

(Communicated by Frank H. Taylor, F.R.E.S., F.Z.S.)

(Thirteen Text-figures.)

[Read 30th April, 1941.]

## LIOSCINELLA Duda.

*Knowia*, viii, 1929, 168; *Folia zool. hydrobiol.*, ii, 1930, 71 and 106.

This genus was recently erected for the reception of those species of the old genus *Oscinella* Becker that have the frontal triangle glossy. I have attempted to clarify the distinctions between it and *Conioscinella* Duda, *Botanobia* Lioy, and *Oscinella* Becker in the present paper and hope that students of the family will be able correctly to assign their specimens by means of my key to the genera and the notes under each genus. The task is undoubtedly a difficult one and beginners in the study will have some trouble in placing the species.

In my concept of *Lioscinella* I include species that have the frontal triangle large and almost entirely or wholly glossy, though not always black. No species has the thorax entirely grey dusted, and nearly all have it either yellow with black markings or largely or entirely glossy-black, the mesopleura being without grey dust except in some of the species that may be doubtfully referred to *Botanobia*. No species of *Conioscinella* has yellow markings on the thorax, and though there are many species in *Botanobia* that have yellow thoracic markings, in the latter the frontal triangle is smaller, rarely extending to the middle of the frons, and it is usually grey dusted on the edges as in *Conioscinella*, or the edges are not sharply defined. There is one group of species that I have placed in the following key with some hesitation. This is the one in which the frontal triangle is almost entirely dull and preponderantly yellow. It contains species that are in the main yellow-coloured, with black or partly black mesonotal vittae, and the aristaes always very short pubescent, in which respect they differ from the larger and darker coloured species of *Botanobia*, the latter having the aristaes longer pubescent.

In order to prevent as far as possible misinterpretations of the species I am including all those in the complex in a single key. I have, after a careful consideration of the characters of the genotype of *Gaurax* Loew, decided that no species definitely referable to the genus is amongst those now available to me.

*Key to the Species.*

- |   |                              |
|---|------------------------------|
| 1. Thorax and scutellum entirely, usually glossy, black, at most with a brown patch on each side at the mesonotal suture .....  | 2                            |
| Thorax largely yellow, if preponderantly glossy-black then at least the apex of the scutellum, or the entire humeral angles, yellow or brownish-yellow .....  | 16                           |
| 2. Halteres black or blackish-brown; triangle and mesonotum with a rather noticeable violet tinge or lustre; palpi dark brown; genae shiny dark brown, becoming yellow in front; legs pale yellow, only the mid and hind femora except their extremities, and the basal halves of the hind tibiae, black; face white; frons blackened on posterior half ..... | <i>nigroviolacea</i> Malloch |
| Halteres pale yellow; frontal triangle and mesonotum without a violet tinge; remainder of characters not all as above .....   | 3                            |

\* Continued from These PROCEEDINGS, lxxv, 1940, 261.

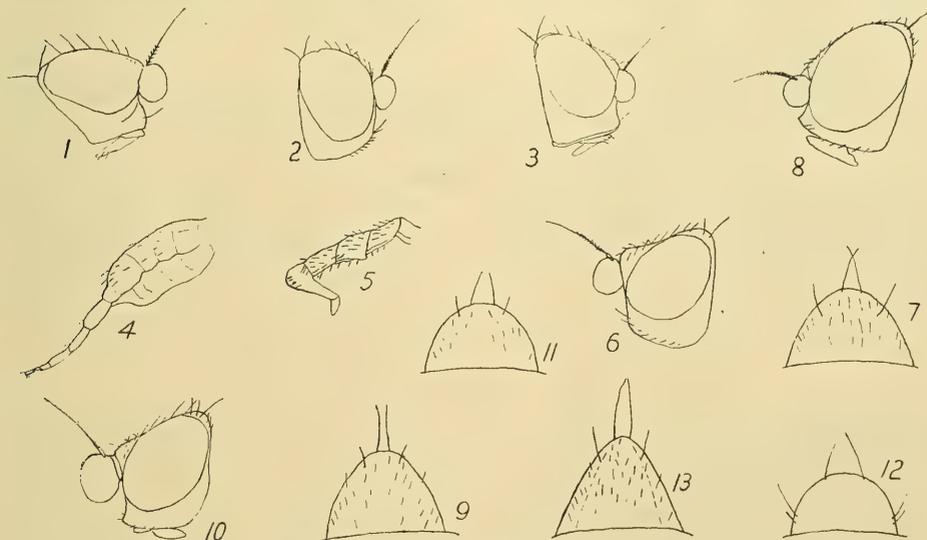
3. Palpi dark brown to black ..... 3a  
 Palpi yellow; mesonotum and scutellum without grey dusting; hairs normal ..... 4
- 3a. Mesonotum and scutellum glossy-black, smooth, the lateral margins of mesonotum and the disc of the scutellum slightly grey dusted; frontal triangle poorly defined, extending to middle of frons, slightly grey dusted and dull on margin, glossy-black on the ocellar orbit; mesonotal hairs longer than usual, erect ..... *Botanobia hirtipes*, n. sp.  
 Mesonotum and scutellum glossy-black, quite closely and coarsely piliferous-punctate, without dusting; frontal triangle narrow, sharply defined, extending to well beyond middle of frons, entirely glossy-black, remainder of frons orange-yellow; mesonotal hairs short and subdecumbent ..... *cairnsi*, n. sp.
4. Frons entirely black or dark brown, the triangle glossy-black, the area laterad of it in front dark brown and distinctly shiny; legs entirely honey-yellow; mesonotum with fine hairs, indistinctly punctured; scutellum with distinct piliferous-punctures, the hairs stiff and decumbent ..... *unifrons*, n. sp.  
 Frons partly yellow or dull brown; other characters not as above ..... 5
5. Frons red or yellow, not blackened or distinctly browned posteriorly between the triangle and eyes; genae and face yellow or whitish-yellow; mesonotum rather distinctly punctured, closely and rather coarsely so in the dorsocentral depressions ..... 6  
 Frons yellow, merging into black or dark brown between the triangle and eyes; mesonotum more finely haired, not distinctly punctured except finely in the dorsocentral lines .. 9  
 Frons yellow in front, merging into black or dark brown posteriorly between the triangle and eyes; triangle alutaceous; mesonotum and scutellum quite coarsely and closely piliferous-punctate ..... *albifacies*, n. sp.
6. Legs entirely yellow ..... *waterhousii*, n. sp.  
 Legs yellow, the mid and hind femora and tibiae largely black ..... 7
7. Robust species, with the mesonotum quite deeply and uniformly piliferous-punctate; hairs on sides of frons, and mesonotum, long; genae largely dark brown; profile of head as Figure 1 ..... *crassa*, n. sp.  
 Slender species, with the mesonotum finely and shallowly piliferous-punctate; hairs on the sides of frons, and on mesonotum, shorter; genae orange-yellow ..... 8
8. Head in profile as Figure 2, the vibrissal angle suppressed ..... *simulata*, n. sp.  
 Head in profile as Figure 3, the vibrissal angle distinct ..... *predatoris*, n. sp.
9. All the tibiae yellow and with two narrow brown annuli ..... *biannulata*, n.n.  
 Tibiae either entirely yellow or with one broad black mark ..... 10
10. Penultimate sections of third and fourth wing-veins subequal in length, or the latter slightly the shorter; all coxae, femora, and tibiae, preponderantly black ..... *nigropolita*, n. sp.  
 Penultimate section of the third wing-vein very much shorter than that of fourth ..... 11
11. Coxae and femora almost entirely, and all the tibiae, preponderantly black ..... 12  
 At least the fore and mid tibiae entirely yellow ..... 14
12. Genae black or dark brown below, brownish-yellow above, not over one-third as high as width of the third antennal segment, and about one-tenth as high as eye ..... *similis*, var. *femoralis* novum  
 Genae yellow below, white above, about half as high as width of the third antennal segment and one-sixth as high as eye ..... 13
13. Frons seen from the side with the face towards the light in front and along the eye margins with silvery white dust; femora and tibiae entirely brownish-black; marginal cell of the wing just beyond the apex of first vein not wider than the submarginal at the same point ..... *albiceps*, n. sp.  
 Frons without pale dust in front and along eye margins when seen from any angle; knees and apices of the tibiae orange-yellow; marginal cell of the wing just beyond the apex of first vein over 1.5 times as wide as submarginal cell at the same point ..... *nigropolita*, n. sp.
14. Legs entirely yellow, rarely with a slight pale brown cloud near middle of ventral surface of the hind femur ..... *similis*, var. *apicta* Malloch  
 Legs with a brown or black mark on each mid and hind femur ..... 15
15. Mid and hind femora each with a brown or black mark ..... *similis*, var. *similis* Becker  
 Mid and hind femora and basal halves of hind tibiae blackened ..... *similis*, var. *fuscibasis* Malloch
16. Legs entirely yellow ..... 17  
 Legs in part black or dark brown, sometimes only the fifth tarsal segment dark ..... 43
17. Scutellum blackened on at least a part of base, the black colour visible from above .. 18  
 Scutellum yellow, rarely with a small blackish mark on each side at base that is not visible from above, but only from the side ..... 26
18. Mesonotum glossy orange-yellow, with the presutural lateral margins and the posterior portions of the humeri lemon-yellow to white, the disc of mesonotum with five glossy-black vittae, the central one usually divided by a yellow line; scutellum whitish-yellow, narrowly black across the base, the apex produced papilliform between the apical pair of bristles; notopleurals 1+2; frons orange-yellow, the triangle with a broad black central vitta from over the posterior ocelli to anterior extremity; legs orange-yellow;

- pleura largely black, sternopleura with yellowish-white upper margin; gena about one-fourth as high as eye ..... *excepta*, n. sp.
- Mesonotum broadly black on disc, not with narrow black vittae, and not white on lateral margins in front of the suture; scutellum usually more broadly black across base, and not produced papilliform between the apical pair of bristles ..... 19
19. Frons black or very dark brown on upper third or more between the triangle and eyes; only two strong notopleural bristles present (1+1) ..... 20
- Frons orange-yellow or yellow on the entire area outside the triangle; three notopleurals present ..... 24
20. Pleura with three or four black spots; scutellum blackened at base, the black mark reduced to a mere line or broken in centre; notopleurals 1+1, and sometimes a short setule above the posterior one; no depressions of the posterior portions of the dorsocentral lines, the hairs more numerous there but the punctures not pronounced; prelabrum black in female, yellow or faintly browned in male; triangle glossy-black, vertex black on each side of the triangle; abdomen of male with long stiff, erect hairs ..... *discolor*, n. sp.
- Pleura either entirely black, or with but two black marks ..... 21
21. Notopleurals 1+1, no setule above the posterior one ..... 22
- Notopleurals 1+1, and a distinct setule above the posterior one; pleura with but one black mark, on the mesopleura ..... 23
22. Pleura entirely black; mesonotum glossy-black, yellowish on only a patch on each notopleural area; scutellum blackish-brown, fading into yellowish-brown at apex, the pale colour most evident below ..... *impura* Becker
- Pleura yellow, with but traces of one or two brownish marks; mesonotum pale yellow along the notopleural region and on the postalar callosities; scutellum distinctly pale yellow at apex ..... *pallidipleura*, n. sp.
23. Mesonotum glossy black except on the lateral margins ..... *flavolateralis*, n. sp.
- Mesonotum with the large black discal mark quite widely broken at suture .. *suturalis*, n. sp.
24. Mesonotum with the large discal black portion distinctly shiny, but with evident greyish dust; scutellum with a very small dark mark on side of each basal angle, sometimes not visible from above ..... *communis*, n. sp.
- The discal black portions of the mesonotum glossy, undusted; scutellum broadly black at base, yellow beyond ..... 25
25. Triangle yellow across vertex at or just below edge; prosternum yellow; humeri usually entirely yellow ..... *tasmaniensis* Malloch
- Triangle entirely black; prosternum black in centre; humeri largely or entirely black ..... *varidorsata*, n. sp.
26. Frontal triangle highly glossy, largely or entirely black, very wide on upper edge where it extends almost across the entire vertex, and at least half the length of frons ..... 27
- Frontal triangle not highly glossy, sometimes distinctly shiny on the central part of the black mark that rarely extends outside of the ocellar orbit, the posterior lateral angles well removed from eyes ..... 30
27. Frontal triangle entirely black, extending to near middle of frons; abdomen of male with quite long erect stiff black hairs and the hypopygium large and pendulous, or projecting forward below abdomen at least to middle of venter ..... *discolor*, n. sp.
- Frontal triangle not entirely black, extending to or nearly to anterior margin of the frons; male with the usual fine abdominal hairs and small hypopygium ..... 28
- Frontal triangle entirely black, extending to anterior margin of frons; abdomen of male normal in hairing and structure ..... *mesopleuralis* Becker
28. Mesopleura yellow; sternopleura with lower half black ..... *sternopleuralis*, n. sp.
- Mesopleura with a black mark below; sternopleura yellow ..... 29
29. The black discal mark on mesonotum broken at suture ..... *mesopleuralis* Becker, var.
- The black discal mark on mesonotum not broken at suture ..... *mesopleuralis* Becker
30. The three or five mesonotal vittae fused, forming a broad black discal mark ..... 31
- The three or five black mesonotal vittae partially or entirely separated ..... 33
31. Scutellum with four quite strong black bristles, the anterior pair nearer to the base than to the apical pair, a setule in front of each anterior bristle, and no noticeable discal hairs ..... *communis*, n. sp.
- Scutellum with the short anterior pair of bristles nearer to the apical longer pair than to the base, the disc with many quite distinct hairs ..... 32
32. Occiput, vertex, and the frontal triangle except its apex, glossy-black; third antennal segment blackened at only upper apex; hairs on mesonotum and abdomen almost entirely black or dark brown ..... *tonnoiri* Malloch
- Occiput laterally, and vertex, yellow, triangle blackened except on lateral edges, shiny centrally, greyish dusted on sides; third antennal segment brownish-black; hairs on mesonotum and abdomen white, fine, and longer than usual ..... *albohirta*, n. sp.
33. Mesonotal vittae bicoloured, black and red; antennae entirely orange-yellow ..... 34
- Mesonotal vittae either entirely black, or the antennae are not entirely yellow ..... 36

34. Thoracic vittae black, the central one red at suture ..... *minutula*, n. sp.  
 Thoracic vittae rufous, blackened at both extremities ..... *extremitata*, n. sp.  
 Thoracic vittae red, blackened at one or other of the extremities, not at both ..... 35
35. Thoracic vittae red, blackened at anterior extremities ..... *flavocapitata*, n. sp.  
 Thoracic vittae red, blackened at only the posterior extremities; female genital processes  
 setulose ..... *semiatra*, n. sp.
36. Thoracic vittae bicoloured, red and black; third antennal segment partly or entirely  
 infuscated ..... 37  
 Thoracic vittae entirely black ..... 38
37. Third antennal segment large, narrowly infuscated above and at apex; female genital  
 processes fine haired ..... *nigrohirta* Malloch  
 Third antennal segment small, entirely black-brown; female genital processes setulose ....  
 ..... *bivittigera*, n. sp.
38. Third antennal segment and the palpi bright orange-yellow ..... 39  
 Third antennal segment and sometimes the palpi darkened apically ..... 40
39. Small species, averaging about 1 mm. in length; the black thoracic vittae dull, overlaid  
 with grey dust, the central vitta divided longitudinally and not extending to posterior  
 margin of mesonotum; female genital processes slender, finely haired .....  
 ..... *quadristriata* Becker  
 Larger species, averaging about 2 mm. in length; the black mesonotal vittae glossy, the  
 central one not divided longitudinally, entire ..... *luteicornis* Malloch
40. All the hairs and bristles on thorax yellow or luteous ..... *luteohirta* Malloch  
 At least the bristles of the thorax black ..... 41
41. Mesonotum with four narrow black vittae, the central one divided longitudinally, extending  
 to only midway between suture and hind margin, shorter than the submedian pair; inner  
 cross-vein a little beyond apex of first vein; marginal cell of the wing not wider than  
 the submarginal just beyond apex of first vein ..... *quadristriata* Becker  
 Mesonotum with three broad black vittae, the central one attaining the hind margin and  
 usually undivided longitudinally, and sometimes a short sublateral postsutural streak  
 on each side; inner cross-vein of the wing slightly proximad of apex of first vein;  
 marginal cell of wing wider than submarginal just beyond apex of first vein ..... 42
42. Palpi black; the black mark on the frontal triangle confined to ocellar orbit .....  
 ..... *confluens*, n. sp.  
 Palpi yellow; the black mark on frontal triangle extending outside the ocellar orbit .. 42a
- 42a. Occiput largely yellow; mesonotal vittae glossy-black, usually separated; scutellum  
 slightly elongated, with two long and two much shorter preapical bristles, the latter  
 much nearer the apical pair than to base, and the disc with many distinct black  
 hairs ..... *tincticornis*, n. sp.  
 Occiput black; mesonotal vittae shiny black, overlaid with grey dust, fused in front and  
 but indistinctly separated behind; scutellum short, rounded in outline, with a pair of  
 moderately long apical and a pair of slightly shorter lateral bristles, the latter as near  
 to base as to apical pair ..... *communis*, n. sp.
43. Legs yellow, all the coxae, and a stripe on the anterior and another on the posterior side  
 of the fore femora, and the palpi, black ..... *tonnoiri* Malloch, male.  
 Legs not coloured as above, some part of the mid and hind pairs besides the coxae black  
 or dark brown ..... 44
44. Legs yellow, fifth tarsal segment on all legs black or dark brown ..... 45  
 Legs otherwise marked with black or dark brown ..... 46
45. Antennae entirely orange-yellow; mesonotum glossy orange-yellow, with a black mark in  
 centre of anterior margin, and five diffuse black postsutural vittae, the anterior portions  
 of the vittae indistinct; scutellum blackened; fore tarsus with fourth and fifth, other  
 segments with only the fifth dark brown, fifth segment not dilated; thoracic bristles  
 black ..... *brunneoapicata*, n. sp.  
 Antennae yellow, third segment black; mesonotum orange-yellow, with five glossy-black  
 vittae, the discal three fused in front, tapered behind, median one entire, submedian  
 pair not attaining hind margin, the sublateral pair consisting of short postsutural  
 streaks; scutellum yellow; all tarsi with the fifth segment deep black and distinctly  
 dilated; thoracic bristles yellow ..... *nigrimana*, n. sp.
46. Wings hyaline, with a blackish mark on the costal margin from just beyond third vein  
 to a little beyond apex of fourth that is hyaline in centre .... *apicipunctata* (Malloch)  
 Wings hyaline, without a blackish costal mark as above ..... 47
47. Hind tarsi with the apical three segments black or blackish-brown, the third sometimes  
 yellow at base, and all three usually noticeably dilated; palpi infuscated apically .. 48  
 Hind tarsi yellow or only slightly brownish apically, the apical three segments not at all  
 dilated ..... 50
48. Hind tarsus with the apical three segments brownish-black, but little dilated, the fourth  
 segment longer than wide; hind tibia black from near middle to apex; all femora with  
 a broad blackish-brown central band; fore coxae with brown mark at base; scutellum  
 yellow only around the margin, disc black; mid tibial spur black and strong; upper  
 posterior notopleural bristle minute ..... *nigroannulata* Malloch

- Hind tarsus with the apex of third segment and the fourth and fifth entirely deep black, very distinctly dilated, the fourth segment broader than long; hind tibia with at most a narrow preapical brown ring; fore coxae yellow; scutellum entirely yellow or with only a narrow black central vitta; mid tibial spur yellow and weak ..... 49
49. Upper posterior notopleural bristle almost as long as the lower one; scutellum yellow, rarely slightly darkened centrally at base ..... *dilatata* Malloch  
Upper posterior notopleural bristle lacking; scutellum yellow, with a narrow black central vitta ..... *latitarsis*, n. sp.
50. Legs yellow, all the tibiae with a narrow central brown annulus or spot .... *tibiella* Becker  
Legs yellow, with more extensive or different black marking ..... 51
51. Femora yellow, fore or hind pairs faintly browned; scutellum entirely yellow ..... 52  
Femora largely black ..... 53
52. Fore femora darkened below; hind tibiae yellow; third antennal segment largely yellow; thoracic bristles yellow ..... *luteohirta* Malloch  
Fore femora yellow, hind tibiae browned on basal halves; third antennal segment entirely black; thoracic bristles black ..... *froggatti*, n. sp.
53. The black mark on the frontal triangle confined to the ocellar orbit, dull; mesonotum with three black vittae that are interrupted or red at suture; scutellum entirely yellow, narrowed at apex and with the apical pair of bristles much closer at bases than usual (Fig. 9); antennae yellow; all femora largely black, the tibiae yellow .. *robusta*, n. sp.  
Black mark on the frontal triangle extending outside the ocellar orbit; scutellum partly or entirely black; mesonotum broadly black on disc, the usual vittae fused ..... 54
54. Scutellum entirely black; frontal triangle black, rather dull, appearing microscopically shagreened or greyish dusted; thorax shiny black, the humeri reddish-brown ..... *subopacifrons*, n. sp.  
Scutellum not entirely black; frontal triangle partly glossy, without distinct grey dust on disc; some part of the thorax besides the humeri pale, usually bright yellow ..... 55
55. Humeri and scutellum entirely yellow; apical ventral spur on mid tibia brownish-yellow ..... *flavohumeralis*, n. sp.  
Humeri yellow, anterior portions black; scutellum more or less broadly black at base; apical ventral spur of mid tibia black ..... 56
56. Genae not white dusted; scutellum very narrowly yellow at apex ..... *tinctipes* Malloch  
Genae distinctly silvery white dusted; scutellum with the apical two-thirds yellow ..... *argenteiceps*, n. sp.

N.B.: The arrangement of the species in the text is not intended to indicate relationships except in a general manner.



Figs. 1-13.

- 1.—*Lioscinella crassa*, n. sp. Head in profile. 2.—*L. simulata*, n. sp. Head in profile.  
3.—*L. predatoris*, n. sp. Head in profile. 4, 5.—*L. discolor*, n. sp. 4. Abdomen of female from the side. 5. Abdomen of male from the side. 6.—*L. bivittigera*, n. sp. Head in profile.  
7.—*Botanobia tonnoiri* Malloch. Scutellum from above. 8, 9.—*B. robusta*, n. sp. 8. Head in profile. 9. Scutellum from above. 10.—*B. nigrohirta* Malloch. Head in profile. 11.—*B. tincticornis*, n. sp. Scutellum from above. 12.—*B. communis*, n. sp. Scutellum from above.  
13.—*Prohippелates nigricornis* var. *flavus* Thomson. Scutellum from above.

## GROUP I.

Thorax and scutellum black, generally glossy, nowhere yellow, at most brownish on each side at the suture.

## SECTION A.

Frons usually yellow of various shades in front, but always black across vertex and on each side of the triangle.

## LIOSCINELLA NIGROVIOLOACEA Malloch.

PROC. LINN. SOC. N.S.W., lvi, 1931, 63.

A small glossy black species that is distinguished from all the others in the group by the dark brown to black knobs of the halteres, and the more or less distinct violet tinge on the frontal triangle and mesonotum. The notopleurals are arranged 1 + 2, and as usual the eyes are distinctly haired. Length, 1.5-2 mm.

Localities, N.S.W.: Sydney, Como.

## LIOSCINELLA SIMILIS Becker.

Ann. Mus. Nat. Hung., ix, 1911, 153.

This species in all its varieties has the thorax glossy-black, without dusting, with usually a faint brownish patch on each side at the notopleural suture, and the scutellum without a trace of yellow colour. The face and genae are pale yellow, densely silvery white dusted, and the halteres yellow.

I have already described two varieties which are included in the foregoing key, and now describe a third variety below.

Originally described from Sydney, N.S.W., from which locality I have a series of specimens.

## LIOSCINELLA SIMILIS, var. APICTA Malloch.

PROC. LINN. SOC. N.S.W., lvi, 1931, 66.

Originally described from Sydney, N.S.W. I have a series of specimens before me from the type-locality.

## LIOSCINELLA SIMILIS, var. FUSCIBASIS Malloch.

Op. cit., lvi, 1931, 66.

The type-locality and that of some additional specimens before me is Sydney, N.S.W. All of these specimens are from the collection of the Health Department.

## LIOSCINELLA SIMILIS, var. FEMORALIS, n. var.

♀. This variety differs from the others already described in having the femora and tibiae all extensively blackened. As in the other varieties the two posterior notopleural bristles are well developed. The peculiar globular basal half and the very slender apical half of the abdomen in the female are maintained throughout all the varieties.

Type and 2 paratype females, N.S.W.: Sydney (Health Dept.).

## LIOSCINELLA ALBICEPS, n. sp.

♂. Agrees very closely in colour and general structure with *similis*, the main distinctions being as follow: Frons when seen from in front and a little to one side white dusted on anterior half, most noticeably so on a narrow line on each side; triangle extending barely beyond middle of frons; genae higher than in *similis*, about one-sixth of the height of eye, yellow below, white dusted above; eyes very indistinctly haired. Notopleural region brownish-yellow, mesonotum glossy-black, with fine moderately long black hairs at bases of which there are no distinct punctures; scutellum similar to the mesonotum, convex above; the upper posterior notopleural bristle reduced to a mere setule. Abdomen rather dull blackish-brown, ovate, tapered behind. Legs blackish-brown, apices of fore coxae and all tarsi paler brown. Wings greyish-hyaline, veins black. Knobs of halteres yellow. Length, 1.75 mm.

Type, N.S.W.: Sydney, 26.x.1924 (Health Dept.).

## LIOSCINELLA NIGROPOLITA, n. sp.

♂, ♀. Similar to *similis* and *albiceps* in general colour and structure, differing mainly as follows: Genae and face in female yellow, in male white as in *similis*, frons not so extensively blackish-brown on the sides, dark for only a short distance before vertex; gena about one-sixth of the eye height, the latter quite densely and distinctly pale haired; arista a little longer pubescent than in *similis*; scutellar hairs longer than in that species; posterior notopleurals both long. Legs fulvous-yellow, fore coxae anteriorly, femora except apices, and tibiae except their extremities, glossy black. Wings greyish-hyaline, with a faint dark shading on costal portion over apex of the first vein that is also seen in some specimens of *similis*; penultimate section of third vein usually a little longer than that of fourth; extreme apices of third and fourth veins divergent. Halteres yellow. Abdomen of the female almost normally tapered to apex. Length, 2-2.5 mm.

Type, ♀, N.S.W.: Yass, 27.vi.1930 (K. English); allotype, A.C.T.: Molonglo R., 10.iv.1930 (L. F. Graham); paratype females, N. Territory: Darwin (Palmerston), April 1931, ex new swedes, and ex rotten swedes (W. Cottier).

The above records are all that are known to me of the habits of the larvae of species of this group.

## LIOSCINELLA ALBIFACIES, n. sp.

♂. Frons about two-fifths of the head width and a little longer than wide, orange-yellow on anterior third or less, blackened behind, the triangle glossy, slightly shagreened, remainder of surface not shiny, triangle extending a little beyond the anterior third, sharp in front; surface hairs brown, about six orbital setulae on each side, the verticals longer than these and the ocellars; face and upper part of the genae densely white dusted, lower margin of genae brown; eye a little higher than long, slightly oblique, and about ten times as high as gena, with distinct pale hairs; genal hairs pale brown, upcurved, vibrissal setule pale yellow, the angle not developed. Antennae orange-yellow, inserted below middle of eye in profile, third segment about twice as wide as gena; arista brown, microscopically pubescent; palpi orange-yellow; prelabrum blackened. Thorax glossy-black, with but slight trace of grey dusting on lateral margins of the mesonotum, the hairs brownish, and moderately long, the bristles black, surface of the mesonotum distinctly and closely piliferous-punctate, the scutellum more coarsely so; notopleurals 1 + 2; scutellum with three pairs of bristles, longer to the apical pair. Legs rather stout, orange-yellow, coxae, femora except their apices, and the hind tibiae centrally, blackened. Wings brownish-hyaline, veins brown. First costal division four-fifths as long as the second and longer than the third, the latter about 1.5 times as long as fourth; third vein ending before, fourth slightly behind the wing tip; penultimate section of fourth vein distinctly longer than penultimate section of third and about one-fourth as long as its own penultimate section. Halteres with yellow knobs. Abdomen broadly ovate, glossy brownish-black, the hairs dark. Length, 1.75 mm.

Type and one paratype, A.C.T.: Blundell's, 26-27.ix.1930 (L. F. Graham).

## LIOSCINELLA UNIFRONS, n. sp.

♀. Head black, frontal triangle glossy-black, almost entirely filling the vertex and extending to nearly the anterior margin, the remainder of surface shiny blackish-brown; face and genae red-brown. Frons at vertex about two-fifths of the head width, very slightly narrowed to anterior margin and as long as its vertical width, bristling and hairing normal, rather fine, black. Eye about 1.25 times as high as long, finely haired; gena about one-tenth as high as eye and one-third as high as width of the third antennal segment, the latter disc-like, orange-yellow; arista pubescent; palpi orange-yellow. Thorax glossy-black, with black hairs and bristles, mesonotum with rather distinct piliferous punctures, especially in the dorsocentral depressions; scutellum slightly flattened on disc, round in outline, with many quite coarse piliferous punctures, the hairs coarse, two long apical and two much shorter preapical bristles; notopleurals 1 + 2. Legs

including the coxae entirely pale yellow. Wings hyaline, veins dark brown. First costal division about three-fourths as long as second and subequal to third, the latter about 1.25 times as long as fourth; third vein ending well before, fourth slightly behind, wing tip; penultimate section of third vein over half as long as penultimate section of fourth, the latter about two-thirds as long as ultimate section of fourth. Knobs of halteres pale yellow. Abdomen ovate, glossy-black, black haired. Length, 1.75 mm.

Type, N.S.W.: Como (Peterson).

Unfortunately after the description when the type was damaged, losing the head, so that the main distinguishing characters are unavailable for study in the specimen.

*LIOSCINELLA BIANNULATA*, new name.

*Oscinosoma nigroannulata* Malloch, PROC. LINN. SOC. N.S.W., lvi, 1931, 61; *nec. op. cit.*, 1, 1925, 338 (*Botanobia*).

Through an inexcusable oversight the writer described two species with the same name as above indicated and now makes a change in the name of the second species.

SECTION B.

Species with the frons except the triangle in various shades of yellow, not becoming black or dark brown on the upper part between the triangle and eyes.

*LIOSCINELLA WATERHOUSII*, n. sp.

♂. Head orange-yellow, frons dull, not darkened above, triangle glossy brownish-black, occiput black, with a narrow yellow line across vertex; face much paler than frons; antennae and palpi yellow; arista dark brown; all hairs and bristles black. Frons longer than its vertical width, narrowed in front, triangle narrowly separated from eyes at vertex, its sides slightly sinuate, apex at about one-third from anterior margin of frons; outer vertical bristles about two-thirds as long as inner pair, the latter barely as long as the post-verticals, ocellars about two-thirds as long as latter; surface hairs stiff, longer and proclinate in centre in front, the upper orbital series erect and setulose. Eye higher than long and erect, with short stiff hairs. Gena about one-eighth as high as eye and less than half as high as width of third antennal segment, the latter wider than long and broadly rounded at apex; longest hairs on arista about half as long as their basal diameter. Parafacial not visible in profile; face rather deeply sunken. Thorax glossy-black, notopleural area and pleural sutures brownish-yellow; all hairs and bristles dark. Mesonotum with minute piliferous punctures, densest in the dorsocentral lines where they are congregated posteriorly; humeral, notopleural (1 + 2), posterior pair of dorsocentrals, and both postalar bristles quite long and strong. Scutellum noticeably flattened on disc, rather short and somewhat pointed between the apical pair of bristles, the latter much longer than the scutellum, the preapical bristles reduced to mere hairs, discal hairs sparse, in minute punctures. Legs honey-yellow, quite strong, mid-tibial spur brown, longer than the tibial diameter. Wings hyaline, veins pale brown. Fourth vein ending almost in, third vein well in front of, wing tip, the costal division between apices of third and fourth veins about four-fifths as long as third section, the latter fully two-thirds as long as second; marginal cell about 1.5 times as wide as submarginal at apex of first vein; inner cross-vein a little proximad of apex of first vein; penultimate section of third vein about half as long as penultimate section of fourth; outer cross-vein at about twice its own length from inner; ultimate section of fourth vein about four times as long as penultimate, bent down at apex; ultimate section of fifth vein over half as long as penultimate. Halteres yellow. Abdomen shiny-black, yellow on centre of basal two tergites and very narrowly so on apices of the other tergites. Length, 2 mm.

Type, N.S.W.: Sydney, 16.xi.1924; paratype, same locality, 1.i.1925 (Health Dept.).

This species is dedicated to Dr. G. A. Waterhouse, who kindly presented several of the papers of this series before the Linnean Society of New South Wales.

## LIOSCINELLA CAIRNSI, n. sp.

♂. A rather aberrant species, resembling in some respects certain species of the genus *Macrostyla*, but there are no evident hairs on the posterior upper portion of the mesopleura, and the wing venation is quite characteristic of *Lioscinella*. Head glossy-black, frons except the triangle orange-yellow, darker above, face yellow above, slightly darkened below, genae brownish-black, with grey dust; antennae orange-yellow, arista orange-yellow at base, fuscous beyond; palpi blackish-brown. Triangle narrow, not nearly filling vertical width, extending to anterior fifth of frons, glossy, entirely smooth and bare; surface hairs dark except in centre in front, the bristles black and not very strong. Antennae inserted at middle of eyes in profile, rather small, third segment with rounded apex; arista distinctly pubescent. Eye haired, distinctly higher than long, erect; over ten times as high as the very narrow gena. Thorax glossy-black, mesonotum rather coarsely and closely piliferous-punctate, the hairs subdecumbent and dark brown; scutellum as mesonotum, rather short and rounded in outline, with two moderately long apical and a number of lateral short bristles and many dark discal hairs, no warts at bases of the bristles. Notopleurals 1 + 2; mesonotum slightly wider than long. Legs orange-yellow, all coxae, and femora except their apices, glossy-black. No exceptional armature present, mid-tibial apical ventral bristle short and luteous; fore tarsi slender and as long as its tibia. Wings brownish-hyaline, veins dark brown. First costal section nearly as long as second and distinctly longer than third; inner cross-vein almost directly below apex of first vein; penultimate section of third vein subequal in length to that of fourth; first posterior cell widened to apex; fourth vein ending a little behind, third farther before wing tip; ultimate section of fourth vein about six times as long as penultimate. Halteres pale yellow. Abdomen broadly ovate, depressed, glossy-black, the surface hairs short and pale. Length, 2 mm.

Type, Queensland: Cairns District (F. P. Dodd).

I place this species provisionally in *Lioscinella*, but believe that it may yet be removed to a separate genus. Nothing is indicated on the label as to the habits of the species, and these may yet be made use of in generic segregations.

## LIOSCINELLA CRASSA, n. sp.

♂. Head brownish-black, frons subquadrate, nearly half the head width, entirely shiny, red except on the glossy-black frontal triangle which extends almost six-sevenths of the distance to anterior margin, hairs brown, rather sparse, each orbit with about six erect setulae that are about as long as the vertical and ocellar bristles. Antennae orange-yellow, third segment infuscated above and at apex; arista fuscous, distinctly pubescent. Profile as Figure 1. Face and upper part of genae yellow, greyish dusted, lower part of genae brownish-black, shiny. Palpi orange-yellow. Eyes distinctly haired. Thorax glossy-black, upper edges of pleura and its sutures brownish-yellow. Mesonotum quite coarsely piliferous-punctate, especially in the dorsocentral lines which are broad behind; notopleurals 1 + 2; surface hairs long and dark; scutellum subtriangular, disc convex, but with irregular piliferous punctures, the six marginal bristles rather long. Legs stout, brownish-yellow, mid and hind coxae, all femora, and the hind tibiae, largely dark brown. Wing brownish-hyaline, veins brown. First costal division about three-fourths as long as second and subequal to third, the latter nearly twice as long as fourth; fourth vein ending a little behind apex of wing, third ending farther before it; penultimate section of fourth vein about one-third as long as ultimate section and twice as long as penultimate section of third; ultimate section of fifth vein over half as long as penultimate. Halteres yellow. Abdomen ovate, shiny blackish-brown. Length, 2.5 mm.

Type, S. Australia: Mt. Lofty Ranges (A. H. Elston).

The subquadrate wide frons with its entirely shiny surface is a good distinguishing character for this species.

## LIOSCINELLA SIMULATA, n. sp.

♂, ♀. Similar to *waterhousii* in all respects except that in the male the mid and hind femora and the hind tibiae, and in the female the fore coxae, all femora, and

the hind tibiae, are predominantly black. Head in profile as Figure 2. The second wing-vein is less abruptly curved forward at its apex, and the second costal division is proportionately longer than in that species. Length, 2-2.5 mm.

Type, male, and two male paratypes, A.C.T.: Blundell's, 4.i.1930; allotype, same locality, 18.ii.1931 (A. L. Tonnoir).

It is possible that this is *subpilosa* Becker, and that it is merely a dark legged variety of *waterhousii*, but the latter appears to me to be improbable because of the lack of variation in the males in the two species. The wing venation, though somewhat inclined to be variable, does not vary as a rule in the characters cited above.

#### LIOSCINELLA PREDATORIS, n. sp.

♀. Differs from the female of *simulata* as follows: Vibrissal angle developed and the genae comparatively higher (Fig. 3); frontal triangle a little longer and the frons not curved down at anterior edge; mesonotum more glossy; fore coxae and the entire prosternum black; hind tibiae more conspicuously blackened; marginal cell of wing above the outer cross-vein fully 1.5 times as wide as the submarginal at the same point, not subequal to it; and the penultimate sections of third and fourth veins subequal, the fourth not distinctly longer than the third. Length, 2.5 mm.

Type, Tasmania: Eaglehawk Neck, 15.xi.1922 (A. L. Tonnoir).

#### GROUP II.

Thorax and scutellum partly yellow.

#### SECTION A.

Legs entirely yellow.

#### *Subsection a.*

Scutellum blackened more or less broadly across the base, or on basal angles.

#### LIOSCINELLA EXCEPTA, n. sp.

♂, ♀. Head orange-yellow, face and genae paler yellow, the triangle glossy-black, with the extreme apex and the posterior lateral angles broadly yellow; antennae yellow; arista dark brown; hairs and bristles of the frons and genae black except those on the lower margin of latter which are brownish-yellow. Triangle shorter and broader than in *tasmaniensis*, extending about three-fourths of the distance to the anterior margin. Inner verticals about three-fourths as long as the outer pair, slightly proclinate and incurved. Third antennal segment wider than long, broadly rounded at apex; arista subnude, second segment about five times as long as thick. Gena higher than in *tasmaniensis*, not as high as width of third antennal segment and about one-fourth as high as eye, the marginal hairs not so strong as in that species. Eyes distinctly haired. Mesonotum with five glossy-black vittae on an orange-yellow ground, the sublateral pair short, postsutural, the central broad vitta sometimes divided by a longitudinal yellow line; pleura glossy-black, yellow on lower part of the propleura, posterior upper part of the mesopleura, and on the sutures, the sternopleura with a whitish-yellow elongate mark above (not present in *tasmaniensis*). The posterior margin of the humeri and the region in front of the suture and laterad of the submedian black vitta also whitish-yellow. Mesonotal hairs inserted in minute punctures, most numerous on the yellow lines between the median and submedian black vittae; notopleurals 1 + 2; inner postalar bristle about half as long as the outer. Scutellum quite narrowly black across base, lemon-yellow, subtriangular, convex on disc, papillate between the apical pair of bristles, the latter a little longer than the scutellum and nearly twice as long as the preapical pair; discal hairs fine. In *tasmaniensis* the preapical pair of scutellar bristles is comparatively longer than in *excepta*, and situated about midway between the apical pair and the base instead of much nearer to the apical bristles as here. Legs rather stout, entirely yellow; mid femur with a rather pronounced apical flange-like scale on ventral edge on anterior surface; apical ventral spur on the mid tibia dark brown, slightly curved, and as long as the apical diameter of the tibia. Wings hyaline,

veins brown. Penultimate section of third vein distinctly shorter than that of fourth; ultimate section of fifth vein not half as long as penultimate section. Abdomen yellow, second tergite with three black spots or broadly black, tergites 3 to 5 inclusive broadly black at bases. Length, 3 mm.

Type, female, and allotype, A.C.T.: Blundell's, 26.ix.1930 (L. F. Graham); paratype female, N.S.W.: Como, from flowers (Peterson).

*LIOSCINELLA TASMANIENSIS* Malloch.

PROC. LINN. SOC. N.S.W., lvi, 1931, 62.

This species is very similar to *excepta*, but the broad black discal mark on the mesonotum presents a ready means of separation. The scutellum in this species is sometimes very slightly produced between the apical pair of bristles. Besides the type material I have seen one specimen from Blundell's, A.C.T.

*LIOSCINELLA SUTURALIS*, n. sp.

♂, ♀. Head orange-yellow, occiput, vertex, and frontal triangle glossy-black, upper portion of frons between triangle and eyes dull brownish-black; third antennal segment infuscated above at apex; palpi yellow; prelabrum partly brown or black. Triangle extending to a little beyond middle of frons, rather blunt in front. Eye a little higher than long, apparently bare, and about six times as high as gena, the latter white dusted above, the lower margin brown. Antennae of moderate size; aristae dark and with distinct pubescence. The orbits each with about six quite long erect setulae. Thorax orange-yellow, pleura with an elongate glossy-black mark on lower margin of the mesopleura, humeri and lateral edge of mesonotum to wing base lemon-yellow, disc of mesonotum glossy-black in front and behind, red across the suture on a rather broad band; scutellum yellow, more or less broadly blackened at base; postnotum glossy-black. Notopleurals 1 + 2; scutellum rather short and rounded in outline, with four almost equally spaced marginal bristles, the lateral pair the shorter, and some very short surface hairs. Legs entirely yellow, mid tibial apical ventral spur pale. Wings hyaline, veins blackish-brown. First costal section a little shorter than the second and distinctly longer than the third; inner cross-vein a little proximad of apex of first vein; first posterior cell slightly widened at apex; third vein ending farther before apex of wing than fourth does behind it; penultimate section of third vein shorter than that of fourth, but apparently this character is rather variable. Halteres yellow. Abdomen broadly ovate, shiny black except narrowly at base, where it is brownish-yellow. Hairs black or dark brown. Genital processes of female slender, finely haired. Length, 1.5 mm.

Type, female, Queensland: Brisbane, no other data (Dr. A. J. Turner); allotype, N.S.W.: Sydney, 23.i.1925 (Health Dept.).

The type-specimen has the scutellum discoloured owing to the pin passing through the thorax near to it, a condition that one meets with quite frequently in pale coloured species of this genus.

*LIOSCINELLA VARIDORSATA*, n. sp.

♂, ♀. Head orange-yellow, the occiput except a small patch near the inner upper angle of each eye, and the triangle except its anterior extremity, glossy-black. Antennae with a slight infuscation at insertion of arista; genae yellow, the lower marginal hairs yellow, becoming darker in front. Antennae moderate in size, aristae pubescent. Triangle extending to anterior fifth of frons, and almost filling the vertex. Eyes very indistinctly haired, about six times as high as gena. Thorax glossy-black, humeri behind and a large subtriangular mark on lateral margin behind each lemon-yellow, upper margin of mesopleura, the pleural sutures, a spot on each postalar callosity, and the apex of the scutellum orange-yellow. Notopleurals 1 + 2; scutellum with sometimes a minute elevation between the apical bristles, the latter much longer than the quite well developed preapical pair, the disc with some fine black hairs; mesonotum with but a few piliferous punctures which are extremely small. Legs orange-yellow; mid tibial apical ventral bristle brown. Wings hyaline, veins pale brown. First section of costa about

two-thirds as long as the second and distinctly longer than third; inner cross-vein slightly proximad of apex of first vein; penultimate section of third vein distinctly shorter than that of fourth. Halteres pale yellow. Abdomen shiny orange-yellow, each tergite with a broad black central fascia; genital processes of female black, slender, and finely haired. Length, 1.5-2 mm.

Type, male, and allotype, N.S.W.: Broken Hill, 9.vi.1925 (Health Dept.); paratypes, Como, 21 specimens taken on flowers (Peterson).

Judging from the fact that there were many more specimens in the miscellaneous lot of material sent to me by the late Carl F. Baker this must be a very common species where it occurs and ought to be readily obtained on flowers in the Sydney district.

*LIOSCINELLA DISCOLOR*, n. sp.

♂, ♀. Frons on anterior half bright orange-yellow, alongside of the triangle on upper half merging into dark brown, the triangle glossy-black, extreme apex sometimes yellow, occiput black, genae and the face pale yellow, with white dust; antennae orange-yellow; aristae dark brown; prelabrum brown; palpi and proboscis yellow. Frons a little longer than wide, triangle appearing to fill the vertex because of slight distinction between its texture and that of the frons at its upper extremity, and extending to well beyond the middle, the surface almost smooth. Bristles all well developed and the orbital setulae strong. Third antennal segment wider than long, broadly rounded at apex; arista minutely pubescent. Eye slightly oblique, about as high as long, without hairs. Gena about as high as length of third antennal segment, and at centre about one-seventh as high as eye. Mesotum glossy-black, posterior and lower edges of humeri, a large notopleural patch, and a spot on the postalar region orange-yellow; pleura orange-yellow, with a dark brown or black mark on each of the following sclerites: mesopleura, sternopleura, hypopleura, and pteropleura, sometimes faint on the last; scutellum orange-yellow, blackened across base, more broadly so on the sides. Mesonotum with rather dense fine black hairs inserted in almost indistinguishable punctures, most numerous and distinct on the dorsocentral lines; upper posterior notopleural reduced to a fine setule; posterior postalar a mere hair. Scutellum short, rounded in outline, apical pair of bristles longer than disc and much longer than the preapical pair. Legs honey-yellow, rather slender, the hind femora stoutest, mid tibia with a black apical ventral spur that is longer than the apical diameter of the tibia. Wings hyaline, veins brown. Penultimate section of third vein shorter than that of fourth, ultimate section of fifth vein curved, a little over half as long as its penultimate section. Knobs of halteres pale yellow. Abdomen stout, ovate, dark brown, glossy on dorsum. Basal half in females globular or almost so, the apical half appearing very slender (Fig. 4), with erect bristly hairs in male (Fig. 5). Length, 1.5-2 mm.

Type, female, N.S.W.: Sydney, 9.xi.1925; allotype, topotypical, 23.i.1925; and 3 paratypes, topotypical, 15.x.1924, 28.x.1924, and 29.i.1925 (Health Dept.).

*LIOSCINELLA IMPURA* (Becker).

*Ann. Mus. Nat. Hung.*, ix, 1911, 150.

♀. This species, as I accept it, is very close to *discolor*, differing mainly in having the pleura almost entirely black, glossy, and the scutellum not pale yellow, only yellowish-brown, at its apex. The postalar region is not yellow, the yellowish notopleural mark is smaller and duller, and each femur is sometimes slightly browned centrally. The eyes have some very short but distinct hairs, while in *discolor* these are practically invisible in all the specimens before me. Length, 1.5 mm.

Type locality, N.S.W.: Sydney, the original locality is given as Parramatta. I have before me four females from Sydney, and Como.

*LIOSCINELLA PALLIDIPLEURA*, n. sp.

♂. Head pale yellow, face and genae densely white dusted, anterior yellow part of frons less distinctly white dusted, triangle, sides of frons from near apex of the triangle to vertex, and the occiput, black; palpi pale yellow; frontal bristles and hairs

black, genal hairs pale yellow. Eyes indistinctly short haired. Triangle extending to anterior fourth of frons; vertical, postvertical, ocellar, and orbital bristles distinct. Gena about one-sixth as high as eye. Mesonotum glossy-black, orange-yellow on posterior margin of humeri, a large patch on notopleural region, and a spot on each postalar callosity; pleura entirely yellow; scutellum yellow at apex, most broadly so centrally. Notopleurals 1+1; discal hairs fine and situated in minute punctures; apical pair of scutellars longer than the rounded scutellum, and much longer than the preapical pair. Legs entirely yellow. Apical ventral spur of mid tibia straight, black, longer than the apical diameter of the tibia. Wings hyaline, veins black. Penultimate section of third vein shorter than that of fourth. Halteres yellow. Abdomen glossy blackish-brown, paler on sides and below. Length, 1.5 mm.

Type, N.S.W.: Sydney, 29.x.1924; paratype, topotypical, 30.xi.1924 (Health Dept.). The paratype has faint traces of brownish pleural spots.

*LIOSCINELLA FLAVOLATERALIS*, n. sp.

This may be the same as *pallidipleura*, but for the presence of a setule above each posterior notopleural bristle *inter alia*.

Abdomen yellow, each tergite with a broad black fascia in centre, widest centrally. Length, 2-2.5 mm.

Type, female, and one paratype, N.S.W.: Broken Hill, allotype and 18 paratypes, Como, in writer's collection.

*Subsection b.*

Scutellum entirely yellow.

*LIOSCINELLA MESOPLEURALIS* (Becker).

*Ann. Mus. Nat. Hung.*, ix, 1911, 150.

Frontal triangle yellow, broadly blackened centrally, extending to almost the anterior margin of the frons; occiput blackened across the entire upper half except narrowly below the vertex. The postvertical pair of bristles are much longer and stronger than the ocellars. Eyes haired. Disc of the mesonotum broadly glossy-black, the black mark rather deeply notched on each side at the suture. Notopleurals 1+2. Mesopleura with a black mark on lower margin. Scutellum entirely yellow. Legs yellow. Wings hyaline; venation much as in *varidorsata*. Length, 2-2.5 mm.

Originally described from Queensland: Brisbane. I have it from the type-locality and from Sydney, N.S.W.

*LIOSCINELLA STERNOLEURALIS*, n. sp.

♀. Very similar to *mesopleuralis*, differing in having the black discal mark on the mesonotum almost straight on the sides, not deeply notched on each side at the suture, no dark mark on the mesopleura below, and the lower half of the sternopleura black. Length, 2.5 mm.

Type, N.S.W.: Sydney, 20.v.1925 (Health Dept.).

*Species of doubtful generic location.*

The species from here to those listed under *Botanobia* are about intermediate between *Lioscinella* and *Botanobia*. Those that are mainly yellow in colour with the mesonotum variably marked with black, or black and red, may require a separate genus when the relationships are finally worked out, preferably in connection with life-history investigations in Australia, the others may be assigned to one or other of the already recognized genera.

*LIOSCINELLA QUADRISTRIATA* Becker.

*Ann. Mus. Nat. Hung.*, ix, 1911, 154.

This species as I accept it on the basis of Becker's description is represented by only one specimen in the material now before me, but it may be that several others that I list below as species are merely varieties of it. Becker stated that the head in all

its parts is yellow, but in the specimen before me there is a small deep black mark on the ocellar orbit, and the third antennal segment has a slight apical infuscation. The triangle is rather dull and reaches to the middle of the frons, the vertex has the usual six bristles of moderate length, the frontal hairs are short and dark, with a few stronger erect setulae on the orbits, most evident above. The eyes are nearly round, very short, but not very densely haired, and about four times as high as the gena at middle. Antennae rather small, third segment slightly darkened at insertion of the arista; the aristae subnude, quite short; palpi yellow. The occiput has a pair of black marks that diverge above and do not extend to vertex. Thorax orange-yellow, almost glossy, mesonotum with four black, shiny but slightly grey dusted, vittae, the central pair ceasing about midway between suture and hind margin, the submedian pair a little longer but not attaining the anterior margin like the others, no postsutural vittae; pleura entirely without black marks. All hairs and bristles black. Scutellum entirely yellow, rather short and rounded in outline, with two moderately long apical and two much shorter subapical bristles and a number of black discal hairs. Postnotum black. Notopleurals 1+2. Legs entirely yellow. Wings hyaline, veins pale brown. First costal section about two-thirds as long as second and subequal to third; inner cross-vein slightly beyond apex of first vein; marginal cell just beyond apex of first vein not as wide as submarginal at same point; penultimate section of third vein about half as long as that of fourth. Abdomen shiny brownish-yellow. Genital processes of female slender, finely haired. Length, 1 mm.

Type-locality, N.S.W.: Sydney. One female Tarro, Hunter R., 18.x.1922 (Health Dept.).

LIOSCINELLA SEMIATRA, n. sp.

♀. Very similar in many features to *quadristriata*, but the head colour, especially above, is more lemon-yellow than orange-yellow, the antennae are entirely pale yellow, the third segment is slightly angulate at apex above, the aristae are dark and subnude, the hairs and bristles are yellow, and the occiput has a single large triangular central black mark the point of which is just below the vertical margin; palpi yellow. Thorax pale orange-yellow, shiny, the mesonotum with three red vittae, the posterior extremities of which are black, the central one entire, the others abbreviated behind, no postsutural sublateral vittae; postnotum black; scutellum yellow, with a small black mark low on each lateral basal angle that is not visible from above. All hairs and bristles luteous. Scutellum as in *quadristriata*. Pleura with a single deep black glossy elongate oval mark on lower half of the mesopleura. Notopleurals 1+2. Legs entirely yellow. Wings hyaline, veins brownish-yellow. First costal section not two-thirds as long as second and subequal to third; inner cross-vein slightly proximad of apex of first; penultimate section of third vein about half as long as that of fourth; marginal cell just beyond apex of first vein about 1.5 times as wide as submarginal at same point. Halteres yellow. Abdomen shiny orange-yellow, third and fourth tergites largely dark brown; genital processes brown, rather broad and with numerous stiff setulae or bristles and a few fine hairs. Length, 1 mm.

Type, Queensland: Eidsvold, 21.iv.1924 (T. L. Bancroft); paratypes, N.S.W.: Bourke, Sydney, 20.ii.1925 (Health Dept.).

LIOSCINELLA MINUTULA, n. sp.

♂. Quite similar to *semiatra*, differing in having the third antennal segment much larger, though this may be a sexual character. Thorax shiny orange-yellow, the mesonotum with three broad glossy-black vittae, the central one entire except for a rather wide red patch at the suture, the others less widely interrupted at suture; mesopleura with a similar mark to that in *semiatra*. Scutellum with a very small black basal lateral mark as in *quadristriata*, shape rather short and outline quite evenly rounded, the apical pair of bristles much longer than the subapical pair, the latter distinctly nearer to apical pair than to base, some black discal hairs present. In *semiatra* the basal pair of scutellar bristles are more nearly of the same length as the

apical pair and much nearer to base than to the latter. Notopleurals 1+2. Legs entirely yellow. Wings hyaline, veins brownish-yellow. Venation almost as in *semitra*. Halteres yellow. Abdomen orange-yellow, extensively dark brown on dorsum centrally. Length, 1 mm.

Type, N.S.W.: Sydney, 16.xi.1924.

A specimen from Bourke, N.S.W., is very similar to *minutula* in thoracic markings, but the scutellum has the armature of *semitra* and I provisionally refer it to that species.

LIOSCINELLA EXTREMITATA, n. sp.

♀. Similar to *minutula*, differing from it in having the anterior and posterior extremities of the mesonotal vittae black.

Type and paratype, N.S.W.: Sydney, 30.xi.1934.

This may be the female of *minutula* with which it agrees very closely in general colour and structure. The third antennal segment is very much smaller and the breaks in the black mesonotal vittae are wider. The genital processes are broad, black, and furnished with a number of erect black setulae and a few fine hairs.

LIOSCINELLA FLAVOCAPITATA, n. sp.

♂. A very small pale orange-coloured species, with the black frontal spot confined to the ocellar orbit, the mesonotum with a black central mark on the anterior margin that is hardly visible from above, and the abdomen slightly brownish. The antennae and palpi are yellow, the third segment of the former yellow and almost evenly rounded in front, the arista fuscous and subnude. Eyes almost round, very short haired, and about four times as high as the gena; frontal triangle shiny, extending to or slightly beyond middle frons, bristles short, black, some of the hairs centrally in front brownish. No dark spots on pleura. Hairs brownish, bristles black. Notopleurals 1+2; scutellum short, rounded in outline, with a pair of moderately long apical and a much shorter pair of preapical bristles that are slightly nearer the apical pair than the base, and some black discal hairs; no bristles between the single pair of dorsocentrals. Legs entirely yellow. Wings hyaline, veins almost colourless. First costal section about four-fifths as long as second and subequal to third; inner cross-vein very slightly beyond apex of first; marginal cell not wider than submarginal just beyond apex of first vein; outer cross-vein oblique. Length, 1 mm.

Type and one paratype, N.S.W.: Tarro, Hunter R., 18.x.1922 (Health Dept.); paratype, Como (Peterson).

LIOSCINELLA BIVITTIGERA, n. sp.

♀. A slightly larger species than most of the group with the general colour yellow. The entirely brownish-black third antennal segment also readily distinguishes it from all the others. Head (Fig. 6) orange-yellow, with a small black spot on the ocellar orbit, and a large subquadrate one on the central half of the occiput that is sometimes narrowed at vertex. Frontal triangle rather poorly defined, shiny, extending to middle of frons; frontal hairs mainly yellow, the bristles yellowish-brown. Eye higher than long, short haired, about five times as high as the gena at middle, the latter with yellow marginal hairs. Antennae of moderate size, basal two segments orange-yellow, third brownish-black; arista pale brown, distinctly pubescent; palpi orange-yellow. Thorax shiny orange-yellow, the mesonotum glossy, with three dark vittae that may be black on only the posterior extremities and the anterior extremity of the central one or also on the presutural portions of the submedian pair; pleura and scutellum yellow, the latter with the apex slightly produced, two moderately long apical and two much shorter preapical bristles, and numerous discal hairs, all black, the mesonotal hairs preponderantly yellow, bristles dark brown. Notopleurals 1+2; no setulae between the dorsocentrals. Legs entirely orange-yellow, mid tibia with the apical ventral bristle luteous. Wings hyaline, veins brownish-yellow. First costal section hardly two-thirds as long as the second and distinctly longer than third; inner cross-vein very slightly

proximal of apex of first vein; penultimate section of third vein over half as long as that of fourth; fourth vein ending slightly behind third much farther before wing tip; marginal cell just beyond apex of first vein a little wider than submarginal at same point. Halteres yellow. Abdomen shiny orange-yellow, with broad dark brown or black fascia on each of the intermediate tergites; genital processes blackish-brown, rather broad, with some setulose hairs and fine pile. Length, 2 mm.

Type and one paratype, N.S.W.: Collaroy, 22.i.1924, no collector's name or other data on label (Health Dept.).

LIOSCINELLA TINCTIPES Malloch.

PROC. LINN. Soc. N.S.W., lvi, 1931, 63 (*Oscinosoma*).

♀. A glossy-black species, the head yellow, genae pale yellow, without white dust, darker yellow below, triangle glossy-black, apex yellowish, extending to anterior third of frons, the latter yellow to hind margin; occiput black, brownish on lateral edges. Antennae orange-yellow, arista dark brown, subnude; palpi orange-yellow. Thorax glossy-black, with a lemon-yellow mark along each lateral margin that is widest at suture, the hind margins of humeri and a mark on each postalar region yellowish; scutellum narrowly brownish-yellow at apex. Mesonotum sparsely black haired, most numerous so in the dorsocentral lines, but without distinct punctures; notopleurals 1+2. Scutellum convex, with two long apical and two much shorter lateral bristles and some discal hairs, not distinctly punctate. Wings hyaline, veins fuscous. Second costal section about 1.5 times as long as second; penultimate section of third vein about half as long as penultimate section of fourth; marginal cell just beyond apex of first vein about twice as wide as submarginal at same point. Halteres with yellow knobs. Legs fulvous-yellow, coxae and femora preponderantly black, hind tibiae blackened on basal two-thirds.

Tasmania: Eaglehawk Neck.

LIOSCINELLA ARGENTICEPS, n. sp.

♀. Very similar to *tinctipes*, differing as follows: Frontal triangle shorter, entirely black, occiput entirely black, genae distinctly silvery-white dusted, a little narrower than in *tinctipes*, brown on lower margins, scutellum lemon-yellow, black on the basal third on sides, more narrowly so in centre; wings brownish-hyaline, veins dark brown, penultimate sections of third and fourth veins subequal, marginal cell just beyond apex of first vein subequal in width to submarginal cell at same point. Length, 2 mm.

Type, Victoria.

The type lacks the antennae so that I cannot make a comparison of these organs with those of *tinctipes*.

LIOSCINELLA TIBIELLA Becker.

*Ann. Mus. Nat. Hung.*, ix, 1911, 155.

This species is unknown to me, but if Becker's description is correct it ought to be easily identified. If he erred in saying tibiae for femora and did not notice the black apical three segments of the hind tarsi it may turn out to be the same as *dilata* Malloch.

N.S.W.: Sydney.

LIOSCINELLA SUBOPACIFRONS, n. sp.

♂, ♀. Back of head, vertex and a small portion of upper orbits and the entire triangle black, face and anterior half or more of the frons orange-yellow, the latter with whitish dust on edges, parafacials and genae whitish, the latter yellow below and behind, triangle evenly though rather inconspicuously grey dusted on the entire area. Antennae and palpi orange-yellow, third segment of former at arista insertions and the arista dark brown. Frontal hairs and bristles and genal hairs dark brown, hairs on eyes pale. Frons at vertex about half the head width, narrowed to anterior margin where it is hardly more than half as wide as long; triangle not reaching beyond middle of frons, quite blunt; vertical and postvertical bristles distinctly longer than the

cruciate ocellar pair; orbital hairs quite long. Antennae normal; arista thickened at bases, distinctly pubescent, the longest hairs about as long as the basal diameter. Parafacials not visible in profile, much as in *simulata*; eyes a little longer than high. Thorax brownish-black, humeri, propleura and anterior portion of mesopleura red or reddish-brown, edges of the mesonotum and the upper half of the mesopleura slightly grey dusted, the mesonotum glossy on disc; scutellum glossy-black; sometimes the notopleural region is red. Hairs and bristles dark, the hairs fine, not inserted in punctures. Notopleurals 1+2; scutellum with six marginal bristles, only the apical pair long, disc convex, not punctate. Legs including the coxae fulvous-yellow, all femora with a broad dark brown band on apical half that does not attain the apex, and all tibiae with a corresponding even broader band on basal half or more that does not attain the base. Hairs and mid tibial spur dark. Wing hyaline, veins brown. First costal division about three-fourths as long as second and distinctly longer than third, the latter nearly twice as long as fourth; marginal cell just beyond apex of first vein wider than submarginal at same point; penultimate section of third vein distinctly shorter than penultimate section of fourth, the latter about one-fifth as long as its ultimate section; third vein ending before wing tip, fourth almost in it; ultimate section of fifth vein about half as long as penultimate in female, longer in male. Halteres yellow. Abdomen ovate, blackish-brown, shiny, with fine hairs. Genital processes of female slender; hypopygium of male with spike-like process. Length, 2-2.5 mm.

Type, male, allotype, and 17 paratypes, N.S.W.: Sydney (Health Dept.).

#### BOTANOBIA Lioy.

*Atti Ist. Veneto*, (3) ix, 1864, 1125.

This genus is so similar to *Lioscinella* that I have included the species in my composite key given above. I have in one or two of my previous papers indicated that this course might be adopted by me to prevent errors in generic assignment and specific identifications. The typical forms are stouter than is the general rule in *Lioscinella*, and they are more noticeably haired, having the frontal and mesonotal hairs longer, though in *L. hirtipes* these distinctions do not hold good. The frontal triangle is usually about half the length of the frons and not sharply limited, nor filling the entire vertex, glossy-black on the greater portion of its extent, the arista are distinctly pubescent, and the thorax is always partly yellow, though the scutellum may be entirely black. I place in this group the following Australian species:

#### BOTANOBIA APICIPUNCTATA (Malloch).

PROC. LINN. SOC. N.S.W., lii, 1927, 444.

This species was originally placed in the genus *Gaurax* Loew, but it appears to be more closely allied to the species now included with it herein. It differs from any other species so included in having the wings hyaline, with a blackish costal mark from just before the apex of the third to a little beyond the apex of the fourth veins that usually is partly hyaline in centre. Scutellum entirely black.

N.S.W.: Sydney. Type in collection of Health Department.

#### BOTANOBIA NIGROANNULATA Malloch.

Op. cit., 1, 1925, 338.

This species has the disc of the mesonotum sometimes largely black, the vittae being more or less distinctly fused, with greyish dust, the scutellum yellow on only the margin, the legs largely blackened, fore coxae yellow with a dark brown basal mark, the apical three segments of hind and apical two segments of mid tarsi blackish-brown, the former but little dilated. The upper posterior notopleural bristle is minute or lacking, second costal section about twice as long as first, penultimate section of third vein but little shorter than that of fourth, inner cross-vein very slightly proximad of level of apex of first vein.

N.S.W.: Sydney. Type in collection of Health Department. I have seen a third female specimen of this species, also from Sydney.

## BOTANOBIA DILATA Malloch.

Op. cit., 1, 1925, 339.

This species has usually no black mark at base of the scutellum. The mesonotal vittae are rather variable in extent, and the upper posterior notopleural bristle is always about as well developed as the lower one. The brown mark on each femur is sometimes quite faint, pale brown, and confined to the ventral surface, but the apical three segments of the hind tarsus except the base of third are deep black and quite noticeably dilated.

N.S.W.: Sydney. Type in collection of Health Department. I have seen four additional specimens of the species from the type locality.

## BOTANOBIA TONNOIRI Malloch.

Op. cit., lvi, 1931, 62.

This species was described from a male, in which sex the fore femora are furnished with a black streak on the anterior and another on the posterior surface, and the hind tarsi are entirely yellow. The palpi and the quite long fore coxae are black. Scutellum as Figure 7. It is entirely probable that there will be some sexual differences in this species, but I have no specimen of a female that would pass for that of this species from the type-locality. I believe that females that run down to Caption 32 in my key belong to this species although there are many points in which they differ from the male and it is with some misgiving that I adopt the course of accepting them as belonging to *tonnoiri*.

Tasmania: Burnie.

## BOTANOBIA LATITARSIS, n. sp.

♂, ♀. Very similar to *dilata*, but readily distinguished from it by the presence of a black central stripe on the scutellum and the lack of the upper posterior notopleural bristle. The third antennal segment is rather broadly infuscated above and at apex, the triangle is broadly black centrally, only the posterior lateral angles being yellow. The eyes are very short closely pale haired, and the aristaе are short pubescent. Palpi yellow. The thorax is testaceous-yellow, shiny, with three broad black vittae on the mesonotum that are fused in front, the central one entire, the submedian pair falling short of the hind margin and tapered behind, and two short outer black postsutural vittae; pleura with a large black mark on the anterior spiracular region, a streak over the centre covering the lower part of the mesopleura and the hypopleura, and the lower half of the sternopleura, and the postnotum also black; scutellum with a posteriorly tapered central black streak; the mesonotal black markings very slightly greyish dusted. Posterior notopleural undeveloped. Scutellum of the short rounded type, with four quite strong black bristles, the anterior pair shorter than the posterior pair and about midway between the latter and base, disc with a few weak short black hairs. Legs yellow, hind tarsi with the apical three segments except the narrow base of the third segment deep black, and distinctly dilated, the fourth segment distinctly wider than long. In the female I can detect a very faint brownish ventral mark at middle of the hind femur and a similarly coloured narrow ring on the mid and hind tibiae near their apices. Apical ventral spur of mid tibia short and luteous. Wings hyaline, veins pale brown. First costal section about two-thirds as long as second and subequal to third; inner cross-vein slightly proximad of level of apex of first vein; penultimate section of third vein fully half as long as penultimate section of fourth; marginal cell just beyond apex of first vein about twice as wide as submarginal cell at same point; first posterior cell widened at apex, the third vein bent slightly forward at apex. Abdomen subopaque testaceous-yellow, each tergite except the composite basal one with a postmarginal fascia that is widened in centre. Length, 2 mm.

Type, female, A.C.T.: Blundell's, 27.ix.1930; allotype, lacking the head, topotypical, 26.ix.1930 (L. F. Graham).

## BOTANOBIA LUTEICORNIS Malloch.

Op. cit., lvi, 1931, 64 (*Oscinosoma*).

In addition to the type material from Tasmania I have seen a specimen that I refer here from Sydney, N.S.W. (Health Dept.).

## BOTANOBIA NIGRIMANA, n. sp.

♂, ♀. A robust glossy orange-yellow species that is distinguished from all the others dealt with herein except *brunneoapicata* by the yellow legs and dark fifth tarsal segment. Head orange-yellow, a black mark on the frontal triangle that extends more or less widely outside the ocellar orbit, and the third antennal segment black. Hairs and bristles yellow. Eyes distinctly pale haired. Genae about one-fifth as high as eye. Antennae rather large, the third segment not regularly rounded at apex, with a slight indication of an angle at upper apex; arista black, short pubescent; palpi yellow. Triangle rather poorly defined, not nearly filling the vertex and falling short of attaining middle of frons. Thorax shiny orange-yellow, mesonotum with three glossy-black vittae that are confluent at anterior extremities, the central one reddish at suture, laterals tapered behind and not attaining the posterior margin, central one entire, a short black streak each side behind suture; anterior spiracular region slightly infuscated, mesopleura, pteropleura, sternopleura, and hypopleura, each with a large black mark; postnotum black; scutellum yellow. All hairs and bristles yellow. Notopleurals 1+2; hairs moderately long and fine; scutellum not elongated, with a moderately long pair of apical and a much shorter pair of preapical bristles and numerous quite long discal hairs. Legs orange-yellow, fifth tarsal segment on all legs deep black and distinctly swollen, apical mid tibial ventral spur luteous. Wings hyaline, veins pale brown. First costal section about four-fifths as long as second and about 1.5 times as long as third; inner cross-vein distinctly proximad of apex of first vein; penultimate section of third vein about half as long as that of fourth; first posterior cell but slightly widened at apex. Halteres yellow. Abdomen orange-yellow, dorsum black except at base and apex, hairs yellow. Hypopygium of male small, genital processes of female slender. Length, 2.5 mm.

Type, male, and allotype, mounted on same card with an empty puparium, N.S.W.: Young, reared from brachyscelid gall, 10.x.1900 (W. W. Froggatt). Two paratypes, same data.

The specimens are rather teneral, but the description will, I believe, be found to be reliable for identification of the species.

## BOTANOBIA BRUNNEOAPICATA, n. sp.

♂. This species agrees with the one described immediately above mainly in having the fifth tarsal segment dark and the legs otherwise orange-yellow, but the fourth segment of the fore tarsi is also dark, the colour is brown, not black, and the fifth segment is not noticeably swollen. The species is like *nigrimana* in being quite stout. Head with a black spot in the ocellar orbit and a brown mark in centre of occiput, the antennae entirely orange-yellow, third segment much smaller than in *nigrimana*, evenly rounded at apex; arista dark brown, short pubescent. Gena about one-seventh as high as eye. Eyes distinctly haired. Bristles and hairs of frons black; triangle very small and poorly defined. Thorax glossy orange-yellow, mesonotum with a black mark in centre of anterior margin and three or five diffuse black vittae on posterior half that are fused behind and taper off in front; scutellum blackened; pleura marked as in *nigrimana* except that the propleura is not infuscated; postnotum black. Thoracic hairs and bristles black. Scutellum tapered behind, damaged by the pin, most of the bristles rubbed off, but the surface with many black hairs. Notopleurals 1+2. Legs orange-yellow, tarsi as described in first paragraph. Wings hyaline, veins pale brown. Venation almost as in *nigrimana*. Halteres yellow. Abdomen rather dull black, yellowish at base and below. Length, 2.5 mm.

Type, N.S.W.: Wahroonga, Sydney, 31.x.1926, no collector's name on label.

## BOTANOBIA ROBUSTA, n. sp.

♂. Very similar to *brunneoapicata* in general appearance, being stout, and of a glossy orange-yellow colour. The black frontal spot is confined to the ocellar area, and the antennae are entirely orange-yellow, the arista are dark brown and short pubescent, there is a brown mark in centre of the occiput, the eyes are distinctly haired, and the palpi are orange-yellow. The gena is about one-ninth as high as the eye (Fig. 8). Frontal hairs and bristles black. Thorax shiny orange-yellow, glossy on mesonotum, the latter with three broad glossy-black vittae that are broken rather diffusely at the suture, the break sometimes consisting of a quite extensive red patch, the central vitta extending to posterior margin, the other two ceasing short of it; pleura with the usual four black spots rather large; scutellum not blackened on disc, longer and more tapered than usual, with the apical pair of bristles more closely placed than in the closely related species, two much shorter preapical bristles, and many moderately long discal hairs (Fig. 9); postnotum black. Dorsal hairs and bristles black. Notopleurals 1+2. Legs orange-yellow, all femora dark brown or blackish-brown except at extremities. Mid tibial apical ventral spur moderately strong, luteous. Wings hyaline, veins brown. First costal section nearly as long as second and almost twice as long as third; penultimate section of third vein about one-third as long as that of fourth; marginal cell about twice as wide as submarginal cell just beyond apex of first vein. Halteres yellow. Abdomen coloured as thorax, without black markings. Hairs pale brown. Length, 2.5 mm.

Type and one paratype, A.C.T.: Blundell's, 30.iv.1930 (A. L. Tonnoir).

## BOTANOBIA FLAVOHUMERALIS, n. sp.

♀. Very similar to *discalis*, differing essentially in having the occiput mainly orange-yellow, only slightly browned in centre, the vertex yellow, darkened behind the ocelli, the posterior lateral angles of the triangle yellow, remainder of triangle glossy-black except the edges which are narrowly brownish, and the yellowish-white instead of black or dark brown mesonotal hairs. Despite the rather teneral nature of the type-specimen the legs show dark brown except at the extremities of the hind femora, and dark brown on the basal half or more of the hind tibiae; the mid femora show but little trace of darker colour.

Frontal triangle reaching to a little beyond middle of frons, the latter with numerous short black hairs and a series of rather closely placed setulae on each orbit; bristles normal; eye longer than high, slightly oblique, distinctly haired; gena entirely yellow, at middle about one-third as high as eye, with yellow lower marginal hairs; third antennal segment with infuscation above and at apex, shaped as in *tonnoiri*, but slightly smaller; arista short pubescent. The large black discal mark on mesonotum glossy, larger than in the type-specimen of *discalis*, extending over almost the entire area behind the suture, the pleural black marks so large that only the propleura and sutures are yellow; postnotum glossy-black. Notopleurals 1+2; scutellum rather shorter than usual in this group, with four black bristles, the apical pair not very closely placed, the preapical pair much shorter and placed rather high, nearer to apicals than to base, the discal hairs fine and yellow. Legs slender, the hind tarsi noticeably so, with the fifth segment slightly brownish, mid tibial apical ventral spur luteous, moderately long. Colour yellow, with brownish marks as noted in the introductory paragraph. Wings hyaline, veins brown. First costal section about 1.25 times as long as third and four-fifths as long as second; inner cross-vein a little proximad of apex of first; penultimate section of third vein fully half as long as that of fourth; veins 3 and 4 divergent at apices. Halteres yellow. Abdomen crushed in type, entirely dark brown, hairs yellow, genital processes slender. Length, 2.5 mm.

Type, A.C.T.: Blundell's, 30.i.1930 (L. F. Graham).

## BOTANOBIA FROGGATTI, n. sp.

♂, ♀. This species is very similar in general features to the one described immediately above, but differs from it in having the third antennal segment entirely

black, the mesonotum with five glossy-black vittae, the hairs on scutellum mainly black, and the brownish-black leg marks confined to the basal half or more of the hind tibiae. Head orange-yellow, upper occiput mainly black, with a yellow patch on each side near angle of eye; frontal triangle with a black central stripe that covers the ocelli and tapers slightly to anterior extremity; frontal hairs mostly dark, the bristles black; basal two antennal segments brownish-yellow, third entirely black, not as large in either sex as in *tonnoiri*, and with less marked upper apical angle; aristaе black, short pubescent; palpi orange-yellow; genae yellow, with yellow marginal hairs, at middle about one-fifth as high as eye, the latter slightly oblique, about as high as long, distinctly haired. Thorax glossy orange-yellow, the mesonotum with five glossy-black vittae, the outer pair short, postsutural, the central one broad, entire, almost fused with the submedian pair in front of suture, the latter attaining neither anterior nor posterior margin of mesonotum and with a narrow break at the suture; pleura with five large black marks, one on the anterior spiracular area, the others on mesopleura, pteropleura, sternopleura, and hypopleura, the last usually faint or reddish; scutellum yellow, hairs black or partly so; armature as in the species described immediately preceding. Hairs on mesonotum mainly yellow, bristles black. Legs orange-yellow, with the basal halves or more of the hind tibiae dark brown, mid tibial apical ventral spur luteous, of moderate length. Wings hyaline, veins pale brown. Venation almost as in *flavohumeralis*. Halteres yellow. Abdomen orange-yellow at base and extreme apex, dark brown centrally, hairs brown. Length, 2.5 mm.

Type, male, allotype, and one female paratype, mounted on the same card, N.S.W.: Sydney, 16.iv.1921, from longicorn larva in *Acacia* sp. (W. W. Froggatt).

It appears entirely probable to me that this and some other related species that are labelled as "parasitic" or in such a manner as to indicate parasitism will be found to be inquilines, the larvae living in the burrows upon the fermenting frass or even upon dead or dying larvae of the burrowing species.

#### BOTANOBIA NIGROHIRTA Malloch.

PROC. LINN. SOC. N.S.W., liv, 1931, 65 (*Oscinosoma*).

♂. An orange-yellow species, with entirely concolourous legs, the black mark on the frontal triangle confined to the ocellar orbit, with a slight brown suffusion beyond it, the mesonotum with three glossy-black vittae, the central one more or less extensively red at the suture, and the pleura with two black marks, one on the mesopleura and the other on the pteropleura, the sternopleura sometimes slightly darkened below. The head is as in Figure 10, the third antennal segment quite large, broadly rounded in front, and with the apex narrowly infuscated, the aristaе dark and with the hairs fully as long as the basal diameter.

♀. Similar to the male in general characters, but with smaller third antennal segment, a black mark on the lower part of the sternopleura, and a fuscous mark on each humeral angle that is fainter in the males before me. The abdomen is blackish-brown except at base and apex, the genital processes are yellow at bases, blackish at apices, slender, and finely haired.

Type-locality, Tasmania. I have a male from A.C.T.: Blundell's, 10.x.1930 (A. L. Tonnoir), one from Queensland: Eidsvold, 26.iv.1924, reared from cotton boll (Bancroft), in teneral condition, and the female above described from N.S.W.: Sydney, 24.viii.1924 (Health Dept.).

#### BOTANOBIA ALBOHIRTA, n. sp.

♂. Head very similar to that of *nigrohirta*, but the antennae a little smaller, with the third segment entirely black. The frontal triangle is black centrally, the dark colour fading out as it approaches the margin which latter is yellow with greyish dust; occiput with a broad brown central mark. Aristaе distinctly pubescent, a little longer than in *nigrohirta*.

Thorax glossy orange-yellow, the disc of mesonotum broadly glossy-black, postsuturally entirely so; pleura with dark brown marks over anterior spiracular area, on

mesopleura, pteropleura, sternopleura, and hypopleura; postnotum entirely glossy-black; scutellum yellow. Mesonotal hairs quite long and fine, white, the bristles black. Notopleurals 1+2; scutellum slightly elongate, with four black bristles, the apical pair longer than the preapical, the discal hairs pale. Legs orange-yellow, yellow haired; mid tibial apical ventral spur luteous. Wings hyaline, veins pale brown. First costal section almost as long as second and about 1.25 times as long as third; inner cross-vein distinctly proximad of apex of first vein; penultimate section of third vein about half as long as that of fourth; third and fourth veins subparallel at apices. Halteres yellow. Abdomen shiny dark brown, paler at base, the hairs quite long and white. Length, 2.5 mm.

Type, N.S.W.: Myall Lakes, 3.ix.1922 (Nicholson).

BOTANOBIA TINCTICORNIS, n. sp.

♂, ♀. Very similar to *albohirta* in general characters, differing in having the antennae yellow, with only the apex of the third segment infuscated, and the mesonotum with quite broad glossy-black vittae, the submedian pair abbreviated in front and behind, the central one entire. Frontal triangle with a black mark that extends faintly outside the ocellar orbit; aristae distinctly pubescent. Marks on pleura black, three or four in number, the hypopleural one sometimes lacking; scutellum entirely yellow. Hairs on mesonotum usually whitish-yellow, those on the scutellum partly or almost entirely black, the margin of scutellum almost evenly rounded, the apical pair of bristles much longer than the preapical pair (Fig. 11). Legs entirely yellow, the hairs concolourous, apical ventral spur on mid tibia pale. Wings hyaline, veins pale brown. Venation as in *albohirta*. Halteres yellow. Abdomen blackish-brown, shiny, with pale hairs and some darker setulose hairs at apices of the tergites. Genital processes of female slender, finely haired. Length, 2 mm.

Type, male, A.C.T.: Blundell's, 27.ix.1930 (L. F. Graham); allotype and one paratype, Queensland: Brisbane (Dr. A. J. Turner); paratypes, Queensland: Southport (Dr. A. J. Turner); A.C.T.: Canberra, 7.xi.1929 (A. L. Tonnoir); N.S.W.: Ballina, iii.1926, "bred from beans".

I have no further information on this last listed specimen and am inclined to think that it may have been reared from larvae that were feeding on decaying beans. Many of the species in this subfamily are found in such habitats though very few, such as *Oscinella frit*, actually are responsible for damage to vegetation.

BOTANOBIA COMMUNIS, n. sp.

♂, ♀. Head dull yellow, the black frontal mark extending slightly outside the ocellar orbit; third antennal segment slightly darkened above at apex; aristae dark and with short pubescence; all the hairs and bristles on frons black, the hairs quite long and strong; palpi yellow. Triangle slightly greyish dusted even on the black part, extending to middle of frons; eyes haired, higher than long and five times as high as gena, the latter yellow, with several series of pale hairs behind, one dark upcurved bristle in front above the hairs; orbital setulae hardly longer than the erect hairs near anterior margin of triangle. Thorax pale orange-yellow, shiny, mesonotum with five black vittae, the three central fused in front and very narrowly separated by yellow lines behind, the outer pair short and postsutural, all with coating of grey dust; pleura with four black marks, the largest on the lower half or more of the sternopleura; scutellum yellow, with a minute black mark low on each lateral basal angle not visible from above. Notopleurals 1+2; scutellum short, rounded in outline, with four moderately strong bristles, the basal pair nearer to base than to apical pair, the disc with one or two hairs in front of basal bristles (Fig. 12). Prosternum yellow, with black central line, postnotum black, humeri sometimes with a faint brown mark in front. Hairs dark, bristles black. Legs yellow, apical ventral bristle on mid tibia black. Wings hyaline, veins dark brown. First costal section about two-thirds as long as second and subequal to third; marginal cell just beyond apex of first vein about 1.25 times as wide as submarginal at same point; penultimate section of third vein

about half as long as that of fourth. Halteres yellow. Abdomen shiny brownish-black, with dark hairs. Genital processes of female rather broad, with fine hairs only; hypopygium of male yellow, small. Length, 1.75 mm.

Type and allotype, mounted on same cardpoint, and 6 paratypes mounted on another along with a chironomid, Queensland: Eidsvold, no date or collector's name. One paratype, N.S.W.: Como, Dec., 1923, swept from flowers (Peterson).

I assume from the mass mounting and the presence of the chironomid with the type-series that the specimens were either taken on flowers or on a window.

BOTANOBIA HIRTIPES, n. sp.

♂, ♀. Head brownish-yellow, paler on anterior margin of the frons, the triangle largely glossy-black, its edges poorly limited and slightly dusted; antennae dark brown, third segment paler below and basally, sometimes almost entirely blackish-brown to black, aristaе concolourous; palpi fuscous to black; hairs and bristles on frons and genae black, hairs on eyes yellow. Frons at vertex almost half the head width, narrowed to anterior margin, triangle not extending across vertex, appearing narrower because of the indistinct edges, not reaching beyond middle of frons; hairs quite long, vertical and postvertical bristles longer than the ocellar pair; orbital setulae quite long. Face concave in profile, the parafacial narrowly visible; epistome produced as in most species of *Conioscinella* to which genus the species has some resemblance; gena about one-fifth as high as eye though not as high as width of third antennal segment, the latter rather larger than usual; the aristaе short pubescent. Thorax glossy-black, finely grey dusted along the margins of mesonotum, on upper half of mesopleura, and on the disc of the scutellum; hairs and bristles black. Mesonotum without distinct piliferous punctures, but with in most cases slight depressed dorsocentral lines; scutellum convex, with six marginal bristles, the apical pair much the longest, and some fine erect discal hairs; notopleurals 1+2. Postnotum glossy-black. Hairs longer than usual, erect. Legs black, or brownish-black, the tarsi usually more noticeably brown, the hairs dark, longer and more numerous in the male than usual. Wing greyish-hyaline, veins dark brown. First costal division almost as long as second and distinctly longer than third; fourth vein ending almost in wing tip, third well before it; penultimate section of third vein distinctly shorter than that of fourth, the latter about one-fifth as long as ultimate section; marginal cell just beyond apex of first vein distinctly wider than submarginal at same point; ultimate section of fifth vein about half as long as penultimate. Knobs of halteres yellow. Abdomen narrowly ovate, glossy-black, with rather long dark hairs, especially in the male. Genital processes of female slender, finely haired; hypopygium of male concealed. Length, 2-2.5 mm.

Type, male, allotype, and 4 paratypes, A.C.T.: Blundell's (L. F. Graham); paratype, Tasmania: Advent Bay (A. L. Tonnoir).

A rather aberrant species with some of the characters of *Conioscinella*.

BOTANOBIA CONFLUENS, n. sp.

♀. This species is readily distinguished from its allies by the black palpi and third antennal segment, and the yellow coloured thorax with three broad glossy-black vittae, the central one entire, the submedian pair abbreviated behind, and all three fused in front of the suture. Head orange-yellow, with a small black spot on the ocellar orbit, the triangle entirely dull and extending to only the upper third of frons. Hairs pale centrally, brown laterally, those on upper part of the orbits rather long, the bristles brownish-black, normal. Eye almost round, densely short haired, and about eight times as high as the yellow gena, the marginal hairs on latter yellow, two on vibrissal angle longer and brown. Antennae yellow, third segment brownish-black, broadly rounded at apex; aristaе dark brown, densely short pubescent; palpi rather thick, dark brown to black. Occiput dark brown, yellow on vertical margin. Thorax shiny orange-yellow, the mesonotum with three glossy-black vittae, the central one entire, the submedian pair tapered behind and not attaining posterior margin; pleura with four black spots; scutellum yellow. Hairs on mesonotum and scutellum mainly yellow,

bristles black. Scutellum rather short and rounded in outline, with a moderately long apical and one or two very short preapical pairs of bristles. Notopleurals 1+2. A small black spot at the anterior extremity of the notopleural suture against the humeri. Legs entirely orange-yellow, the apical ventral bristle on mid tibia yellow. Wings hyaline, veins brown. First costal section two-thirds as long as second and about 1.5 times as long as third; inner cross-vein distinctly proximad of apex of first vein; penultimate section of third vein a little over half as long as that of fourth; veins 3 and 4 slightly and evenly divergent to apices. Halteres yellow. Abdomen ovate, shiny orange-yellow, the tergites extensively dark brown, more broadly so centrally; genital processes dark brown, slender, and with some fine hairs. Length, 2.5 mm.

Type, N.S.W.: Sydney, 25.i.1925 (Health Dept.).

#### ADDENDA.

##### PSEUDOFORMOSINA Malloch.

PROC. LINN. SOC. N.S.W., lxiii, 1938, 355.

I erected this genus for the reception of *Chlorops nicobarensis* Schiner. I believe this species is a synonym of *Oscinis noctilux* Walker, described from New Guinea and included in the genus *Oscinella* by Becker in his revision of the Indo-Australian Chloropidae. The name of the genotype will therefore be *Pseudoformosina noctilux* (Walker).

##### CADREMA Walker.

*J. Proc. Linn. Soc. London* [1859], iv, 1860, 117.

In my revision of the North American species of this subfamily that have the hind tibia with a distinct apical or preapical ventral spur\* I erected a genus *Prohippелates* for the reception of *Hippelates pallidus* Loew on the basis of the elongate dorsally flattened scutellum and its armature, the very long and strong hind tibial spur, and the possession in the male of two long fine hairs on the proboscis. Later in papers on the Pacific Islands species, I accepted as the same species one that had been named *nigricornis* by Thomson. I have some doubts about the propriety of accepting all the varieties, *bilineatus* de Meijere, *flavus* Thomson, and the typical form in which the third antennal segment is black as one species. The insect is found feeding in the larval stages in dead shell-fish and ought to be easy to rear so that the question of specific identities could be readily settled by anyone having access to such pabuli where the species occurs. I have now before me one female that is referable to this complex.

##### PROHIPPELATES Malloch.

*Proc. U.S. Nat. Mus.*, xlvi, 1913, 260.

This genus will run down to *Cadrema* in my key to the genera given on a preceding page, but will be readily distinguished therefrom by the long hind tibial spur, which extends to the apex of the hind metatarsus, and by the flattened and elongate scutellum (Fig. 13).

##### PROHIPPELATES NIGRICORNIS FLAVUS Thomson.

The single specimen before me has the mesonotum entirely yellow except for a faint trace of two reddish vittae near the hind margin; the antennae are entirely yellow. In the variety *bilineatus* de Meijere the mesonotum has two black vittae and the antennae are yellow; in typical *nigricornis* Thomson the third antennal segment is black, and the mesonotum may have two dark vittae or be entirely yellow. Length, 2.5 mm.

Queensland: Townsville (F. H. Taylor).

This form is the one I accepted as *pallidus* Loew. It is common in the West Indies.

#### POSTSCRIPT.

EFFTAYLORIA, new name.

*Tayloria* Malloch, PROC. LINN. SOC. N.S.W., lv, 1930, 98;  *nec. Tayloria* Bourguignat, *Moll. Afr. Equat.*, iii, 1889, 38.

\* *Proc. U.S. Nat. Mus.*, xlvi, 1913, 260.

STUDIES ON *CORTICIUM ROLFSII* (SACC.) CURZI (*SCLEROTIUM ROLFSII* SACC.).

I. CULTURAL CHARACTERS AND PERFECT STAGE. II. MECHANISM OF PARASITISM.

By F. L. MILTHORPE, B.Sc.Agr.

(Plate v; seven Text-figures.)

[Read 30th April, 1941.]

*Sclerotium rolfsii* Sacc. was first recorded in New South Wales in 1902 (Noble *et al.*, 1934), and since then has resulted in severe losses in many crops. It is an extreme facultative parasite, causing a crown and root rot of a large number of plants, Weber (1931) listing over 150 known hosts.

The terminology of this species is somewhat confused. Owing to the difficulty of inducing sporulation, the appearance and size of the sclerotia and other vegetative characters are generally used in classification. *S. rolfsii*, for example, is distinguished from the closely-related *S. Delphinii* Welch by the production of numerous, fairly small, globose sclerotia (Stevens, 1931). Curzi (1932) recognizes two species, usually termed *S. rolfsii*, on the characteristics of the hymenia, styling them *Corticium rolfsii* and *C. centrifugum*. He also finds a correlation between certain vegetative characters and the perfect stage of either species, and assumes that these characters may be employed in identification. Goto (1933, 1933a) finds a similar relationship between groups of characters and sporulating capacity of various Formosan strains. In these studies, however, the extent to which the composition of the substratum, temperature, and other factors influence the nature of the growth has been overlooked.

The effects of temperature, and composition of the media, on the vegetative growth of several Australian isolates, a description of the perfect stage, recorded for the first time in Australia, and the method of parasitism are set out in this paper.

## I. CULTURAL CHARACTERS AND PERFECT STAGE.

(a). *Materials and Methods.*

Eight isolates were grown on potato-dextrose agar (Riker, 1936), onion agar and carrot agar (Goto, 1933), onion-proteose-peptone agar (Mundkur, 1934), peptone-dextrose broth (peptone 35 gm., dextrose 35 gm., distilled water 1,000 ml.) and pectin broth (MgSO<sub>4</sub> 0.26 gm., K<sub>2</sub>HPO<sub>4</sub> 0.26 gm., citrus pectin 20 gm., distilled water 1,000 ml.). In the temperature studies, the isolates were grown on potato-dextrose agar at 15°, 20°, 25°, 30° and 37°C.

(b). *Observations.*(i). *Effect of media on growth.*

Both the type and rate of growth of the mycelium depend largely on the composition of the substrate, little difference being displayed by various isolates grown on the same medium, although the lower rate of S3 (Table 1) would suggest that rate of growth is also an inherent factor. Sclerotial characters are largely inherent, being influenced only slightly by the substrate composition. On carrot agar, growth is more abundant, being thicker and denser than on the other media (Pl. v, fig. 1). The white, dense, feathery growth, similar to that described by Stevens (1931) for corn-meal agar, is in direct contrast to the thinner, straighter, less-feathery growth, with more abundant aerial mycelium, typical of the other media. Potato-dextrose agar encourages rather dense, thick mycelium, with equal development of aerial and surface mycelium, growth being more vigorous and abundant than on onion and onion-proteose-peptone agars. The

TABLE 1.  
*Rate of Diameter Spread of Colony at 30° C. (Mm. per 24 hours.)*

Culture.	Medium.				Mean of Culture.
	Potato-dextrose Agar.	Onion Agar.	Onion-proteose-peptone Agar.	Carrot Agar.	
S1	28	32	24	23	27
S2	28	29	28	24	27
S3	29	22	22	25	24
S4	28	28	28	28	28
S5	29	27	29	27	28
Mean for Medium	28	28	26	25	27

mycelium is more silky on onion agar, with abundant strands of aerial mycelium. It is more abundant than that produced on onion-proteose-peptone agar, which is relatively sparse and thin, and confined to the surface with very little aerial mycelium. This medium is far less suitable for the vegetative growth of the organism than any of the other solid media, but the ease with which hymenial production occurs indicates its suitability in inducing sporulation. Hymenia were not produced on any of the other media except to a very limited extent on potato-dextrose agar. Very feathery, thick, densely flocculent mycelium is produced on peptone-dextrose broth. It spreads rapidly over the surface of the broth and up the sides of the flask, contrasting with the slowly spreading, scarce mycelium on pectin broth, which is very thin and lacking in aerial mycelium. A gel was formed beneath the mycelium on this broth.

The sclerotia are little affected by the quality of the substrate, their size, shape and colour being constant on all media during the early stages of growth (i.e., during the first three weeks). There is some variation in the number produced, however, production being much less frequent on onion-proteose-peptone agar than on carrot agar, and more frequent on potato-dextrose agar than on onion agar. Their size, shape and abundance are largely inherent. Two isolates (S2 and S3) produced large, rather irregular, and relatively few sclerotia, while the remaining isolates had typically small, globose, uniform, and numerous sclerotia.

The sclerotia produced during the later stages of growth of a culture, i.e., when mycelial growth had apparently ceased and sclerotial production was progressing slowly, were usually very much larger than those produced during the earlier phases. These sclerotia were globose and of the typical brown colour, the chief variation being in size only. That this is connected with variation in the substrate—probably staling conditions—was demonstrated by growing these large sclerotia on fresh media, when the typical small types were produced in the earlier stages and larger ones produced again towards the end of the growth period.

(ii). *Effect of temperature on growth.*

Growth proceeds very slowly at 15°C., increases rapidly as the temperature is raised to 25°C., and reaches an optimum growth temperature at about 30°C. At higher temperatures it decreases rapidly, becoming very slow at 37°C. There appears to be no significant difference between the growth rates of these five isolates (Table 2). These observations are in accord with those of Higgins (1927) for several American isolates.

Considerable variation in the type of growth produced at various temperatures was noted (Pl. v, fig. 3). At 15°C. the mycelium was more sparsely distributed than at any other temperature, producing aerial mycelium far more abundantly. With higher temperatures, the production of aerial mycelium became less distinctive, giving way to a denser and more vigorous surface growth. The tendency for the sparse aerial hyphae to be lost and a more compact habit to be assumed with increased temperature was very marked, but was less apparent between 25° and 30°C. than between any other two temperatures.

TABLE 2.  
*Effect of Temperature on Colony Growth.*

Isolate.	Increase in Diameter of Colony. (Mm. per 24 hours.)				
	15° C.	20° C.	25° C.	30° C.	37° C.
S1	5	13	24	28	6
S2	7	15	27	28	7
S3	5	11	21	29	7
S4	5	11	24	28	9
S5	4	10	21	29	4
Mean of 5 isolates	5	12	23	28	7

The time of first appearance and the number of sclerotia were also greatly affected by temperature. At 15°C. no sclerotia had appeared after fourteen days in any culture, but at the other temperatures sclerotia had appeared in all plates. Sclerotial production was more rapid at 37° than at 20°C., but less rapid than at 25° and 30°C. (Table 3).

TABLE 3.  
*Effect of Temperature on Sclerotial Production.*

Isolate.	15° C.		20° C.		25° C.		30° C.		37° C.	
	First Appearance.	Production.*	First Appearance. (Days.)	Production.*						
S1	—	—	8	+	2	+++	2	++++	6	++
S2	—	—	—	—	7	++	7	++	11	+
S3	—	—	12	+	4	+++	3	++++	7	++
S4	—	—	10	+	3	+++	2	+++	4	+++
S5	—	—	11	+	4	+++	4	+++	5	+++

\* + denotes relative abundance of sclerotia after 14 days.  
— denotes absence of sclerotia after 14 days.

The number of sclerotia produced was greatest at 25° and 30°C., but decreased with both higher and lower temperatures, being more abundant at 37° than at 20°C.

(iii). *The perfect stage.*

During the present investigations, three isolates produced hymenia. Considerable difficulty was experienced in inducing fructification, which occurred on both onion-proteose-peptone and potato-dextrose agars, but more vigorously on the former than on the latter medium. Of various methods tried to induce sporulation, the most successful was to culture the organism on onion-proteose-peptone agar and incubate at 30°C. for two to three weeks, after which time, vegetative growth had practically ceased. The cultures were exposed to direct sunlight at room temperatures for two days, then re-incubated at 30°C. Vigorous sporulation usually followed about two weeks later. Exposure to light and maintaining the cultures at 30°C. appeared to be necessary conditions for sporulation.

In a series of cultures in which combinations of pairs of the isolates were grown under the above conditions, hymenia were only produced in those tubes containing an isolate which fructifies readily by itself. It would appear that the failure of certain isolates to fructify is not due to heterosexuality, but rather to the loss of the inherent capacity to do so, or the absence of suitable conditions.

Hymenia developed as small irregular areas, not exceeding 2 sq. mm. in extent, over the surface of the slopes. Two to fifteen separate hymenia were found in different cultures. No correlation could be found between the amount of hymenia produced and any single factor. It did not appear to depend on the capacity of the particular strain to sporulate.

Hymenia appeared as dense crustiform masses, white in colour and closely adhering to the substrate. During the early stages of development, drops of a glistening crystal-white liquid, similar to that found on the sclerotia, were exuded. The subhymenial layer consists of closely interwoven hyphae which branch monopodially. The branchlets are basally septate and rise as clavate-shaped hyphae to form the basidia. Two or more basidia frequently arise close together on the one hypha. The basidia are hyaline, club-shaped and very closely aggregated (Figs. 1*a*, *b*). Usually four sterigmata are borne at the apex, these structures tapering towards the end (Fig. 2*b*). Basidiospores arise as small spherical bodies, but they elongate and when mature are pyriform-globose in shape (Figs. 2*a* to 2*f*). They are usually apiculated at the base, and are smooth

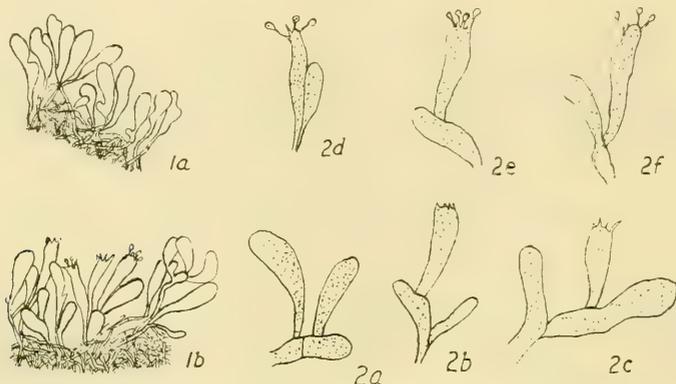


Fig. 1.—Hymenia of *C. rolfsii*. (a) Immature. (b) Mature.  $\times 530$ .

Figs. 2*a*-2*f*.—Stages in the development of the basidium of *C. rolfsii*.  $\times 1080$ .

and hyaline. The dimensions of the structures were found to be constant in size for the three isolates; the basidia ranging from  $2.01\mu$  to  $5.61\mu$  (mean  $4.16\mu$ ) in length and  $1.67\mu$ - $3.61\mu$  ( $2.47\mu$ ) in breadth, the sterigmata  $1.34\mu$ - $2.57\mu$  ( $1.95\mu$ ) in length, and the basidiospores  $1.64\mu$ - $2.51\mu$  ( $1.94\mu$ ) in length and  $1.00\mu$ - $1.72\mu$  ( $1.37\mu$ ) in breadth.

Curzi (1932) distinguishes two species whose vegetative stages are usually known as *Sclerotium rolfsii*:

- (1). *Corticium rolfsii* (Sacc.) Curzi.—Mycelium never flocculent and mostly creeping; sclerotia numerous, relatively small, globose, scattered, not aggregated and not coalescing; form and size almost constant; hymenia dense, crustiform, adhering to substrate; basidiospores globose.
- (2). *C. centrifugum* (Lév.) Curzi.—Mycelium flocculent, abundantly aerial; development usually centrifugally; sclerotia not very numerous, irregularly scattered, aggregated and coalescing; hymenia loose, never crustiform, with the basidia-bearing hyphae in white tufts, mostly aerial; basidiospores long, oval or pyriform.

The three strains which sporulated in culture (S1, S3, S4) have similar mycelial and sclerotial characters to those described for *C. rolfsii*; although on some media, as carrot agar, the mycelium is definitely flocculent. Aerial mycelium is also common, in which respect they resemble *C. centrifugum*. Strains S2 and S8 resemble *C. centrifugum* generally in vegetative habit, aerial mycelium being common, and sclerotia being less numerous, larger and irregularly scattered. As these strains were non-sporulating, it was impossible to refer them to their correct group. They resemble very closely the description given by Goto (1933) for several non-sporulating Japanese strains. The variation in type of growth produced on different media, however, makes it impossible to identify any isolate on vegetative characters. The hymenia of the sporulating strains more closely resemble *C. rolfsii* than *C. centrifugum*, although the shape of the basidiospores is slightly different. It is probable that environmental effects and strain variation will also influence these characters and a certain degree

of laxity must be allowed. It is therefore suggested that the name *Corticium rolfsii* should be applied to these Australian isolates.

(iv). *Variation in the cultures originated from basidiospores.*

Seven monobasidiosporidial cultures were obtained by the following method. A petri dish was poured with clear agar and allowed to cool. A portion of the hymenium was then placed on the lid of the dish and kept at 30°C. for one hour. The temperature and moisture conditions were found to be satisfactory for spore discharge, but during the period allowed, only relatively few spores were obtained. The discharged spores were observed under the high power objective, isolated by means of a fine-pointed harpoon, and transferred to potato-dextrose agar. The cultures were examined until germination had well proceeded to confirm the authenticity of the cultures, which were kept at 30°C. during germination and growth.

Considerable variation was noticeable in the growth habit of the cultures (designated as B1, B2, B3, B4, B5, B6, B7) both between each other and respective mother cultures (Pl. v, fig. 4). B1, B4, B5 and B7 were very similar in appearance. During the first three days of growth, they produced an abundance of fine aerial mycelium, surface or compressed growth being relatively slight. On the other hand, B2 gave rise to a mass of rather dense surface mycelium, aerial mycelium being entirely lacking. B6 produced aerial and surface growth in almost equal amounts, but the surface mycelium was finer and sparser than in B2. B3 was vastly different from the other cultures, being very slow growing and producing dense mycelium, closely confined to the surface of the medium, and with no aerial mycelium.

Variation in sclerotial production was also apparent. B1, B5 and B7 were rather similar, producing abundant, small, globose sclerotia within four days of inoculation. The sclerotia were irregularly scattered through a band on the plate about one-third the radius in width and situated towards the outer portion of the plate. B6 differed by producing a great abundance of very small, globose sclerotia scattered irregularly over the whole plate. The sclerotia were much smaller and far more numerous in this culture than in any other sporidial or mother culture. B4 formed large sclerotia, with a tendency to aggregate. In B3, the sclerotia were even larger than in B4, were very scarce, and coalesced. Sclerotia took much longer to appear in B3 and B4, being about fourteen days in B3 and seven days in B4. Growth rates for the various cultures on potato-dextrose agar at 30°C. are given in Table 4.

TABLE 4.  
*Increase in Mean Diameter of Colonies.*  
(Mm. per 24 hours.)

Culture.	Diameter Increase.
B1	30
B2	28
B3	10
B4	27
B5	28
B6	29
B7	32

To determine whether the cultures retained the capacity to sporulate, they were grown singly and in combination of pairs under conditions which induced sporulation in the mother cultures. Three cultures only produced hymenia, and again heterosexuality could not be demonstrated. It would appear that sporulation can be induced only under very exact conditions, and this varies with different strains, or else the capacity to fructify is readily lost. The former seems more likely.

(c). *Discussion and Conclusions.*

The composition of the medium upon which *C. rolfsii* is growing greatly affects its mycelial growth and the relative abundance of sclerotia, although it has little effect on the colour or shape of the sclerotia. The size of these bodies varies with the age

of the culture. Great care is therefore necessary in separating various strains (or species) on vegetative characters. Hymenial characters are considered to be the only accurate basis of classification of this group of closely related fungi, often considered as *Sclerotium rolfsii*, but the difficulty in inducing sporulation may make it necessary to consider vegetative characters as points of differentiation. If such a resort be necessary, the organism should be grown on a standard medium for a specified period and at a specified temperature. Such a classification would be tentative and preliminary to sporulation.

The wide range of cultural characters produced under artificial conditions by strains, most of which have an apparently similar host range, make it essential that any classification should be broad, allowing considerable range within the terminology of the species. Curzi's classification (1932) was used in identification in this paper. This was thought to be the best available, but whether it is adequate is yet unknown.

## II. MECHANISM OF PARASITISM.

### (a). *Mode of Infection and Effect on Host Tissue.*

The method of entry of *C. rolfsii* was studied by inoculating hypocotyls of germinating bean seeds with small drops of a mycelial suspension prepared by macerating an actively-growing culture of the pathogen in a tube of sterile water. The inoculated hypocotyls were incubated at 30°C., and sections fixed at intervals until pathogenic action was complete. Sections were fixed in Flemming's osmic acid solution, sectioned and stained with various combinations, including safranin—light green, gentian violet—orange G, and carbol-fuchsin—light green.

#### (i). *Method of entry.*

The hyphae grow rapidly in the suspension drop and form a thick mat over the surface of the host (Fig. 3). From this mat, small mycelial strands grow down towards the cuticle. On reaching the cuticle, appressoria are formed, penetration taking place after the manner described by Blackman and Welsford (1916) for *Botrytis cinerea* (Figs. 4a, b, c, d). Formation of appressoria and penetration rarely precede the establishment of the mycelial mat, although this structure does not appear to have any significant function in penetration. It is more likely to be the natural outcome of ideal growth conditions.

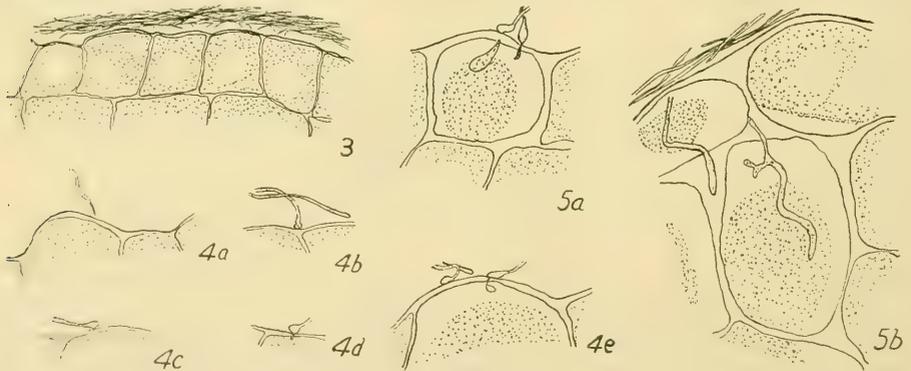


Fig. 3.—Mycelial mat growing over surface of host.  $\times 410$ .

Figs. 4a-4e.—Entry of *C. rolfsii* showing appressoria and penetration hyphae.  $\times 830$ .

Fig. 5.—(a) Growth through epidermal cells showing expansion of hyphae after entry and death of cells in advance.  $\times 410$ . (b) Death of cells in advance and dissolution of middle lamellae. Inter- and intra-cellular hyphae.  $\times 410$ .

The penetration hyphae expand on reaching the epidermal cells, assuming normal dimensions (Fig. 4c). There is no visible action on the host tissue until penetration has taken place, but, immediately after, plasmolysis and death of the invaded cell become visible (Fig. 5a). As the hyphae grow, dying of the protoplasm extends,

the protoplasm being always killed in advance of the invading hyphae, showing that some toxic substance is diffusing from the fungal mycelium.

(ii). *Growth through host tissue.*

The invading mycelium is both inter- and intra-cellular. It readily permeates the whole of the tissue, branching frequently both in the cells and in the inter-cellular spaces. The hyphae are often thickly clustered together, especially in the outer layers. Penetration of all cell walls within the tissue is mechanical, appressoria being formed. In tissue which has been invaded for several days, appressoria are very numerous and can be readily distinguished as enlarged oval structures (Figs. 7*a* and *b*). During the first stages of invasion, the hyphae are coenocytic, few cell walls being formed (Figs. 6*a* and *b*). Later, however, cell walls become more numerous (Figs. 7*a* and *b*). The hyphae are usually multinucleate during all stages of invasion. Generally the invading hyphae grow parallel to the long axis of the cell, less frequently obliquely, but rarely across the cell. No particular preference is shown by the fungus for any portion of the tissue. Growth proceeds as readily through the cells as along the inter-cellular spaces.

Death of the cytoplasm precedes hyphal invasion to a depth of usually one layer, the cells being rarely killed at a distance of more than one layer from the invading fungus. The nuclei remain normal in shape and appearance until the cells are fully

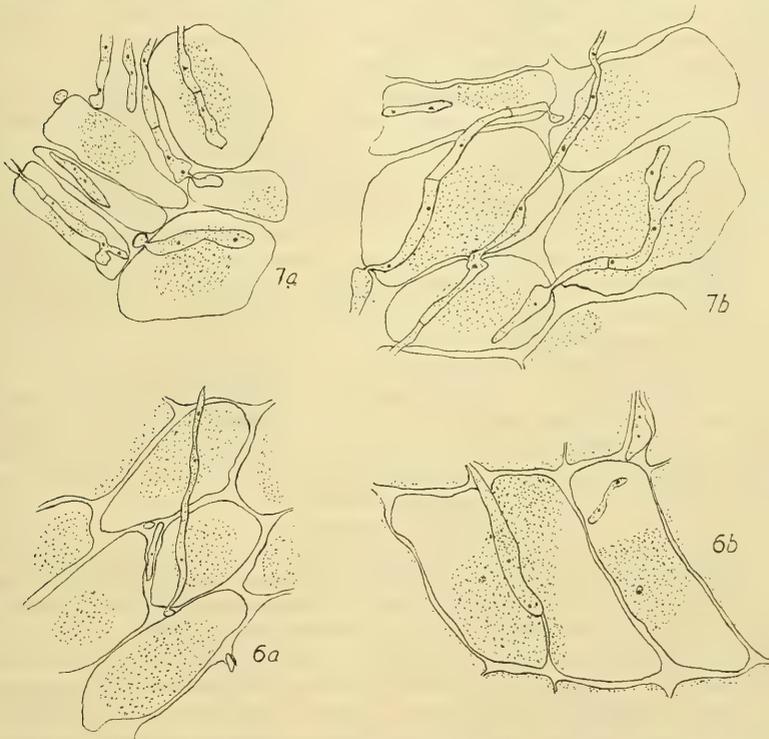


Fig. 6.—(a) Coenocytic hyphae in host tissue.  $\times 450$ . (b) Disintegration of nucleus of invaded cell.  $\times 910$ .

Figs. 7*a*, *b*.—Multinucleate septate hyphae, with killed and disintegrating cells.  $\times 910$ .

invaded by the hyphae. Although in many cases the cytoplasm has been plasmolysed and hyphae are growing in the cell, the nuclei still remain intact (Fig. 6*a*). When the cell has been fully permeated by the hyphae, the nuclei are seen to disintegrate and disappear (Fig. 6*b*). It would seem that invasion must proceed to a marked degree before the nuclei are finally destroyed. This would not necessarily indicate, however, that their function did not cease until then, as it is highly probable that death occurs long before disintegration has taken place, as is the case with the cytoplasm.

Dissolution of the middle lamellae was evident early in the action of the fungus (Fig. 5a). The rapid maceration of the tissue as a result of this action would indicate the presence of a pectilytic enzyme.

(b). *Investigation of the Toxic Principle.*

Considerable controversy exists as to the exact nature of the offensive action of facultative parasites. Enzymes and organic acids, especially oxalic acid, are most favoured. Brown (1936) has recently reviewed the subject, showing that the bulk of the evidence favours the enzyme theory. Higgins (1927) has suggested oxalic acid as the toxic substance of *S. rolfsii*. He isolated large quantities of oxalic acid from carbohydrate broths after thirty-one days' growth. Tests with these filtrates showed that they were extremely toxic. Filtrates boiled for one minute gave positive, but less conclusive, results, which he stated indicated that the toxin was thermostable. Oxalic acid was found to have a bleaching and destructive effect in concentrations of 1:10,000. He does not indicate, however, whether the symptoms of the destructive action are similar in each case, as it is possible that oxalic acid, though toxic, may not be the substance concerned in parasitism. Besides it would seem that his cultures, due to their age, would have an oxalic acid content far greater than that shown by the fungus at the time of parasitism. No knowledge of the concentration of acid in the vicinity of invading hyphae is available, and it is a matter of conjecture whether it is produced in sufficient concentrations to account for the offensive action.

The following investigations were initiated in an attempt to obtain more conclusive evidence as to the nature of the toxic substance. The fungus was grown on pectin and peptone broths (see *Materials and Methods*) and peptone-dextrose broth (peptone 20 gm., citrus pectin 20 gm., distilled water 1,000 ml.). The broths were inoculated with small pieces of three-day-old cultures and incubated at 30°C. for three days, when the mycelium was harvested after the method described by Davison and Willaman (1927). An extract was prepared from the dry mycelium by grinding 0.5 gm. with 25 c.c. sterilized distilled water and allowed to stand for twenty-four hours at 40°C., toluene being added to prevent bacterial activity. (Toluene does not affect enzyme action.) All fragments of the mycelial powder were removed by centrifuging and the clear extract used immediately.

All pieces of mycelium were removed from the broths upon which the fungus was growing by filtering through thinly-woven linen. Filter papers were not used as it was considered they might absorb the enzyme. Toluene was added to the filtrates. Half of each filtrate was used for determining direct macerating effects, the remaining portion being used for enzyme precipitation with equal volumes of 95% alcohol. The precipitate was removed by centrifuging.

(i). *Macerating effect.*

The macerating effects of both filtrate and mycelial extracts, unheated and after steaming for one hour, were tested by their action on potato tissue. Small uniform strips of potato tuber were cut 0.5 mm. in thickness with a razor. Controls were run with sterile water, sterile water plus toluene, sterile broths (i.e., broths upon which no fungus had been growing), and sterile broths plus toluene. Solutions of oxalic acid in concentrations of 1:100, 1:1,000, 1:5,000, 1:10,000 were also tested. Total maceration, the point of ready disintegration of the tissue, was taken as the end-point. The result was judged purely qualitatively by the fingers, but accurate comparative results were obtained.

Total maceration was obtained in the mycelial extracts from pectin broth in six hours, from peptone-pectin broth in eight hours, and from peptone-dextrose broth in twelve hours, and from all three filtrates in twelve hours; no maceration was obtained in the heated filtrates and mycelial extracts, or the controls within five days. Oxalic acid totally macerated potato tissue in sixty hours when in concentrations of 1:100, but in concentrations of 1:1,000 or greater no action was observed within five days.

The fungus produces a thermolabile substance, capable of rapidly macerating plant tissue, and which differs greatly from oxalic acid both in rate of action and in effects

produced. It corresponds to the enzyme described by Davison and Willaman (1927) as protopectinase.

(ii). *Pectase determination.*

To determine the presence of pectase, tests were carried out with filtrates, mycelial extracts, and solutions of the re-dissolved alcoholic precipitates. Two methods were used, the coagulation method of Davison and Willaman (1927) and the calcium mono-methyl tartrate method (Thornberry, 1938). Negative results were obtained in all cases.

(iii). *Pectinase determination.*

The presence of pectinase was determined by Davison and Willaman's method (1927), the reducing sugars obtained being estimated by the picric acid method (Willaman and Davison, 1924). Mycelial extracts from 0.5 gm. mycelial mat and the solutions of alcoholic precipitate obtained from 10 ml. filtrate were used in the determinations. The results are given in Table 5, the amount of reducing sugar expressed

TABLE 5.  
*Reducing Effect of Fungal Solutions on Pectin.*

Solution.	Reducing Sugars in Solution after 24 hours at 40° C.
<i>Mycelial extracts from :</i>	
Peptone-dextrose broth .. .. .	2.57%
Peptone-pectin broth .. .. .	2.71%
Pectin broth .. .. .	2.90%
<i>Alcoholic precipitates from :</i>	
Peptone-dextrose broth .. .. .	1.80%
Peptone-pectin broth .. .. .	2.02%
Pectin broth .. .. .	2.31%
<i>Controls :</i>	
Peptone-dextrose broth .. .. .	0.04%
Peptone-pectin broth .. .. .	0.06%
Pectin broth .. .. .	0.09%
<i>Alcoholic precipitates from :</i>	
Peptone-dextrose broth .. .. .	0.00%
Peptone-pectin broth .. .. .	0.01%
Pectin broth .. .. .	0.01%

being that obtained from the hydrolysis of 20 ml. 3% pectin solution. Controls were run by omitting the pectin, which had no reducing effect.

The enzyme pectinase is produced by *C. rolfssii*, being produced in greater quantities on a pectic medium than on a peptone-dextrose medium.

(c). *Discussion and Conclusions.*

Both protopectinase and pectinase are produced by *C. rolfssii* and are responsible for its destructive action on plant tissue. Although much confusion exists at present as to the nature and effects of pectolytic enzymes, yet the main point that the action is enzymic has been established. Oxalic acid is certainly not responsible. The discrepancy in Higgins's (1927) results is probably due to the very high concentrations of oxalic acid present in the old cultures used. Boiling the solutions for one minute may be insufficient to coagulate all the enzyme in the solution. Steaming for an hour, however, appears to irreversibly precipitate the enzyme. His results also show a more delayed and less effective action with the boiled filtrates, indicating that the toxic action may be somewhat reduced after boiling for so short a period as one minute.

It must be remembered that oxalic acid has a macerating action in high concentrations, but it is difficult to imagine how such concentrations could be obtained during parasitism, as the action of *C. rolfssii* is so rapid. The demonstration of pectolytic

enzymes, however, offers a more feasible explanation for the rapidity and effectiveness of this action.

#### SUMMARY.

*Part i.*—Studies on eight isolates of the organism formerly known as *Sclerotium rolfii* showed that the abundance and type of vegetative growth are determined largely by the nature of the medium and temperature. Abundance and size of the sclerotia, but not shape or colour, are also affected by these factors.

The optimum temperature for growth is 30°C., and this decreases markedly to 15°C. and to 37°C.

The hymenial stage is reported for the first time in Australia, and is designated *Corticium rolfii* (Sacc.) Curzi.

Distinct variations in the growth habit of seven monobasidiosporidial cultures are also noted.

*Part ii.*—The mechanism of the parasitic action of *C. rolfii* is discussed. It penetrates plant tissue mechanically, and gives rise to coenocytic intra- and inter-cellular hyphae. Death of the cytoplasm precedes the invading hyphae by one cell layer. Dissolution of the middle lamellae occurs shortly after entry.

Protopectinase and pectinase, but not pectase, are produced and are responsible for its toxic action.

#### Acknowledgements.

My thanks are due to Dr. W. L. Waterhouse, School of Agriculture, Sydney University, under whose direction the work was carried out, for his kind help and criticism. Thanks are also due to Mr. R. J. Goldacre, Assistant Chemist, New South Wales Department of Agriculture, for the preparation of the half-calcium salt of mono-methyl tartaric acid. I am also indebted to Mr. J. Street for the photographs and to Mr. J. Meade for the translation of Curzi's paper.

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## EXPLANATION OF PLATE V.

- 1.—Growth of isolate S3 on potato-dextrose agar (P.D.A.), carrot agar (C.A.), onion-proteose-peptone agar (O.P.P.A.), and onion agar (O.A.) at 30°C.
  - 2.—Vegetative growth of different isolates on potato-dextrose agar at 30°C.
  - 3.—Growth on potato-dextrose agar at different temperatures after three days.
  - 4.—Variations in growth of basidiosporidial cultures on potato-dextrose agar at 30°C., with cultures from which they were derived.
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## A SURVEY OF THE MISTLETOE OF NEW SOUTH WALES.

By VALERIE MAY, M.Sc.\*

(Plate vi; nineteen Text-figures.)

[Read 30th April, 1941.]

### *Introduction.*

In recent years considerable interest has been aroused by the apparently increasing incidence of Mistletoe (species of the Loranthaceae) on trees in New South Wales. Where infestation is heavy there is little doubt that the economic effects are serious. Fruit and timber trees as well as ornamental and shelter trees are all liable to attack by the members of this group of hemi-parasites.

The germination of the seed, development of the young plant on the host and penetration of its haustoria have been discussed by McLuckie (1923) and need not be considered here. When the parasite has become established on a branch of the host it apparently cuts off supplies of water and mineral salts from the parts of the branch beyond the point of infection. Loss of foliage occurs and often this part of the branch is so injured that it dies and is shed, the Mistletoe thus assuming a terminal position. Because of this the host plant may develop a straggling habit, lack of symmetry caused by the parasite sometimes being extreme. The quality of the timber may be affected adversely by the swellings at the junction of host and parasite; this is of greatest significance when the infection is on the bole itself. Several reports have been received of secondary infection by fungal and insect pests through the gap in the host tissue left by the death of a Mistletoe. Even where the trees are of too poor a quality to be of economic importance as timber, their destruction by the parasite may leave the way open to increased soil erosion and consequent depreciation of land values. Parasitized plants have also been reported to have a lower production of flowers, pollen, honey and fruit. It has also been reported that if trees with and without Mistletoe are felled, the healthy ones give rise to numerous suckers, but the infected trees do so very rarely.

Field observations indicate that the presence of Mistletoe leads to a reduction in the rate of growth of the host tree. As a result of this it assumes a ragged appearance, and, if the tree is not treated, it will finally die. The term "finally" is used advisedly; most observers quote about twenty years as the time needed for Australian Mistletoes to kill a host, although others quote as short a time as six months. The time varies according to the species of host and parasite, age of host, the conditions of growth and the number of infections present.

No experiments in Australia have been recorded which give actual measurements of the reduction in growth rate of the host, but it is of interest to note the observations of workers in other countries where Mistletoe is a pest. Boyce (1925) says: "In eastern Oregon . . . it was found that the height of infected 100-year-old yellow pines was 36% less than normal individuals of the same age, while diameter growth was reduced 17%. These figures for Douglas firs of the same age were 15% and 20%, while for the western larch they were 45% and 41%." Nuessle (1930), from Germany, reports observations on five similarly situated branches of a medium-sized red fir tree.

\* This paper was prepared when the writer held a Linnean Macleay Fellowship in Botany.

One of the branches, which carried a heavy growth of Mistletoe, became devitalized upon reaching a length of only 80 cm., and was bare of needles, while the healthy branches measured 150 cm. Haan (1928), from the Dutch East Indies, reported a 20-30% loss of harvest in kapok plantations, due to Mistletoe infection.

In view of the economic importance of Mistletoe in New South Wales, therefore, it appeared desirable to attempt to survey the species occurring in this State, studying their distribution, abundance and incidence on various species of host, and to co-ordinate existing information on control measures and on conditions affecting their dispersal.

#### *Methods of Investigation.*

The data discussed below have been obtained from field observations by the writer, from records in the National Herbarium, from the monograph on the Loranthaceae of Australia by Blakely (1922-28), and from reports received from observers over a wide area in New South Wales. In order to obtain detailed information as to the present distribution of, and damage caused by, various species of Mistletoe, questionnaires were distributed to agricultural workers, foresters and others interested, and over three hundred replies were received, many answers being accompanied by further information in letter form. Specimens of Mistletoe and host were forwarded in many cases, thus enabling specific determinations to be made. It is recognized that the method of collecting information by means of questionnaires is subject to certain limitations, owing to variability in the methods of observation of those responding. Nevertheless it is felt that an analysis of a large number of replies does yield a considerable amount of valuable information.

#### *Distribution of Mistletoe.*

Blakely (1922-28) has recorded that Mistletoe occurs all over Australia, except in Tasmania. It occurs in varying amounts throughout New South Wales, and in the present survey an attempt has been made to determine its relative abundance in different districts. In Plate vi the total amount of all species for each locality is indicated.

From the answers to the questionnaires received, each locality was classified as belonging to one of the arbitrary groups of 0-1, 1-5, 5-20, 20-50 or over 50% infection, computed on the number of trees infected per hundred, irrespective of the number of infections per tree; Plate vi shows the result obtained from this analysis. The size of the dots is directly proportional to the heaviness of infection in each area. Mistletoe tends to occur in local patches; therefore the density shown in the plate can indicate only an estimate for each district. Any interpretation of this map must therefore be made with caution. Examining the same data by means of histograms (Fig. 19), it appears that there is a lighter infection to the south than the north, and less to the west than the central (Tablelands) or coastal portions of the State. In the central districts there is less very light or very heavy infection than on the coast, i.e., infection in the coastal districts is more sporadic.

From all over the State come reports of an increase in the amount of Mistletoe during the last two or three decades. Some observers suggest that this is due to drought conditions making the effects of infection more noticeable, but others claim that an actual increase has occurred during the last 40 years in their districts.

Twenty-nine species of Mistletoe occur in New South Wales; these are comprised of twenty species of *Loranthus*, four of *Phrygilanthus*, three of *Notothixos*, one of *Korthalsella* and one of *Viscum* (Table 1). Maps have been constructed showing their distribution in this State (Figs. 1 to 14); these are summarized in Table 1. In constructing these maps the shire, or county in the Western Division, has been used as a unit. Against the name of each species quoted (Table 1) is noted whether this plant occurs here on many hosts or is limited to one or a few. In the latter case the distribution of the host plant may, obviously, determine the range of the parasite.

Some trees may be immune in certain localities, but where Mistletoe is very prevalent in their vicinity, they will be found to be attacked. There have been many claims by local observers that certain tree species are resistant to infection in their

TABLE 1.  
Distribution of Different Species of Mistletoe in New South Wales.

Species.	Districts.												Fig.	Remarks.	
	Northern.			Central.			Southern.								
	Coast.	Tablelands.	Plains.	Coast.	Tablelands.	Plains.	Coast.	Tablelands.	Plains.						
<i>Phrygilanthus celastroides</i> (Sieb.)															
Eichl. . . . .	X			X				X						7b	Many hosts.
<i>Notothizos ineanus</i> Oliv. . . . .	X	X		X	X			X	X					—	" "
<i>N. cornifolius</i> Oliv. . . . .	X	X		X	X			X	X					1b	On <i>Brachychiton populneum</i> .
<i>P. eucalyptoides</i> (DC.) Danser. . . . .	X	X		X	X			X	X					2b	Many hosts.
<i>Loranthus vitellinus</i> Muell. . . . .	X	X	X	X	X			X	X	X				10b	" "
<i>L. Cambagei</i> Blakely . . . . .	X	X	X	X	X	X		X	X	X				2a	Usually on <i>Casuarina</i> sp.
<i>L. pendulus</i> Sieb. . . . .	X	X	X	X	X	X		X	X	X				1a	Many hosts.
<i>L. Miquelii</i> Lehm. . . . .	X	X	X	X	X	X	X	X	X	X	X			14	" "
<i>L. Murrayi</i> Muell. et Tate . . . . .			X								X			4a	Usually on <i>Acacia</i> sp.
<i>L. Preissii</i> Miq. . . . .			X	X		X	X			X	X			3a	" " " "
<i>L. Lucasi</i> Blakely . . . . .			X	X		X	X			X	X			8a	Many hosts.
<i>L. Quandang</i> Lindl. . . . .		X	X	X	X	X	X			X	X			7a	" "
<i>L. tinophyllus</i> Fenzl. . . . .	X	X	X	X	X	X	X			X	X			13	Usually on <i>Casuarina</i> sp.
<i>L. miraculosus</i> Miq. . . . .		X	X	X	X	X	X	X	X	X	X			5a	Many hosts.
<i>L. Maidenii</i> Blakely . . . . .			X	X		X	X			X	X			6a	Usually on <i>Acacia</i> sp.
<i>L. grandibracteus</i> Muell. . . . .			X	X		X								9a	Many hosts.
<i>L. Exocarpi</i> Behr. . . . .		X	X	X	X	X	X			X	X			12	" "
<i>Korthalsella articulata</i> (Benth.)															
Blakely . . . . .	X	X	X	X	X	X		X						4b	" "
<i>L. congener</i> Sieb. . . . .	X	X		X	X			X						3b	" "
<i>L. ferruginiflorus</i> Fitz. . . . .	X	X	X											9b	On <i>Eucalyptus</i> and <i>Angophora</i> spp.
<i>N. subaureus</i> Oliv. . . . .	X	X		X	X									6b	Usually on other Mistletoes.
<i>L. gaudichaudi</i> DC. . . . .	X	X		X										—	Usually on <i>Melaleuca</i> sp.
<i>Viscum angulatum</i> Heyne . . . . .	X			X										—	Many hosts.
<i>L. dictyophlebus</i> Muell. . . . .	X	X		X										8b	" "
<i>L. alyxifolius</i> . . . . .	X	X		X										5b	" "
<i>L. Betchei</i> Blakely . . . . .	X													—	" "
<i>L. Mitchellianus</i> (Hook.) Blakely . . . . .		X			X									10a	" "
<i>P. Bidwillii</i> (Benth.) Eichl. . . . .	X	X		X	X			X	X					11	Usually on <i>Callitris</i> sp.
<i>P. myrtifolius</i> (Cunn.) Eichl. . . . .	X													—	One record only.

districts, but in all such cases (provided there have been several reports concerning the same species) reports of infection come from other districts.

Fruit trees furnish an example of plants liable to infection wherever they occur. In New South Wales these are grown on the coastal plains, to a less extent on the Tablelands, and least in the west; the amount of damage suffered follows the same order as the density of cultivation. The Mistletoe species causing most trouble to fruit trees are *Phrygilanthus eucalyptoides*, *Loranthus vitellinus* (including var. *glabrescens*) and *L. congener*. Others that occur are *Korthalsella articulata*, *Loranthus alyxifolius*, *L. Exocarpi*, *L. Cambagei* and *Phrygilanthus celastroides*.

One of the trees which may be attacked in any district where it occurs is Wilga, *Geijera parviflora* Lindl. (Fig. 15). The species attacking this plant are *Korthalsella articulata*, *Loranthus miraculosus* (including var. *Boormani*) and *L. Exocarpi* (including var. *tenuis*), the first two of which are reported to cause severe damage.

The only trees which appear to be free from Mistletoe attack over comparatively wide areas are *Callitris* species and Kurrajong (*Brachychiton populneum* R.Br.). The two most common western tree species of *Callitris*, *C. glauca* R.Br. and *C. calcarata* R.Br.,



Figs. 1-2.—Distribution of certain Mistletoes in New South Wales. Solid circles indicate that the species has been identified from the district (shire, or county in the Western Division) indicated. Hollow circles indicate additional districts where the variety named has been obtained. Crosses indicate that the species has been reported (only) from the district shown.

1.—A. *Loranthus pendulus* Sieb. B. *Notothixos cornifolius* Oliv. 2.—A. *Loranthus Cambagei* Blakely. B. *Phrygilanthus eucalyptoides* (DC.) Danser.

are attacked by the one Mistletoe, *Phrygilanthus Bidwillii*, which is almost confined to species of *Callitris*, and occurs on them both over the same areas (Fig. 16). The zone of heaviest infection is in the Northern Tablelands. Around this there is a zone of lighter infection extending south and westwards. With one slight exception (reported in the Shire of Coreen), *Callitris* growing in the south-central and south-western areas has not been found attacked, even though Mistletoes are present and occur on associated plants. Despite the numerous reports of the absence of Mistletoe infection on *Callitris* in these districts it must be remembered that Mistletoe is less prevalent here on any host, and *Phrygilanthus Bidwillii* has not yet been reported in this district. The map showing the distribution of *P. Bidwillii* (Fig. 11) almost coincides with that showing the infection of these species of *Callitris* (Fig. 16).

As in the case of *Callitris*, the areas where infection on Kurrajong has not been recorded are those where all Mistletoes are relatively rare (Fig. 17). The most important Mistletoe infecting this valuable fodder tree is *Loranthus vitellinus* (including var. *glabrescens*); others are *Notothixos cornifolius*, *N. subaureus* and *Phrygilanthus eucalyptoides*. Infection of Kurrajong by Mistletoe is reported as being extremely serious and rapidly causing much damage.

As species of *Eucalyptus* and *Acacia* are the most abundant elements in the Australian flora, they are the most usual hosts. Other frequent hosts and their infecting Mistletoes are listed in Table 2.

TABLE 2.  
Common Hosts and their Infecting Mistletoes.

Host.	Mistletoe.
<i>Cytisus</i> species .. .. .	<i>Loranthus pendulus</i> , <i>L. vitellinus</i> (incl. var. <i>glabrescens</i> ), <i>Phrygilanthus eucalyptoides</i> .
<i>Eremophila</i> species .. .. .	<i>Korthalsella articulata</i> , <i>L. Cambagei</i> , <i>L. Exocarpi</i> , <i>L. linophyllus</i> , <i>L. miraculosus</i> (incl. var. <i>Boormani</i> ), <i>L. Mitchellianus</i> , <i>L. Quandang</i> , <i>L. vitellinus</i> var. <i>glabrescens</i> .
<i>Flindersia maculosa</i> F. v. M. . . . .	<i>L. miraculosus</i> var. <i>Boormani</i> (N.S.W. ?), <i>L. Mitchellianus</i> (N.S.W. ?), <i>L. Quandang</i> , <i>L. Lucasi</i> .
<i>Heterodendron oleaefolium</i> Desf. . . . .	<i>L. Exocarpi</i> (incl. vars. <i>flavescens</i> , <i>tenuis</i> and <i>vennulosa</i> ).
<i>Pittosporum phillyraeoides</i> DC. . . . .	<i>L. Exocarpi</i> (incl. var. <i>tenuis</i> ), <i>L. miraculosus</i> .
<i>Santalum</i> and <i>Fusapus</i> species. . . . .	<i>K. articulata</i> , <i>L. Exocarpi</i> (incl. var. <i>vennulosa</i> ), <i>L. Quandang</i> , <i>L. miraculosus</i> (incl. var. <i>Boormani</i> ).

*Conditions Affecting the Local Distribution of Mistletoe in New South Wales.*

Although all species of *Eucalyptus* seem liable to infection, reports suggest that in most districts a greater percentage of smooth-barked trees appears to be affected. Plants may become infected at practically any age.

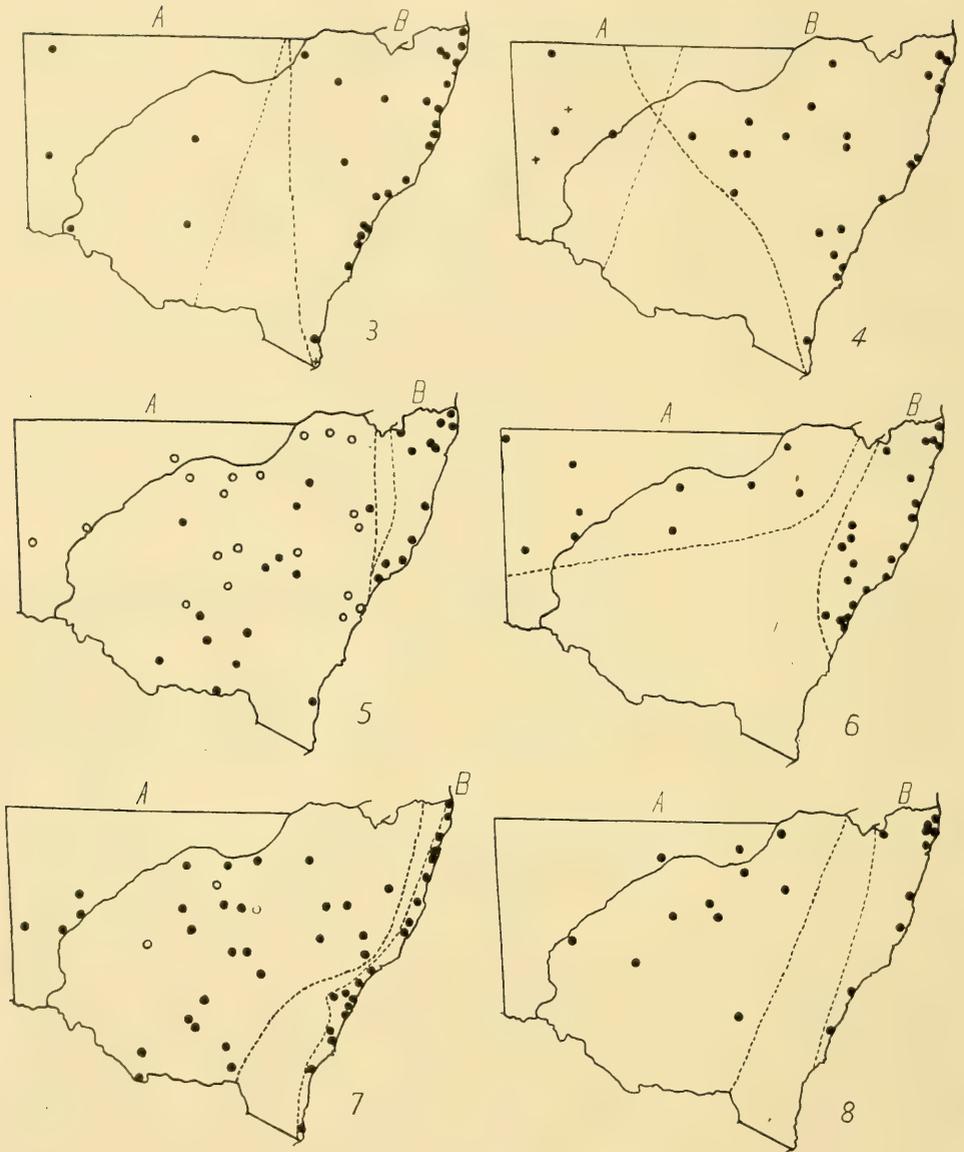
Numerous replies received indicate that Mistletoe is more prevalent where the soil is poor. Mr. E. C. Powell of Parkes has given an estimate (Table 3) of the percentage occurrence of host trees and their percentage infection by Mistletoe on different soils in a locality about twelve miles from Tomingley on the Dubbo-Peak Hill Road. He

TABLE 3.  
Estimate of Percentage Occurrence of Host Trees and Mistletoe Infection on different Soils near Tomingley (Dubbo-Peak Hill Road).

	Iron-bark %	Gum %	Stringy-bark %	White Box %	Yellow Box %	Pine %
On granite ridges (grey) . . . . .	40	45	10	—	—	5
Mistletoe infection . . . . .	20	40	10	—	—	0
On granite soil . . . . .	35	25	—	15	—	25
Mistletoe infection . . . . .	5	15	—	5	—	0
Better soil (mainly granite) . . . . .	15	20	—	35	10	20
Mistletoe infection . . . . .	5	5	—	0	1	0
Granite ridges (red) . . . . .	40	50	—	5	—	5
Mistletoe infection . . . . .	20	35	—	0	—	0

states that the Ironbarks and Gums of the ridges are stunted, lack vigour and are mainly hollow or "piped" (probably 75%). Timber of the granite soil is somewhat better than that on the actual ridges, but is still of poor quality. On the better soil, which, however, is still of a relatively poor type, the trees are healthy and stronger. In this area, it appears that the incidence of Mistletoe decreases as the vigour of the trees improves on the better soils. This result is in agreement with many reports that trees which for some reason are growing less vigorously than the normal tend to become infected.

Reports indicate that, on the western slopes, Mistletoe seems to be more abundant on hills, but that this condition is variable in the mountain and coastal districts; Mistletoe



Figs. 3-8.—Distribution of certain Mistletoes in New South Wales. (For explanatory details see Figs. 1-2.)

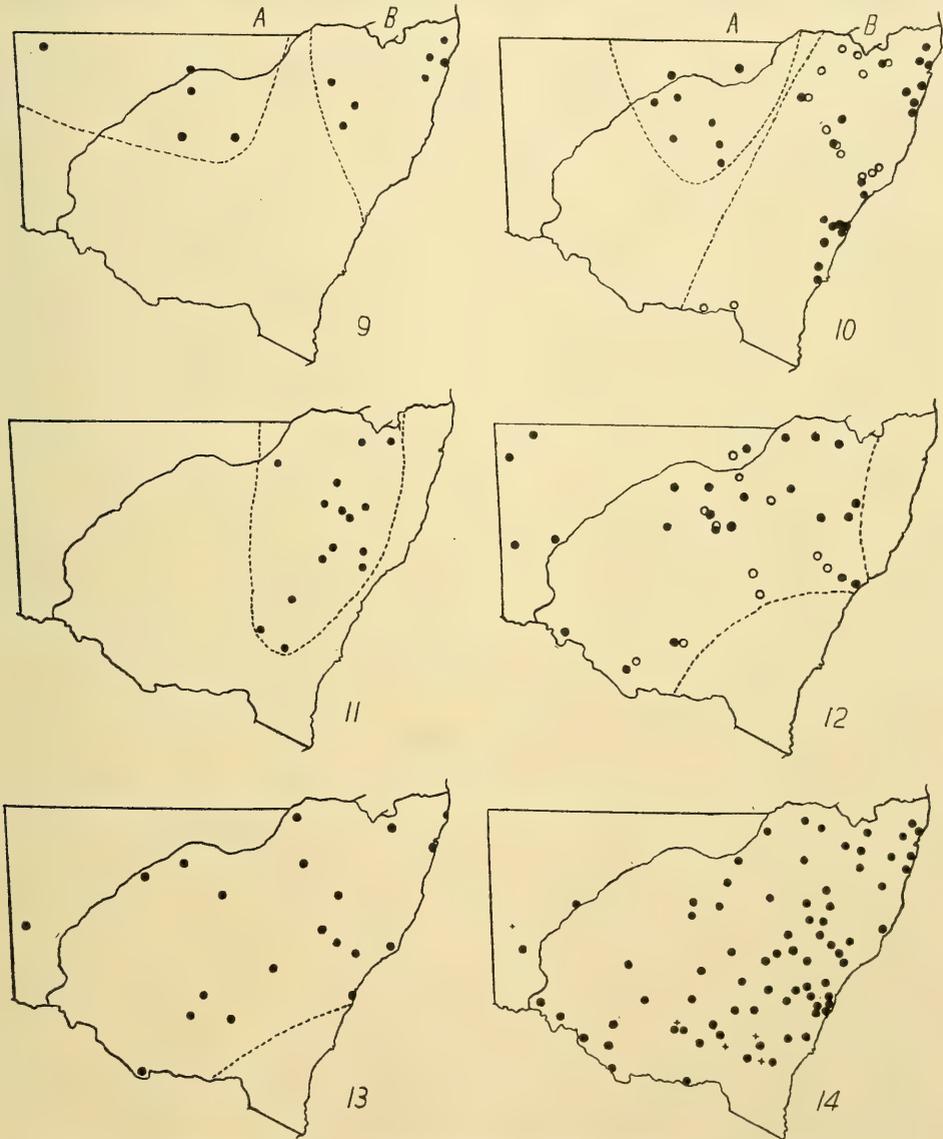
3.—A. *Loranthus Preissii* Miq. B. *L. congener* Sieb. 4.—A. *L. Murrayi* Muell. et Tate. B. *Korthalsella articulata* (Benth.) Blakely. 5.—A. *Loranthus miraculosus* Miq. and var. *Boormani* Blakely. B. *L. alyxifolius* Muell. 6.—A. *L. Maidenii* Blakely. B. *Notothizos subaureus* Oliv. 7.—A. *L. Quandang* Lindl. and var. *Bancroftii* Bail. B. *Phrygilanthus celastroides* (Sieb.) Eichl. 8.—A. *L. Lucasi* Blakely. B. *L. dictyophlebus* Muell.

is absent from high altitudes on the Southern Alps. Some observers say that less Mistletoe occurs on hillsides facing south.

The occurrence of fires may also have an effect on the incidence of Mistletoe. On uncleared land a fire tends to kill the Mistletoes while Eucalypts on which they grow are able to regenerate. On land which has been cleared of undergrowth or which is more or less protected by man, bushfires either do not occur, or, on the rare occasions when they do, are very severe and destroy all timber. Thus the activities of

man result in fire not freeing the host plants of their parasites. This point is worthy of notice, and is perhaps connected with the recent increase in the amounts of Mistletoe.

Where a forest has been partially cleared, the remaining trees tend to be infected much more frequently (this statement however does not seem to apply to the Riverina in the south of New South Wales). For example, Mr. W. A. Crawford (Alstonville) reports that a virgin scrub of two hundred trees bore only one Mistletoe plant, while on a neighbouring area of similar vegetation, but consisting of thinned-out trees and secondary growths, sixteen out of seventy trees had been attacked by Mistletoe. These figures



Figs. 9-14.—Distribution of certain Mistletoes in New South Wales. (For explanatory details see Figs. 1-2.)

9.—A. *L. grandibracteus* Muell. B. *L. ferruginiflorus* Fitz. 10.—A. *L. Mitchellianus* (Hook.) Blakely. B. *L. vitellinus* Muell. and var. *glabrescens* Blakely. 11.—*Phrygilanthus Bidwillii* (Benth.) Eichl. 12.—*Loranthus Exocarpi* Behr. and var. *flavescens* (Muell.) Miq. 13.—*L. linophyllus* Fenzl. 14.—*L. Miquelii* Lehm.

support the statement that trees on semi-cleared land are more liable to infection. It has been noticed also that Mistletoe occurs more on the edge of a forest, in clearings, or near a road, or when in a forest it occurs mostly on boughs projecting above the general level. This preference of Mistletoe for trees or boughs which are not closely surrounded by other trees has been observed also in India and the United States. It is usually attributed to high light requirements of Mistletoe, but may be due to the behaviour of birds which distribute the seeds.

Experiments conducted by the writer on the germination of *Loranthus Miquelii* have shown that embryos placed in the light give a 91% germination, while those kept in darkness give 44%. In the field, of course, such extreme conditions would not exist, since no host would be in absolute darkness.

Reports from all over the State agree that Mistletoe is more abundant near water and in sheltered places. This relationship may be direct as affecting the water needs of host and parasite, or indirect through animal (including bird) behaviour and seed dissemination.

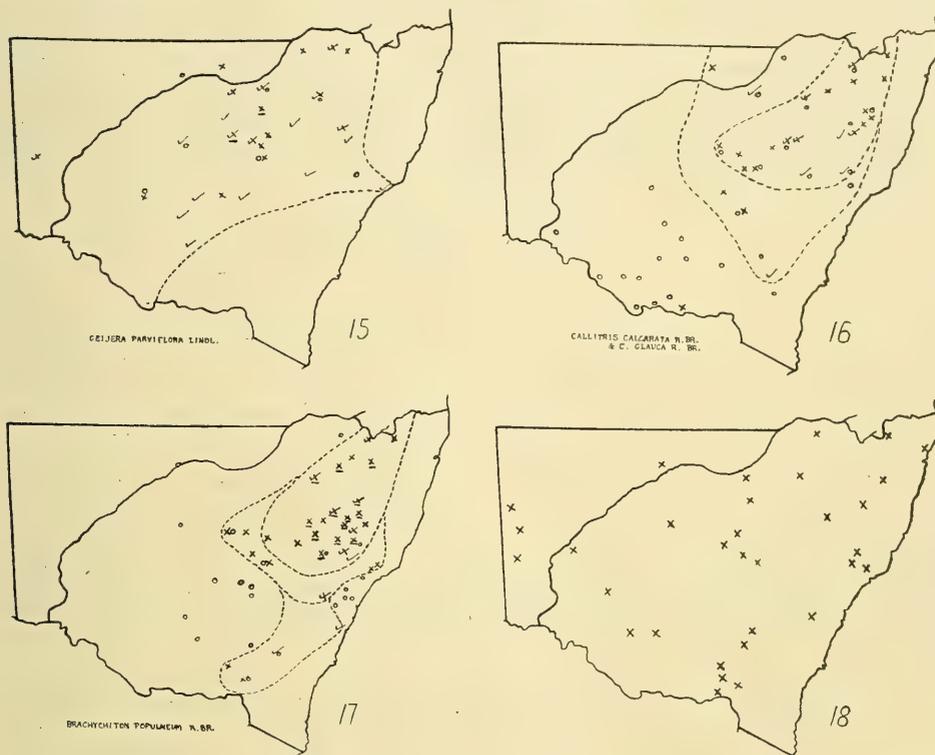
The Mistletoe has a succulent, edible fruit, inside which is the embryo enveloped in mucilage. Experiments indicate that at least in the case of *L. Miquelii*, germination occurs only if the fruit coat has been removed. The young embryos develop readily on inanimate objects or on a potential host plant; often one Mistletoe grows parasitically on another. The writer has found that, in the case of *L. Miquelii*, germination occurs readily even when no additional water is supplied to the embryos. When the "fruit" is eaten by animals, the mucilage-enclosed seed is often either not eaten or it passes through the body unharmed, and so is able to germinate wherever discarded or excreted by the animal. Many birds distribute the Mistletoe seed. In France (Anon., 1934) *Viscum* is reported to be more prevalent along the routes taken by migratory birds. Numerous birds of New South Wales have been reported as eating the fruits and distributing the seeds of Mistletoe. The Mistletoe bird, *Dicaeum hirundinaceum* (Shaw), has been recorded from the far west as well as the coastal and mountain regions, and is regarded by many as the chief distributing agent in this State. Haan (1928) reports another species of *Dicaeum*, *D. flammeum*, as spreading *Loranthus* in kapok plantations in the Dutch East Indies. In New South Wales *Dicaeum* is only one of many birds which distribute the seeds. The King Parrot, *Alisterus scapularis* (Lichtenstein), is reported to chew the fruit, thus destroying the embryo and controlling, not spreading, the Mistletoe. Sugar squirrels and flying-foxes are also reported to distribute Mistletoe. It has been reported that the faeces of the flying-fox contain immense numbers of Mistletoe embryos.

Many claims have been made that the present increase in the amount of Mistletoe is due to a decrease in the number of opossums and/or koalas. The evidence on this point is inconclusive. The Shire Council at Bland (Black, 1928) reports Mistletoe as increasing where koalas have never been known to exist. Mr. N. Burnet, of Koala Park near Sydney, stated (*Sydney Morning Herald*, Nov. 7th, 1935): "At Koala Park, where bears are afforded as much liberty as possible, and where Mistletoe is prevalent, not a single instance of bears or opossums eating such leaves has been observed." (The Mistletoe growing at Koala Park is *Phrygilanthus eucalyptoides*.)

Experimental work in Queensland, by Young (1937), indicated that opossums show a general preference for Mistletoe (*Loranthus vitellinus* and *L. pendulus*), whilst koalas sometimes eat one species (*L. pendulus*), if grown on *Eucalyptus*. It seems that koalas and opossums do eat certain species of Mistletoe, perhaps only as a change of diet, but their significance in the control of Mistletoe in New South Wales is not yet clear. Two-thirds of the reports received concerning opossums claim that they control the spread of Mistletoe, the other third stating that they distribute the seeds of this parasite.

During droughts, Mistletoe is frequently lopped for fodder, so there is less chance of the amount becoming excessive in districts where droughts are common and grazing continuous. From many parts of New South Wales come reports of sheep, cattle or camels eating it when available (Fig. 18); from Hay there is a report that cattle eat

Mistletoe even when they are on green pasture. The species which are eaten include *Loranthus Exocarpi*, *L. linophyllus*, *L. Maidenii*, *L. miraculosus* (including var. *Boormani*) and *L. Mitchellianus*.



Figs. 15-17.—Maps showing the districts in which certain hosts are infected by Mistletoe. Crosses indicate that infected material has been identified, ticks that reports of infection have been received, and underlining that these reports are accompanied by claims of severe damage caused. Circles indicate that the host is here reported as never attacked by Mistletoe.

Fig. 18.—Map showing those districts of New South Wales where stock are reported as eating Mistletoe when available.

#### Control of Mistletoe.

Frequently dead Mistletoe may be seen on living hosts; often such hosts are surrounded by trees bearing living Mistletoe. Mr. F. J. Bendeicht (Belford, via Singleton) describes one area where 80% of the Mistletoe occurring on the Spotted Gum is dead. The reason for this behaviour is not known. It has been suggested by an observer at Wollondilly that scale insects have killed the Mistletoe; but near Sydney scale insects are prevalent without exercising any apparent control over Mistletoe. From Bogan and Woodburn it is reported that wood-boring beetles kill the Mistletoe, but these reports come from districts where Mistletoe is still common. Leaves of *Loranthus Miquelii* which were dying (collected by the writer near Kurrajong) were investigated for the presence of bacteria, but no strains which reinfected the leaves were found. Larvae were found by the writer in fruits of *L. Miquelii*, the plant embryo being completely replaced. These larvae were bred through and the flies identified by Mr. F. A. Perkins (Queensland University) as *Paratrithirum loranthi* (Froggatt). The flies of this group are orchard pests, so are not suitable for use as a practical means of control of Mistletoe. Apparently no effective method of biological control has been discovered as yet in any part of the world. Probably *Loranthus vitellinus*, *Phrygilanthus eucalyptoides* and *L. Miquelii* are the species of Mistletoe whose control in New South Wales is most desirable owing to the damage they cause.

The work of Brooks and Bailey (1919) appears to indicate that a parasitic fungus inside the tree (*Stereum purpureum*) may be killed by the injection of appropriate poisons, without injury to the tree. This suggested the possibility that a substance having a similar action with regard to Mistletoe might be found. The Commonwealth Council for Scientific and Industrial Research initiated experiments along these lines; in most cases, however, host and parasite both died, although the Mistletoe died far more quickly than did the host. It seems the slight difference in tolerance to a toxic substance by host and parasite would not make this method practicable. Further, the effect is not permanent and also the toxic substances are not distributed evenly within the host.

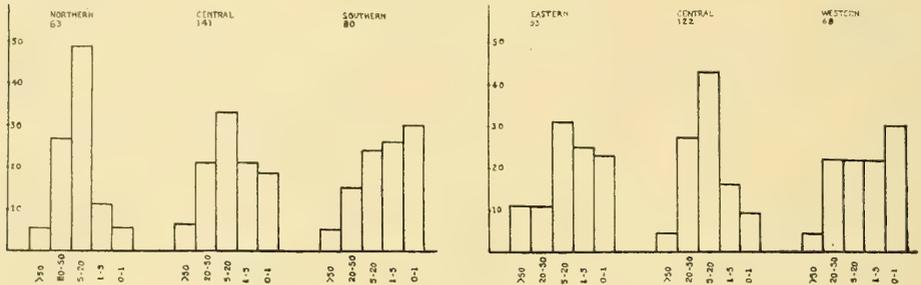


Fig. 19.—Histograms comparing the occurrence of Mistletoe (all species) in various parts of New South Wales. *Left*: Three histograms showing infection in the northern, central and southern areas respectively. *Right*: Three histograms showing infection in the eastern, central and western areas respectively. The 'x' axis indicates the number infected per hundred trees. The 'y' axis indicates the percentage of answers received, for each of the five arbitrary degrees of infection. The number of answers from which each histogram is computed is shown above the figure.

The effects of fire and of opossums on the control of Mistletoe have been discussed earlier.

Measures of controlling Mistletoe usually consist mainly of felling or lopping infected trees. Lopping is carried out in New South Wales as mentioned above in places where Mistletoe is used as drought fodder. Lopping is advised as the chief method of control; where the main trunk is infected, the whole tree may need to be cut down to prevent the Mistletoe from acting as a source of infection to other plants. Bray (1910), in America, suggests lopping the Mistletoe flush with the bark and poisoning the wound with, for example, wood creosote or carbolineum. If the parasite has "rooted" in several places each should be treated. There should be more than one pruning, the second to take place some two to three years after the first. If birds are a serious cause of infection, the lopping must be continued regularly. Since ripe fruit and buds of Mistletoe (e.g., *Loranthus Miquelii*) may be found on the same spray, and since the date of maturing of the fruit on the one species may vary with local conditions, no general optimum date for lopping can be stated. Obviously it is better to lop before fruits ripen, and better still before the flowers mature. Further experiments are necessary to refine the measures of control.

#### SUMMARY.

1. The economic effect of Mistletoe is considered. It appears that the presence of Mistletoe leads to a reduction in the rate of growth, and often the death, of the host tree.
2. It has been shown that Mistletoe in New South Wales is most prevalent and does most damage in the north-east. The Riverina district is least infected.
3. Factors affecting the local distribution of Mistletoe are discussed, and maps have been prepared showing the distribution in New South Wales of the various species of Mistletoes.
4. The distribution of *P. Bidwillii* and the districts of infection by Mistletoe of *Callitris* (western species) are almost, if not quite, coincident. This case appears to

be unique. Most trees of New South Wales appear to be potential hosts to Mistletoe in some district, even if apparently immune in one particular locality. However, Kurrajong is reported free from Mistletoe in many districts, although heavily infected in others.

5. Methods suggested for control of Mistletoe are considered. The topping or felling of infected trees is the only known control.

#### Acknowledgements.

I wish to express my thanks to Professor E. Ashby, Sydney University, and to Mr. R. H. Anderson, National Herbarium, Sydney, for the suggestions and assistance they have rendered, also for sanctioning posting of circulars under their names; to Mr. W. F. Blakely, of the National Herbarium, who has kindly identified numerous specimens sent in response to the circulars; also to the many persons who answered the circulars or assisted in their dispersal.

#### References.

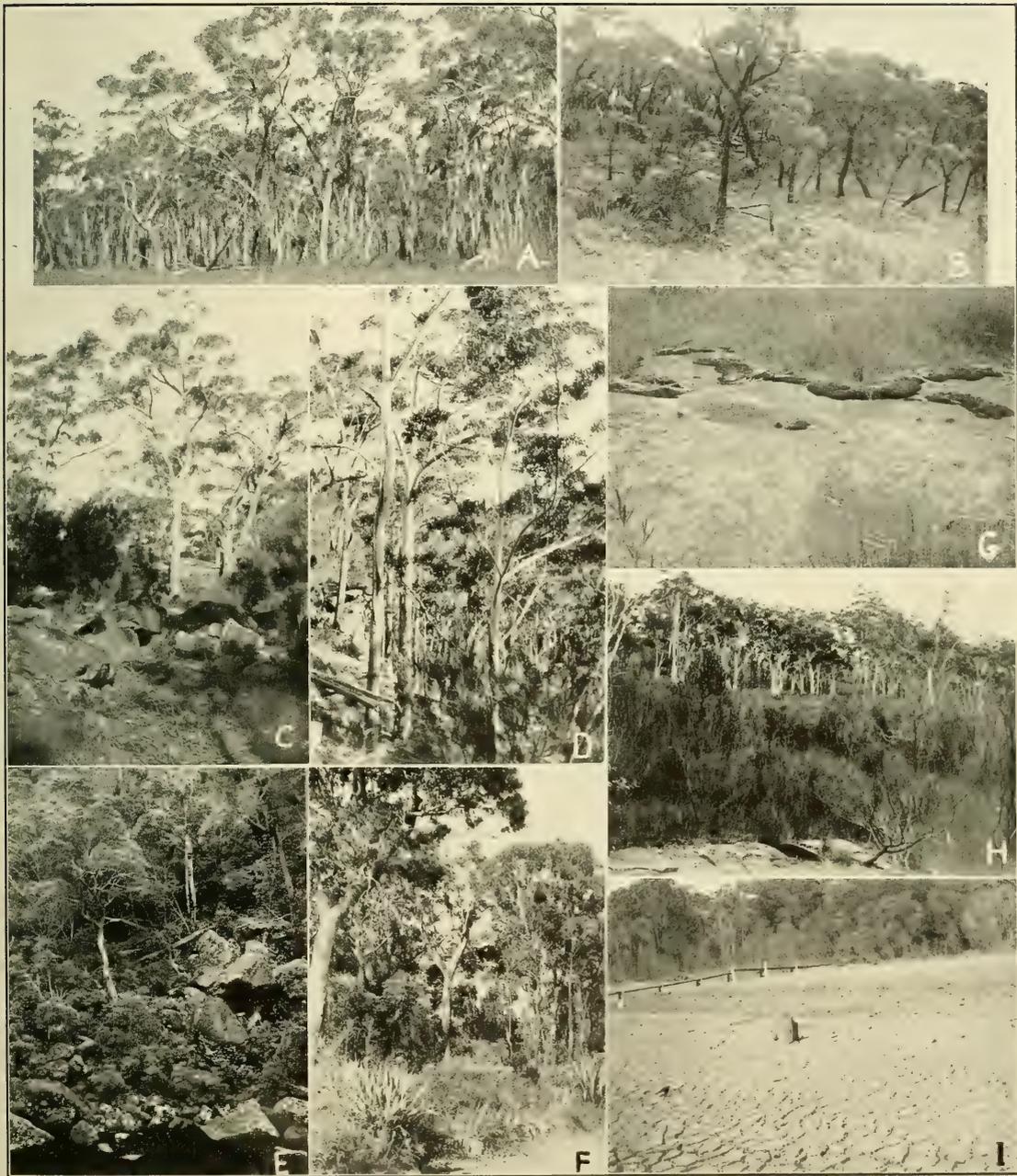
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#### EXPLANATION OF PLATE VI.

A map showing the relative abundance of all species of Mistletoe in New South Wales. Circles indicate places from which estimates of the number infected per hundred host trees have been received. The diameter of the dot is one of five sizes, the largest indicating infection of over 50%, the next infection of 20-50%, the next infection of 5-20%, the next infection of 1-5%, and the smallest infection of 0-1%.

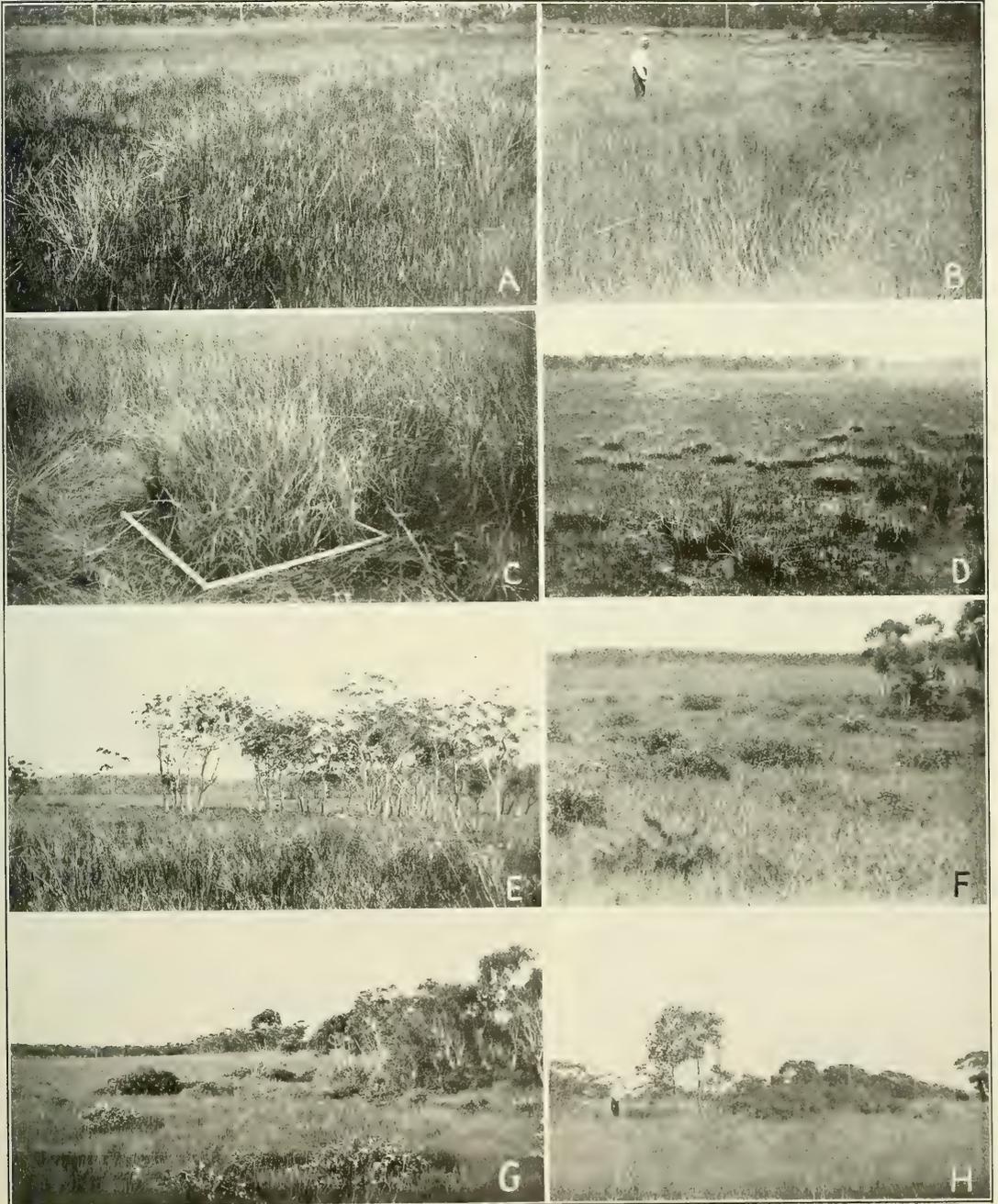
\* Original paper not seen by writer.





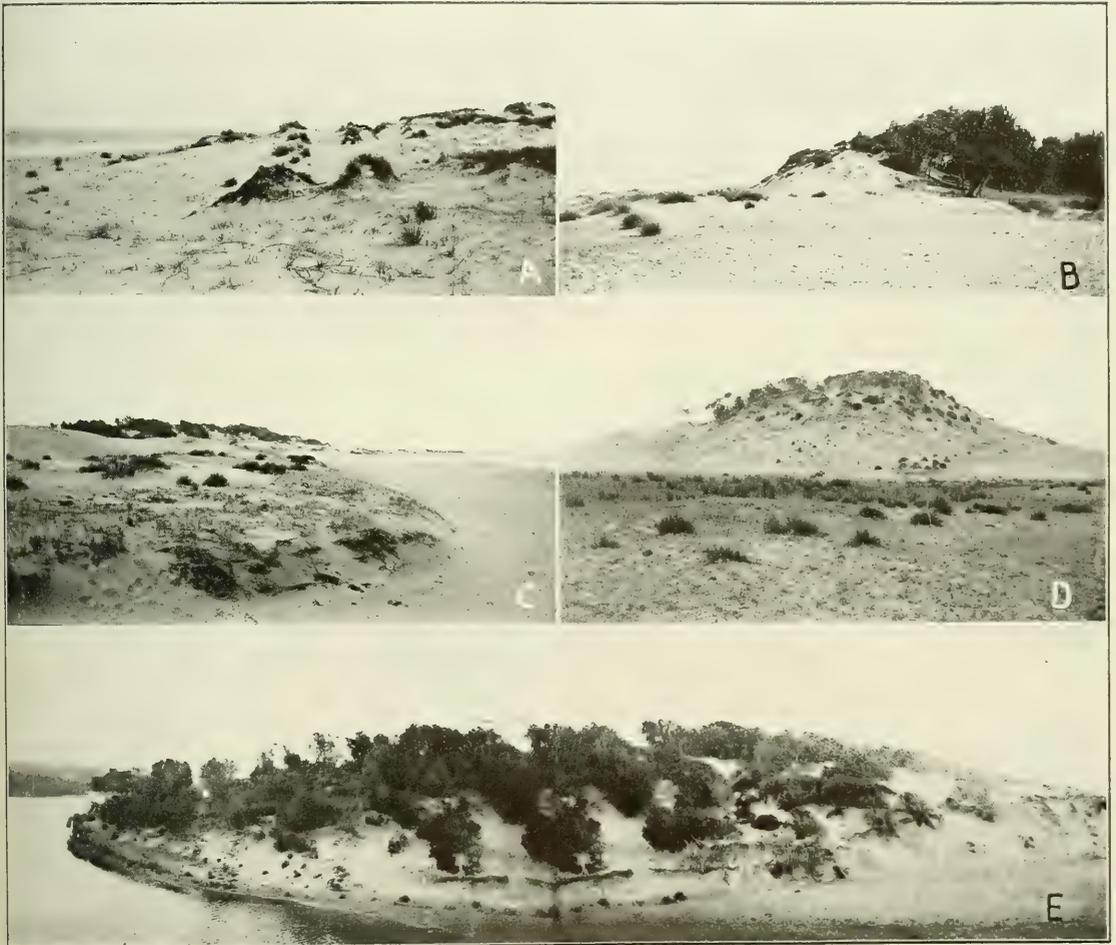
Ecology of the Bulli District.





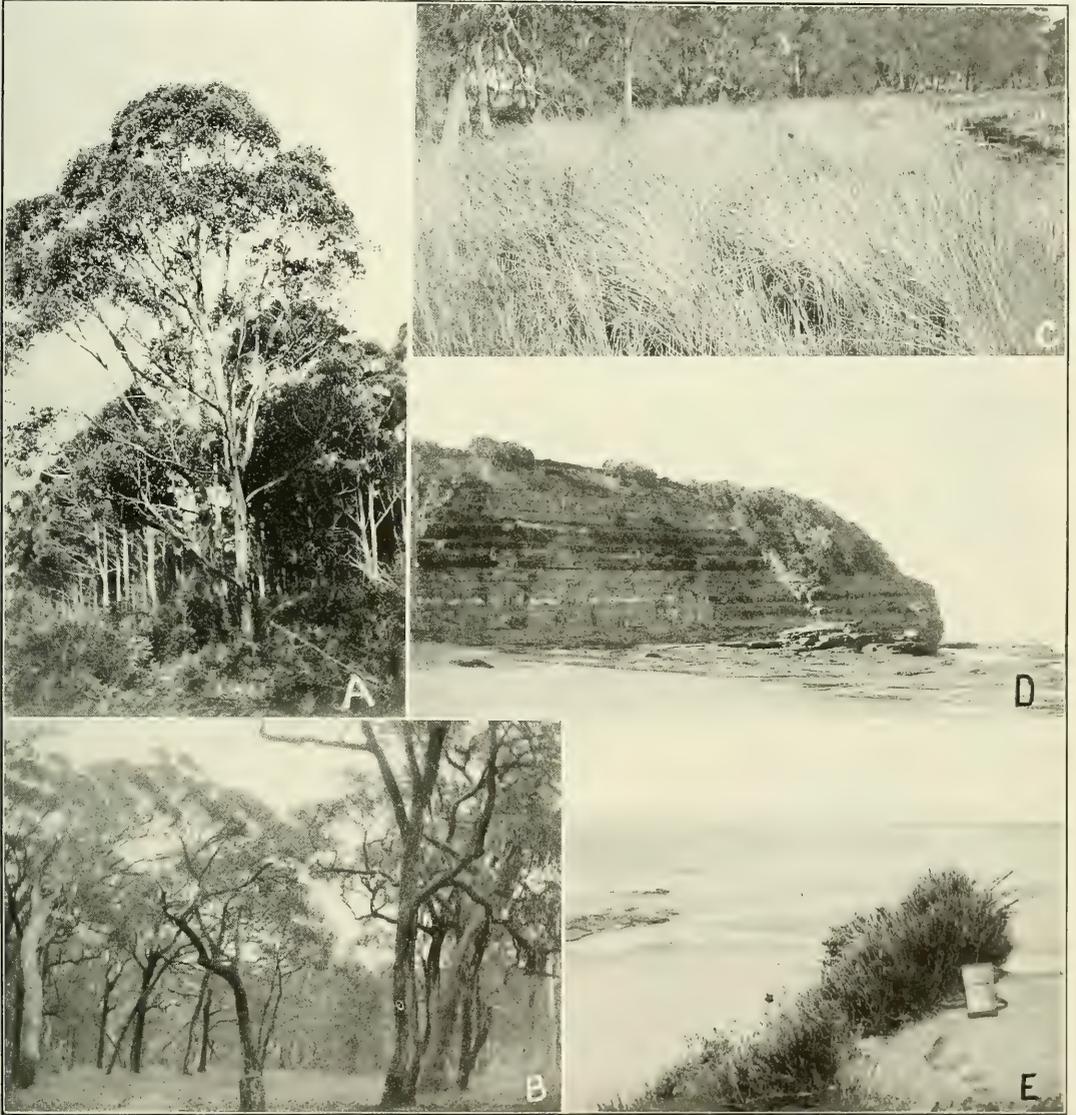
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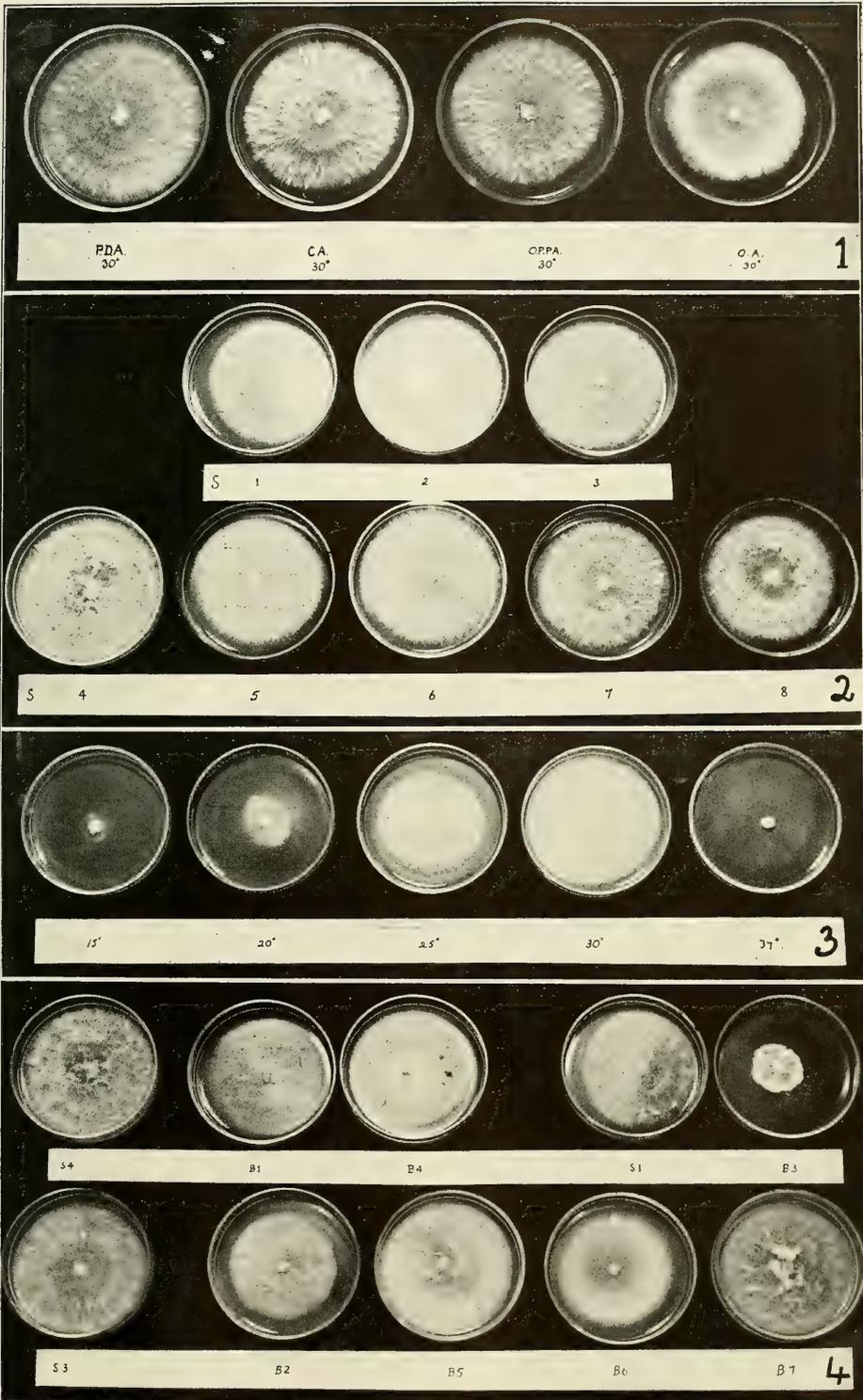
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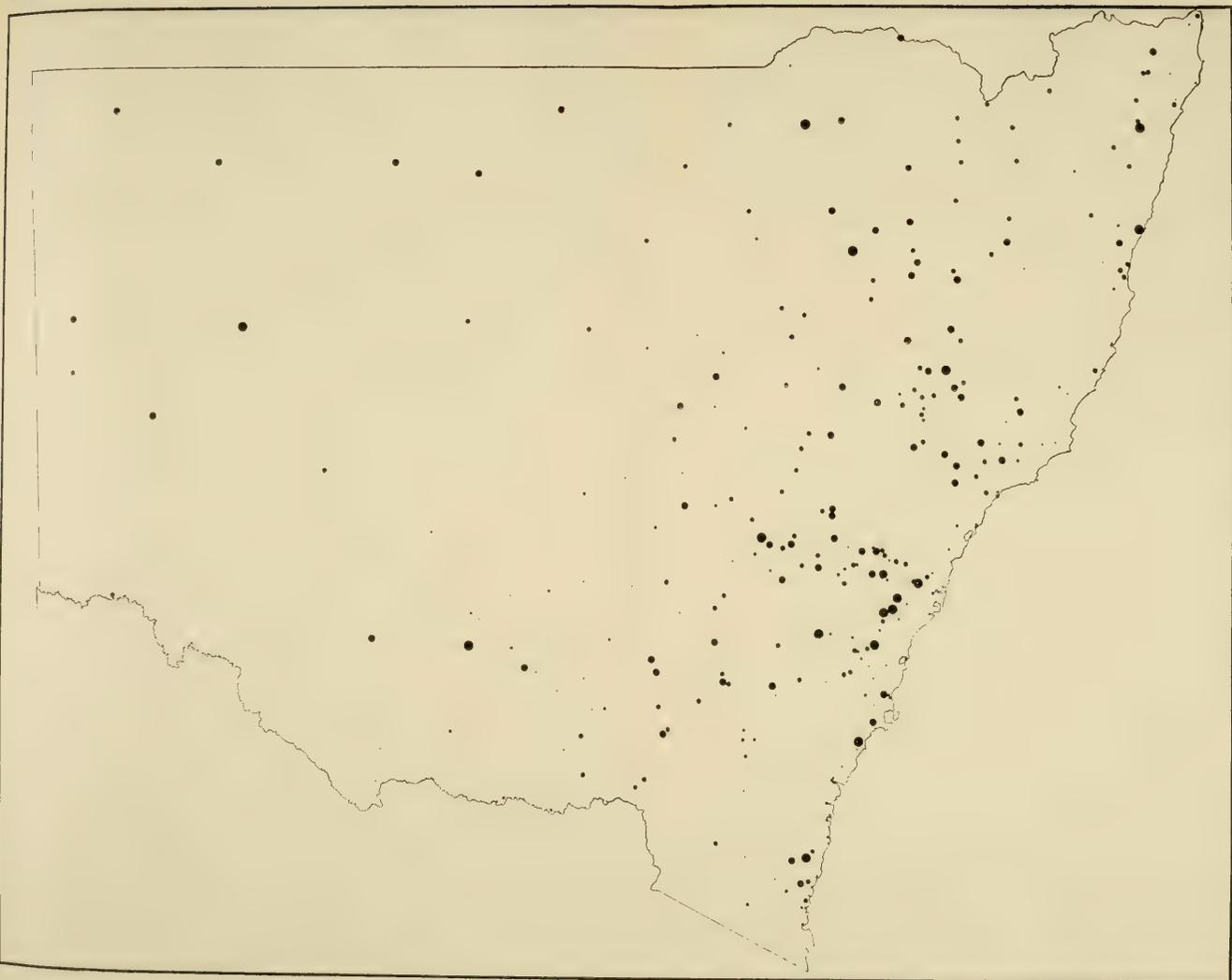
Ecology of the Bulli District.





*Corticium rolfsii.*





Map showing the relative abundance of Mistletoe in New South Wales.



## NITROGEN FIXATION AND CELLULOSE DECOMPOSITION BY SOIL MICRO-ORGANISMS. II.

THE ASSOCIATION BETWEEN AZOTOBACTER AND FACULTATIVE-AEROBIC CELLULOSE-DECOMPOSERS.

By H. L. JENSEN, Macleay Bacteriologist to the Society, and R. J. SWABY,  
formerly Biochemist to the Society.

(From the Department of Bacteriology, University of Sydney.)

(One Text-figure.)

[Read 28th May, 1941.]

### Introduction.

In a previous paper (Jensen, 1940*b*) it was shown that no fixation of nitrogen takes place in combined pure cultures of *Azotobacter* and "typical" aerobic cellulose-decomposing soil bacteria (*Cytophaga*, *Cellvibrio*, etc.), as well as fungi or actinomycetes, but that certain facultative aerobes which decompose the cellulose with formation of organic acids, enable *Azotobacter* to fix appreciable quantities of nitrogen. The present paper gives an account of the quantitative relationship between cellulose decomposition and nitrogen fixation under varying experimental conditions, and the nature of the organic breakdown products of cellulose that serve as energy material for the fixation.

Four strains of cellulose-decomposing bacteria were tested: three species of corynebacteria (*Cor.* 3 (*fini*?), *Cor.* Va and *Cor.* Vb, described previously (Jensen, 1940*b*)), and an authentic strain of *Cellulomonas biazotea*.\* The strain of *Az. chroococcum* used in the previous investigation was used throughout the experimental work, and occasionally *Az. vinelandii*, *Az. Beijerinckii* (?) and *Az. indicum* (the last kindly supplied by Dr. R. L. Starkey, New Jersey Agricultural Experiment Station, N.J., U.S.A.). The basal solution for the combined cultures, unless otherwise stated, contained:  $K_2HPO_4$  0.1%,  $MgSO_4$  0.05%,  $NaCl$  0.02%,  $FeCl_3$  0.01%,  $Na_2MoO_4$  0.001%, besides varying amounts of  $CaCO_3$  and yeast extract (of 10% dry yeast in tap water, autoclaved and filtered). Cellulose was supplied as filter paper—Whatman No. 1. Inoculum consisted of one loopful of a thin suspension of cells from young cultures on agar slopes. Nitrogen was determined by the Kjeldahl method as previously described (Jensen, 1940*a-b*), and soluble organic carbon by the method of Birkinshaw and Raistrick (1931). Residual cellulose was determined by filtration through Jena glass filter crucibles (No. 1-G-1), washing with dil. HCl and distilled water, and drying to constant weight at 98°C. It was found that both cellulose and nitrogen could, without any serious error, be determined in the same culture by removing the dried residue from the crucible and digesting it together with the combined filtrate and washings. Volatile acids were determined by distillation according to Duclaux, and lactic acid by the method of Friedemann *et al.* (1927).

### EXPERIMENTAL.

#### A. Nitrogen Fixation in Associated Cultures.

*Experiment 1:* The four cellulose-decomposing bacteria were tested in combination with *Az. chroococcum*. The basal solution contained 2.0% yeast extract and 0.5%  $CaCO_3$ :

\* A strain of *Cell. rossica* (Kellerman), obtained from the National Collection of Type Cultures, Lister Institute, London, was also tested. This organism, however, was found to have lost its cellulose-decomposing power.

the first series, with *Cor.* 3, was carried out in 250 c.c. round flasks with 100 c.c. solution and 1.0 gm. filter paper, the others in 100 c.c. round flasks with 40 c.c. solution and 0.5 gm. filter paper. Table 1 gives the results.

TABLE 1.

*Nitrogen Fixation in Combined Cultures of Azotobacter chroococcum with Corynebacteria and Cellulomonas biazotea.*

Inoculum.	Incubation Days.	Cellulose, gm.		Nitrogen, mgm.	
		Per Culture.	Loss.	Per Culture.	Gain.
I.					
Control	0	0.951		2.40 2.41	2.40
<i>Corynebacterium</i> 3	48	(a) 0.797 (b) 0.822	0.154 0.129		
.. + <i>Azotobacter</i>	48	(a) 0.728 (b) 0.762 (c) 0.800	0.223 0.189 0.151	(d) 4.04 (e) 4.22 (f) 4.72	1.64 1.82 2.32
II.					
Control	0	0.478		2.66 2.72	2.69
<i>Azotobacter</i>	35			2.65	(-0.04)
<i>Corynebacterium</i> Vb	35			2.80	(0.11)
.. Va	42			2.78	(0.09)
.. Vb + <i>Azotobacter</i>	35	(a) 0.251 (b) 0.238 (c) 0.235	0.227 0.240 0.243	(d) 6.30 (e) 6.68 (f) 5.26	3.61 3.99 2.57
.. Va + <i>Azotobacter</i>	42	(a) 0.332 (b) 0.330 (c) 0.328	0.146 0.148 0.150	(d) 4.31 (e) 4.48 (f) 4.41	1.62 1.79 1.72
III.					
Control	0	0.478		2.36 2.20	2.28
<i>Cellulomonas biazotea</i> + <i>Azotobacter</i>	45	(a) 0.405 (b) 0.404	0.073 0.074	(a) 2.73 (b) 2.53	0.45 0.25
		Average Loss of Cellulose, gm.		Average Gain of N, mgm.	
				Per Culture.	Per gm. of Cellulose Lost.
<i>Azotobacter</i> + <i>Corynebacteria</i> 3		0.188		1.93	10.3
.. + .. Vb		0.237		3.39	14.3
.. + .. Va		0.148		1.71	11.5
.. + <i>Cellulomonas biazotea</i>		0.074		0.35	4.7

The pure cultures of cellulose-decomposers absorb no nitrogen from the atmosphere, and *Azotobacter* does not grow in the absence of cellulose-decomposers (cf. Jensen, 1940b). The associated cultures show in all cases a strong cellulose decomposition and significant gains of nitrogen which, although varying considerably in replicate cultures, correspond to fixation of about 4 to 14 mgm. N per gm. of cellulose decomposed. This figure agrees perfectly with the findings (reviewed by Jensen, 1940a) of many previous investigators who have used crude cultures or natural populations of soil or decaying plant material. Both absolutely and relatively, *Cell. biazotea* appears the least and *Cor.* Vb the most efficient organism. The latter was therefore used in most of the subsequent experiments.

*Experiment 2:* Various other species of *Azotobacter* were tested; in the first series, *Cor.* 3 together with *Az. vinelandii*, in the second, *Cor.* Vb with *Az. vinelandii*, *Az. Beijerinckii* and *Az. indicum*. Cultures were grown in 100 c.c. round flasks with 0.5 gm. filter paper, 0.2 gm. CaCO<sub>3</sub> (not added to the cultures of *Az. indicum*) and 40 c.c. of basal solution which in the first series contained 0.01% peptone, and in the second 2.0% yeast extract. Table 2 shows that the efficiency of fixation in terms of nitrogen per gm. of cellulose lost is similar to that in the cultures of *Az. chroococcum*, although the actual gains are smaller in *Az. indicum*.

TABLE 2.  
*Nitrogen Fixation in Combined Cultures of Corynebacteria and Different Species of Azotobacter.*

Inoculum.	Incubation, Days.	Cellulose, gm.		Nitrogen, mgm.	
		Per Culture.	Loss.	Per Culture.	Gain.
Series I, peptone solution.					
Control, duplicate	0	0.478		1.22	
<i>Corynebacterium</i> 3	28	0.466	0.012	1.28	(0.06)
„ 3 + <i>Azotobacter</i> <i>vine-</i> <i>landii</i>	28	(a) 0.411 (b) 0.428 (c) 0.404	0.067 0.050 0.074	(d) 2.00 (e) 1.97 (f) 1.70	0.78 0.75 0.48
Series II, yeast extract solution.					
Control, duplicate	0	0.478		2.17	
„ single	46	0.477		2.21	(0.04)
<i>Corynebacterium</i> Vb	48	0.392	0.086	2.34	(0.17)
„ „ + <i>Azotobacter</i> <i>vine-</i> <i>landii</i>	42	(a) 0.257 (b) 0.271 (c) 0.260	0.223 0.207 0.218	(a) 5.01 (b) 4.67 (c) 4.72	2.84 2.50 2.55
„ „ + <i>Azotobacter</i> <i>Bei-</i> <i>jerinckii</i>	45	(a) 0.264 (b) 0.275 (c) 0.287	0.214 0.203 0.191	(a) 5.21 (b) 4.59 (c) 4.48	3.04 2.42 2.31
„ „ + <i>Azotobacter</i> <i>in-</i> <i>dicum</i>	48	(a) 0.362 (b) 0.351 (c) 0.317	0.116 0.127 0.161	(a) 3.45 (b) 3.52 (c) 3.93	1.28 1.35 1.76

Average gain of nitrogen per gm. of cellulose lost by:

<i>Corynebacterium</i> 3 + <i>Azotobacter</i> <i>vinelandii</i> :	10.5 mgm.
„ Vb + „ „:	12.2 mgm.
„ Vb + „ <i>Beijerinckii</i> :	12.8 mgm.
„ Vb + „ <i>indicum</i> :	10.8 mgm.

*Experiment 3:* The influence of temperature on the efficiency of fixation was tested. *Cor.* Vb and *Az. chroococcum* were grown in 100 c.c. round flasks with 0.5 gm. filter paper, 0.2 gm. CaCO<sub>3</sub>, and 40 c.c. basal solution + 2.0% yeast extract, at 15°C. and 37°C. The results (Table 2) show no striking difference between the two temperatures, although the efficiency appears lower than at 28–30°C. (cf. Table 1). The hypothesis of Olsen (1932) that a low temperature of decomposition might lead to a more copious formation of organic by-products and consequently stronger nitrogen fixation, finds no support in these data.

*Experiment 4:* This was undertaken with the same organisms and the same medium as Exp. 3, but with incubation at 28–30°C. and analysis at three stages of growth. It appears from the results in Table 4 that the efficiency increases with the age, i.e., the nutrients for *Azotobacter* seem to be formed more abundantly in ageing cultures of the cellulose-decomposers.

TABLE 3.

*Nitrogen Fixation in Combined Cultures of Azotobacter chroococcum and Corynebacterium Vb at Different Temperatures.*

Culture Series.	Incubation, Days.	Cellulose, gm.		Nitrogen, mgm.	
		Per Culture.	Loss.	Per Culture.	Gain. <sup>a</sup>
Control (duplicate) . . . . .	0	0.478		3.94	
<i>Corynebacterium Vb</i> . . . . .	42			3.88	(-0.06)
15° C.		(a) 0.364	0.114	(d) 4.76	0.82
"    "    + <i>Azoto-</i>	42	(b) 0.380	0.098	(e) 4.44	0.50
<i>bacter</i>		(c) 0.398	0.080	(f) 4.45	0.51
<i>Corynebacterium Vb</i> . . . . .	20			(a) 3.74	(-0.20)
				(b) 3.59	(-0.35)
37° C.		(a) 0.319	0.159	(d) 5.06	1.12
"    "    + <i>Azoto-</i>	20	(b) 0.335	0.143	(e) 5.30	1.36
<i>bacter</i>		(c) 0.309	0.169	(f) 5.17	1.23
Average gain of N per gm. of cellulose lost: 15° C.: 6.3 mgm.					
37° C.: 7.9 mgm.					

TABLE 4.

*Nitrogen Fixation in Combined Cultures of Azotobacter chroococcum and Corynebacterium Vb at Different Stages of Growth.*

Inoculum.	Incubation, Days.	Cellulose, gm.		Nitrogen, mgm.	
		Per Culture.	Loss.	Per Culture.	Gain.
Control (duplicate) . . . . .	0	0.478		2.28	
<i>Corynebacterium Vb</i> . . . . .	32	0.394	0.084	2.18	(-0.10)
	52	0.386	0.092	2.04	(-0.24)
	14	(a) 0.374	0.104	(c) 2.78	0.50
		(b) 0.377	0.101	(d) 3.06	0.78
"    "    + <i>Azotobacter</i> . . . . .	32	(a) 0.312	0.166	(a) 3.83	1.55
		(b) 0.308	0.170	(b) 3.88	1.60
	52	(a) 0.286	0.192	(a) 4.44	2.16
		(b) 0.254	0.224	(b) 4.63	2.35
Average gain of N per gm. of cellulose decomposed: 14 d.: 6.2 mgm.					
32 d.: 9.4 mgm.					
52 d.: 10.8 mgm.					

*Experiment 5:* In all the previous experiments the filter paper was added to a liquid medium in a fairly deep layer. At the start of incubation a part of the paper protruded above the liquid, but with advancing decomposition it soon collapsed and was entirely submerged, so that most of the cellulose decomposition probably took place under a somewhat restricted access of oxygen, the tension of which would be further decreased by the vigorous growth of *Azotobacter* on the surface of the medium, where something approaching a true *Azotobacter*-pellicle was often noticeable. An experiment was therefore designed to test the nitrogen fixation when cellulose was being decomposed under strictly aerobic conditions; this was done by placing the filter paper on the surface of an agar medium. The first series was carried out with *Cor.* 3 and *Az. chroococcum* in 250 c.c. Erlenmeyer flasks containing 75 c.c. basal solution + 0.8% agar and 2.0% yeast extract; FeCl<sub>3</sub> was replaced by 0.02% FeSO<sub>4</sub>, which was added separately in solution after melting of the agar, in order to prevent precipitation of the iron as phosphate. After the agar had set, 0.5 gm. finely cut filter paper and 0.2 gm. CaCO<sub>3</sub>, sterilized separately, were distributed evenly over the agar surface, where the

condensation water was just sufficient to moisten the paper thoroughly; two flasks received an extra 10 c.c. of sterile water, thus immersing the paper in a shallow layer of liquid. The second series was carried out with *Cor. Vb* and *Az. chroococcum* in 250 c.c. round flasks with 80 c.c. agar medium, otherwise as in the first series. The paper was rapidly attacked, but vigorous growth of *Azotobacter*, as indicated by pigment formation, was observed only where extra water had been added.

TABLE 5.  
*Nitrogen Fixation in Combined Cultures of Azotobacter chroococcum and Corynebacteria on Agar Surface.*

Inoculum.	Incubation, Days.	Cellulose, gm.		Nitrogen, mgm.	
		Per Culture.	Loss.	Per Culture.	Gain.
I.					
Control .. .. .	0	0.478		3.93 3.88	3.91
<i>Azotobacter</i> .. . . .	42			3.78	(-0.13)
<i>Corynebacterium</i> 3 .. . . .	42			3.91	(0)
„ 3 + <i>Azotobacter</i> .. . . .	42	(a) 0.323 (b) 0.315 (c) 0.320	0.155 0.163 0.158	(d) 4.10 (e) 4.18 (f) 4.41	0.19 0.27 0.50
„ 3 „ +10 c.c. water	42			(a) 4.80 (b) 4.69	0.89 0.78
II.					
Control .. . . .	0	0.478		3.70 3.74	3.72
<i>Azotobacter</i> .. . . .	35			3.51	(-0.21)
<i>Corynebacterium</i> Vb .. . . .	35			3.68	(-0.04)
„ Vb + <i>Azotobacter</i> .. . . .	35	(a) 0.287 (b) 0.287 (c) 0.288	0.191 0.191 0.190	(d) 3.70 (e) 3.80 (f) 3.51	(-0.02) (0.08) (-0.21)
„ Vb „ +10 c.c. H <sub>2</sub> O	35			4.94	1.23

The data in Table 5 show clearly that under strictly aerobic conditions the efficiency of nitrogen fixation is very much lower than under the partly anaerobic conditions obtaining in the solution cultures: in series 1 (*Cor.* 3) it amounts to only about 2 mgm. N per gm. of decomposed cellulose, and in series 2 (*Cor.* Vb) it is altogether insignificant. Where the decomposing cellulose is immersed in a shallow layer of liquid, some nitrogen fixation takes place; abundant supply of moisture thus appears generally essential (cf. Jensen, 1940a).

*Experiments 6-8:* Next the utilization of natural cellulosic materials was tested. The first two series in Exp. 6 were carried out with finely ground and water-extracted wheat straw, 0.5 gm. in 100 c.c. round flasks with 0.2 gm. CaCO<sub>3</sub> and 40 c.c. basal solution + 1.0% yeast extract. Table 6 shows that with this material some nitrogen is also fixed, and the efficiency is about the same as with filter paper, but the actual amounts are much smaller. An additional experiment was carried out (Ser. III, Table 6) with a crude culture of obligate anaerobic cellulose-decomposing bacteria\* in the same medium without yeast extract; this combination with *Azotobacter* gives a vigorous fixation, whereas *Cor.* 3 seems unable to induce fermentation in this medium which contains the N-compounds of the straw only. Experiment 7 was carried out as Exp. 6, in solution with 1.0% yeast extract, but with ground and water-extracted

\* Spore-bearing organisms of the type studied by Khouvine (1923); the culture was found to be free from aerobic cellulose-decomposers.

material of *Paspalum dilatatum*, harvested at the period of early seed formation. The results are given in Table 7, and show that *Azotobacter* + corynebacteria fix nitrogen with approximately the same efficiency as in straw, but in considerably larger amounts. Probably the cellulose in the grass-material is easier to digest than the more lignified straw-cellulose. The crude anaerobic culture again gives a very vigorous fixation. Experiment 8 was designed in a manner similar to Exp. 5 (decomposition under aerobic conditions): 0.5 gm. dry straw or *Paspalum*-material and 0.25 gm.  $\text{CaCO}_3$ , sterilized separately, were placed on the surface of 75 c.c. of agar medium in 250 c.c. round flasks; 1.0% yeast extract was added to the medium in the series in which straw was used. The results, summarized in Table 8, show no nitrogen fixation whatever under these conditions, even with extra addition of water.

TABLE 6.

*Nitrogen Fixation in Combined Cultures of Azotobacter chroococcum and Cellulose-decomposing Bacteria: Straw in Liquid Medium.*

Inoculum.	Incubation, Days.	Dry Organic Matter, gm.		Nitrogen, mgm.	
		Per Culture.	Loss.	Per Culture.	Gain.
I.					
Control .. .. .	0	0.438		0.98	
<i>Azotobacter</i> .. .. .	53			0.98	(0)
<i>Corynebacterium</i> 3 .. .. .	53			0.98	(0)
.. 3 + <i>Azotobacter</i> ..	53	0.391	0.047	1.20	0.22
II.					
<i>Corynebacterium</i> Vb .. .. .	36	0.383	0.055	2.03*	
.. Vb + <i>Azotobacter</i> (tri- plicate) .. .. .	36	0.370	0.068	2.71	0.68
III.					
Control (5 N-determinations) ..	0	0.438		0.78	
<i>Azotobacter</i> .. .. .	21			0.78	(0)
<i>Corynebacterium</i> 3 + <i>Azotobacter</i> ..	21			0.72	(-0.06)
Crude anaerobic culture + <i>Azotobacter</i>	15	0.363	0.075	1.71	0.93
	33	0.336	0.102	2.02	1.24
Average gains of N, mgm. per gm. of dry matter lost:		<i>Corynebacterium</i>	3 + <i>Azotobacter</i> (series I):	4.7	
		..	Vb + .. (series II):	10.0	
		Crude anaerobe	+ .. 15 d.	12.4	
		.. ..	+ .. 33 d.	12.2	

All figures averages of duplicates unless otherwise stated.

\* Control analyses of this series lost; N-fixation therefore calculated as excess over pure culture of *Cor.* Vb.

*Experiment 9: Nitrogen fixation with hemicellulosic material:* In the experiments with straw and *Paspalum* it was thought that some fixation might be due to decomposition products of the hemicelluloses if these were attacked by the cellulose-decomposers. Most cellulose-decomposing fungi and actinomycetes can also attack hemicelluloses (Norman, 1937), but cellulose-decomposing bacteria have scarcely been studied in this respect; *Cytophaga*, according to Shrikande (1933), can decompose some of the hemicellulose in straw, and Verhulst *et al.* (1923) found strong decomposition of the hemicellulose in maize by *Cellulomonas flavigena*. Some tentative experiments were carried out with the organisms involved in the present study. Crude hemicellulose (xylan) was prepared from finely chopped wheat straw by extraction with hot 6% NaOH,

TABLE 7.  
*Nitrogen Fixation in Combined Cultures of Azotobacter chroococcum and Corynebacteria: Paspalum-material in Liquid Medium.*

Inoculum.	Incubation, Days.	Dry Matter, gm.		Nitrogen, mgm.	
		Per Culture.	Loss.	Per Culture.	Gain.
Control	0	0.459		5.91 5.70	5.81
<i>Azotobacter</i>	35			5.83	(0.02)
<i>Corynebacterium</i> 3	71	0.340	0.119	5.75	(-0.06)
„ Vb	71	0.340	0.119	5.94	(0.13)
„ 3+ <i>Azotobacter</i>	40	(a) 0.306	0.153	(c) 7.38	1.57
„	72	(b) 0.236	0.173	(d) 7.34	1.53
„	42	(a) 0.250	0.209	(a) 5.68	(-0.13)
„	42	(b) 0.261	0.198	(b) 7.59	1.78
„ Vb+ <i>Azotobacter</i>	42	(a) 0.327	0.132	(a) 6.62	0.81
„	75	(b) 0.342	0.116	(b) 6.71	0.90
„	75	(a) 0.305	0.154	(a) 7.35	1.54
„	75	(b) 0.311	0.148	(b) 6.92	1.11
Crude anaerobic cellulose-decomposers + <i>Azotobacter</i>	31			(a) 9.25 (b) 9.09	3.44 3.24
<i>Corynebacterium</i> Va+ <i>Azotobacter</i>	45	(a) 0.350	0.109	(a) 6.46	0.65
„	45	(b) 0.355	0.104	(b) 6.50	0.69

Average gain of nitrogen per gm. of dry matter lost:  
*Corynebacterium* Va+*Azotobacter*, 45 d.: 6.4 mgm.  
 „ Vb+ „ 42 d.: 7.0 mgm.  
 „ Vb+ „ 75 d.: 8.0 mgm.  
 „ 3+ „ 40-72 d.: 9.4 mgm. (excluding the abnormal culture (a) after 72d.).

TABLE 8.  
*Nitrogen Content of Cultures of Azotobacter chroococcum and Corynebacteria: Straw and Paspalum-material on Agar Surface.*

Inoculum.	Incubation, Days.	Wheat Straw.		<i>Paspalum</i> -material.	
		Total N, mgm.	Incubation, Days.	Total N, mgm.	Incubation, Days.
Control	0	3.72 3.72	0	5.94 6.07	6.01
<i>Corynebacterium</i> 3	56	3.80	76	6.16	
„ Vb	56	3.82	76	6.17	
„ Vb+ <i>Azotobacter</i>	35	(a) 3.80 (b) 3.63	75	(a) 6.23 (b) 6.13	
„ Vb „ +10 c.c. water	65	(a) 3.74 (b) 3.69	76	(a) 6.25 (b) 6.10	
„ 3+ <i>Azotobacter</i>	35	(a) 3.49 (b) —	75	(a) 6.28 (b) 6.26	
„ 3 „ +10 c.c. water	65	(a) 3.68 (b) 3.33 (?)	76	(a) 6.00 (b) 6.32	

precipitation with alcohol, washing and drying. Qualitative tests showed that, with the exception of *Cytophaga*, all aerobic cellulose-decomposers previously examined (Jensen, 1940b) could attack this material; this was shown by the formation of enzymatic zones on agar and clearing of solution media, in which organic acids were formed by the

corynebacteria, and reducing compounds (sugars?) by the other organisms. Three series of nitrogen-fixation experiments were conducted: (a) 0.4 gm. xylan, 0.2 gm. CaCO<sub>3</sub> and 20 c.c. of basal solution with 1.0% yeast extract in 50 c.c. round flasks; (b) similar, but xylan and CaCO<sub>3</sub> placed on surface of medium with 1% agar in 100 c.c. Erlenmeyer flasks; (c) as (a), but with 0.5 mgm. N as (NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub> instead of yeast extract. The corynebacteria and others demanding organic N were tested in the first and second, and the cellvibrios, actinomycetes and fungi in the third series. The results are given in Table 9.

TABLE 9.

*Nitrogen Fixation in Combined Cultures of Azotobacter chroococcum and Cellulose-decomposing Bacteria, in Crude Hemicellulose.*

Inoculum.	In Solution.			On Agar Surface.		
	Incubation, Days.	Total N, mgm.		Incubation, Days.	Total N, mgm.	
		Per Culture.	Gain.		Per Culture.	Gain.
Control .. .. .	0	1.16		0	1.30	
<i>Azotobacter</i> (1) .. .. .	20	1.39	(0.23)			
" (1) .. .. .	42	0.99	(-0.17)	48	1.22	(-0.08)
<i>Corynebacterium</i> 3 (1) .. .. .	46	0.94	(-0.22)	48	1.29	(-0.01)
" Vb (1) .. .. .	46	1.19	(0.03)	48	1.26	(-0.04)
" 3 + <i>Azotobacter</i> .. .. .	20	1.55	0.39			
" 3+ .. .. .	46	4.07	2.91	48	1.88	0.58
" Vb+ .. .. .	20	1.70	0.54			
" Vb+ .. .. .	46	2.64	1.48	48	1.56	0.26
" Va+ .. .. .	42	2.87	1.71	46	2.00	0.70
<i>Cellulomonas biazotea</i> + <i>Azotobacter</i>	42	3.50	2.34	46	2.26	0.96
<i>Bacterium</i> 43 + <i>Azotobacter</i> .. .. .	35	1.14	(-0.02)			
" G+ .. .. .	35	1.19	(0.03)			

Third series: in (NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub>-solution.

Inoculum.	Incubation, Days.	Total N, mgm.	Inoculum.	Incubation, Days.	Total N, mgm.
Control .. .. .	0	0.57	<i>Cellvibrio</i> G3 + <i>Azotobacter</i> .. .. .	42	0.60
<i>Actinomyces</i> sp. .. .. .	43	0.54	" 17+ .. .. .	42	0.59
<i>Cellovibrio</i> G2 .. .. .	43	0.63	<i>Actinomyces</i> + .. .. .	43	0.61
" G2 + <i>Azotobacter</i> .. .. .	42	0.59	<i>Micromonospora</i> + .. .. .	43	0.57
" G1+ .. .. .	42	0.63	<i>Trichoderma</i> + .. .. .	43	0.58

*Azotobacter* together with the corynebacteria gives a vigorous fixation, and *Cel. biazotea*, so little active in cellulose-media, appears remarkably effective here. Since the organic matter of the impure xylan was not all used up, it is obvious that the efficiency of fixation in cultures of *Cor.* 3 and *Cell. biazotea* exceeds 9-12 mgm. N per gm. of material decomposed. On the agar surface some nitrogen is also fixed, but the amount is only roughly one-sixth to one-third of that in solution (cf. Exp. 5). The cellulose-decomposing spore-formers *Bac.* G and *Bac.* 43, which were previously found unable to feed *Azotobacter* from cellulose (Jensen, 1940b), behave likewise with the xylan. In the cultures of cellvibrios, actinomycetes and fungi there is no trace of nitrogen fixation, and no growth of *Azotobacter* was seen.

#### B. Nitrogen Fixation in Culture Filtrates.

In the associated cultures *Azotobacter* might derive energy from the cellulose either by intercepting hydrolysis products of cellulose before these were taken up by the corynebacteria, or by utilizing the organic acids and possibly other organic by-products of these latter organisms, or finally in both ways. In order to test the value of the by-products as nutrients for *Azotobacter*, this organism was grown in filtrates from cultures of the cellulose-decomposers.

In the first experiment, *Cor.* 3 was grown for 48 days at 28–30°C. in 2.0% yeast-extract solution with filter paper and CaCO<sub>3</sub> (cf. Ser. I, Table 1), and *Cor.* Vb. was grown for 45 days at 37°C. in the same medium. After filtration through glass crucibles and determination of the loss of cellulose, the filtrates were made up to definite volumes. After addition of 0.01% FeCl<sub>3</sub>, 0.001% Na<sub>2</sub>MoO<sub>4</sub>, and 0.2% CaCO<sub>3</sub>, the filtrates were divided into portions of 50 c.c., which were distributed in 250 c.c. Erlenmeyer flasks, sterilized, inoculated with *Az. chroococcum*, and incubated at 28–30°C. A control experiment was run with *Cor.* Vb. in yeast-extract solution without filter paper. The results are set out in Table 10.

TABLE 10.

*Nitrogen Fixation by Azotobacter chroococcum in Culture Filtrates of Corynebacterium 3 and Corynebacterium Vb.*

Source of Filtrate.	Incubation, Days.	Total N, mgm.	Gain of N, mgm.	
			Per Culture.	Per gm. of Cellulose Decomposed.
I.				
<i>Corynebacterium</i> 3, 48 d., 28–30° C. . . . .	0	0.78 } 0.72 } 0.75		
Each culture ≡ 0.057 gm. decomposed cellulose*		(a) 0.92	0.17	3.0
	6	(b) 1.00	0.25	4.4
		(c) 0.96	0.21	3.7
II.				
<i>Corynebacterium</i> Vb, 45 d., 37° C. . . . .	0	2.71 } 2.64 } 2.68		
Each culture ≡ 0.193 gm. decomposed cellulose*	8	(a) 3.13	0.45	2.3
	15	(b) 3.09	0.41	2.2
		(a) 3.55	0.87	4.5
		(b) 3.64	0.96	5.0
III.				
As II, +0.5% glucose . . . . .	15	(a) 5.45	2.77	
		(b) 5.34	2.66	
IV.				
<i>Corynebacterium</i> Vb, 45 d., 37° C. . . . .	0	2.88 } 2.80 } 2.84		
Cellulose-free control medium	14	(a) 2.80	(-0.04)	
		(b) 2.78	(-0.06)	

\* Calculated on the basis of the total amount of cellulose decomposed.

In all filtrates from cellulose cultures, *Azotobacter* grew well, and the gains of nitrogen are significant; no nutrients for *Azotobacter* are produced from the yeast extract itself. Glucose, when added to the medium, is utilized with an approximately normal efficiency. Evidently the nitrogen compounds present in the filtrate, chiefly as bacterial cells, do not interfere with the fixation, nor does the filtrate appear to contain special stimulating factors (cf. Greaves *et al.* (1940), who claim to have observed a strong stimulative effect on *Azotobacter* by small amounts of amino acids. etc.).

In the main experiment the amount of soluble carbon in the filtrate was determined, and an attempt was made to estimate the nutritive value of its volatile and non-volatile constituents. *Cor.* Vb. was grown in ten replicate cultures in 250 c.c. Erlenmeyer flasks with 1.0 gm. filter paper, 1.0 gm. CaCO<sub>3</sub>, and 100 c.c. solution + 4.0% yeast extract. After incubation for 25 days at 37°C. the cultures were filtered through glass crucibles; the total loss of cellulose was 3.35 gm. The combined filtrates and washings with distilled water were made up to 1000 c.c. and treated according to the following scheme:

A. ("Original filtrate").—200 c.c. of filtrate were used for carbon determination, etc.; reducing sugars as well as neutral volatile compounds (alcohol) were found to be absent. To another 300 c.c. of filtrate were added 0.05% K<sub>2</sub>HPO<sub>4</sub>, 0.01% FeCl<sub>3</sub>, 0.1%

CaCO<sub>3</sub>, and 0.001% Na<sub>2</sub>MoO<sub>4</sub>; the medium was then distributed to 250 c.c. Erlenmeyer flasks in six portions of 50 c.c., each of which thus represented the total decomposition products of 0.167 gm. cellulose. The flasks were sterilized, inoculated with *Az. chroococcum*, and incubated at 28–30°C.

B. ("Volatile fraction").—The volatile compounds were removed from 500 c.c. of original filtrate by steam distillation after acidification with sulphuric acid. The distillate was made up to 600 c.c., of which 100 c.c. were used for carbon determination; the remaining 500 c.c. were neutralized with a small excess of CaCO<sub>3</sub>, reduced to about 200 c.c. on a water bath, made up to 240 c.c. and given additions of 0.05% K<sub>2</sub>HPO<sub>4</sub>, 0.02% MgSO<sub>4</sub>, 0.02% NaCl, 0.01% FeCl<sub>3</sub>, and 0.001% Na<sub>2</sub>MoO<sub>4</sub>. This medium was again distributed to 250 c.c. Erlenmeyer flasks in six portions of 40 c.c., each of which represented the volatile decomposition products of 0.233 gm. cellulose. The flasks were sterilized, inoculated with *Azotobacter*, and incubated, as under (A).

C. ("Non-volatile fraction").—The residue after steam distillation of 500 c.c. of original filtrate under (B) was neutralized with CaCO<sub>3</sub>, filtered and made up to 400 c.c., of which 100 c.c. were used for carbon determination, etc. (no reducing sugar). To the remaining 300 c.c. were added 0.05% K<sub>2</sub>HPO<sub>4</sub>, 0.02% MgSO<sub>4</sub>, 0.01% FeCl<sub>3</sub>, 0.001%

TABLE 11.

*Nitrogen Fixation by Azotobacter chroococcum in Culture Filtrate, and Fractions Thereof, from Corynebacterium Vb.*

Culture Series.	Incubation, Days.	Total N, mgm.	Gain of N. mgm.		
			Per Culture.	Per gm. Carbon in Culture.	Per gm. Cellulose Decomposed.
<b>I.</b>					
Original filtrate; each culture ≡ 0.167 gm. decomposed cellulose.	0	2.90 } 2.84 } 2.87			
	10	(a) 3.58 (b) lost	0.71	29	4.2
Total organic carbon at start: 25.3 } 24.2 mgm. per 23.0 } culture	16	(a) 3.67 (b) 3.67	0.80 0.80	33 33	4.8 4.8
<b>II.</b>					
Volatile fraction; each culture ≡ 0.233 gm. decomposed cellulose.	0	0.11 } 0.08 } 0.10			
	10	(a) 0.32 (b) 0.28	0.22 0.18	19 16	0.9 0.8
Total organic carbon per culture at start: 10.7 } 11.4 mgm. 12.0 }	16	(a) 0.33 (b) 0.24	0.23 0.14	20 12	1.0 0.6
<b>III.</b>					
Non-volatile fraction; each culture ≡ 0.209 gm. decomposed cellulose.	0	3.18 } 3.19 } 3.19			
	10	(a) 3.97 (b) 3.81	0.78 0.62	38 30	3.7 3.0
Total organic carbon per culture at start: 20.7 } 20.7 mgm. 20.7 }	14	(a) 3.90 (b) 3.86	0.71 0.67	34 32	3.4 3.2
<b>IV.</b>					
Filtrate from crude culture of anaerobic cellulose decomposers. Each culture ≡ 0.137 gm. decomposed cellulose.	0	0.71 } 0.71 } 0.71			
	7	(a) 1.38 (b) 1.20	0.67 0.49	42 30	4.9 3.6
Total organic carbon per culture at start: 16.9 } 16.1 mgm. 16.0 } 15.4 }	14	(a) 1.33 (b) 1.52	0.62 0.81	38 50	4.5 5.9
Do., sterile control	14	0.80	(0.09)	—	—

$\text{Na}_2\text{MoO}_4$ , and 0.1%  $\text{CaCO}_3$ . The medium was then divided into six portions of 50 c.c., each, representing the non-volatile decomposition products of 0.209 gm. cellulose. Erlenmeyer flasks were sterilized, inoculated and incubated as before.

The results of the nitrogen-fixation experiments are seen in Table 11, which includes a series with filtrate from a crude culture of anaerobic cellulose-decomposing bacteria:  $2 \times 250$  c.c. basal solution with 2.0 gm. filter paper, 0.5 gm.  $\text{CaCO}_3$ , and 0.1 gm. dry matter of *Azotobacter* as source of N. Cultures were incubated 59 days at  $37^\circ\text{C}$ .; 2.05 gm. cellulose had been decomposed. The filtrate was treated as under (A).

The data show that *Azotobacter* utilizes the carbon compounds of the original filtrate very economically, fixing more than 30 mgm. N per gm. of C present, or close to 5 mgm. per gm. of cellulose decomposed (cf. Table 10). Of this total fixation only a minor part appears to be due to the volatile decomposition products, which are also of lesser value per unit of carbon. The bulk of the fixation (3.0-3.7 mgm. N per gm. cellulose) takes place at the expense of the non-volatile products, which appear to be good nutrients, some 30 to 40 mgm. N being fixed per gm. C present; this is similar to the gain in ordinary *Azotobacter*-cultures fixing 12 to 16 mgm. N per gm. of glucose. The decomposition products of the anaerobic cellulose-decomposers seem to be at least equally valuable.

As mentioned above, reducing sugars or substances giving rise to such compounds on acid-hydrolysis were not present in the culture filtrates. A control experiment was therefore made to test the nutritive values of various organic acids in concentrations similar to the carbon content of the filtrates and their fractions. This experiment is recorded in Table 12. The culture medium consisted of 50 c.c. basal solution in 250 c.c. Erlenmeyer flasks, with a trace of  $\text{CaCO}_3$  and calculated amounts of organic acids as Ca-salts.

TABLE 12.  
*Nitrogen Fixation by Azotobacter chroococcum in Dilute Solutions of Organic Acids.*

Series.	Total N per Culture, mgm.*	Gain of N, mgm.		
		Per Culture.	Per gm. Org. C.	Per gm. Acid.
I. 25 mgm. C as formic acid.				
Control .. .. .	0.03	—	—	—
<i>Azotobacter</i> inc. 14 d. .. .. .	0.05	(0.02)	—	—
II. 25 mgm. C as acetic acid.				
Control .. .. .	9.05	—	—	—
<i>Azotobacter</i> inc. 12 d. .. .. .	0.71	0.66	26.6	10.6
III. 50 mgm. C as acetic acid.				
Control .. .. .	0.02	—	—	—
<i>Azotobacter</i> inc. 17 d. .. .. .	0.80	0.78	15.8	6.3
IV. 25 mgm. C as lactic acid.				
Control .. .. .	0.04	—	—	—
<i>Azotobacter</i> inc. 12 d. .. .. .	0.84	0.80	32.0	12.8
V. 25 mgm. C as gluconic acid.				
Control .. .. .	0.07	—	—	—
<i>Azotobacter</i> inc. 8 d. .. .. .	0.73	0.66	26.6	9.8
„ „ 14 d. .. .. .	0.79	0.72	27.8	10.8

\* Averages of duplicates.

Formic acid is not utilized (cf. Gainey, 1928), but acetic acid, especially in the lower concentration, is a favourable source of carbon; the fixation of about 26 mgm. N per gm. acetate-C is consistent with the gain of 12-20 mgm. per gm. C in the mixture of formic and acetic acid which represents the "volatile fraction" in Table 11. Lactic acid is an even better nutrient (cf. Mockeridge, 1915); the fixation of 32 mgm. N per gm. lactate-C agrees with the corresponding figures for "original filtrate" and "non-volatile

fraction" in Table 11. Finally, gluconic acid appears to be only a moderately good source of carbon. So far the results suggest that the bulk of the non-volatile constituents is represented by substances not identical with reducing sugars, but similar or superior to lactic acid in nutritive value.\*

### C. Influence of Aeration on the Formation of Organic By-products.

The slight or negligible nitrogen fixation in cultures with cellulosic material in direct contact with the air (Tables 5, 8, and 9) suggests that the organic by-products under these conditions are formed in smaller amounts or consist of less valuable nutrients (formic acid?). An experiment was designed to find the quantities of total free acid produced from cellulose under varying conditions of aeration. *Cor.* 3 and *Cor.* Vb were grown in 50 c.c. of basal solution with 2.5% yeast extract and 0.5 gm. filter paper, but no CaCO<sub>3</sub>: (a) in 100 c.c. round flasks, the paper thus submerged in a layer of liquid about 2.5 cm. deep; (b) in 250 c.c. Erlenmeyer flasks, layer of liquid about 1 cm. deep, and (c) as (b), but paper resting on a raft of glass tubes of 1 cm. diameter, thus being in contact with the atmosphere. Cultures were incubated at 28–30°C., then filtered through glass crucibles; loss of cellulose was determined, and the filtrates were titrated with approximately 0.035 n NaOH to the same reaction (pH about 7.5) as filtrate from the sterile control medium. The results are given in Table 13.

TABLE 13.

*Influence of Access of Oxygen on Production of Acid from Cellulose by Corynebacteria.*

	Method of Placing Filter Paper.	Cellulose Lost, gm.	Total Free Acid, c.c. 0.1n.			
			Per Culture.	Per gm. Cellulose Lost.		
<i>Corynebacterium</i> 3 (triplicate) inc. 26 d.	Deep layer .. .. .	0.048	1.49	31.0		
	Shallow layer .. .. .	0.045	0.98	21.8		
	In contact with air .. .. .	0.062	0.85	13.7		
<i>Corynebacterium</i> Vb (duplicate).	Deep layer .. .. .	22 d. . . . .	0.032	1.29	40.3	
		42 d. . . . .	0.042	1.58	37.6	
		22 d. . . . .	0.041	1.23	30.0	
	Shallow layer .. .. .	42 d. . . . .	0.064	0.99	15.5	
		In contact with air .. .. .	22 d. . . . .	0.090	0.98	10.9
			42 d. . . . .	0.127	1.15	9.1

This simple experiment shows clearly that the formation of acid in proportion to cellulose decomposition falls off markedly with an increasing degree of aeration, especially in *Cor.* Vb. It is interesting to compare this with the results of nitrogen-fixation experiments on agar surfaces (Table 5), where *Cor.* 3 caused a slight fixation, but *Cor.* Vb none.

Another experiment was designed to test the nutritive value of the by-products formed under complete or restricted aeration. *Cor.* Vb was grown in two series, each of five replicate cultures; the medium consisted of 1.0 gm. filter paper, 0.5 gm. CaCO<sub>3</sub>, and 60 c.c. basal solution with 3.0% yeast extract. Five cultures were grown in 100 c.c. round flasks, and five in 500 c.c. Erlenmeyer flasks, the paper resting on a raft of glass tubes as above. After incubation for 20 days at 37°C. the cultures were filtered, and loss of cellulose determined: 1.23 gm. in the five round flasks, and 0.60 gm. in the five Erlenmeyer flasks. The combined filtrates and washings from each series, before HCl-treatment, were reduced in volume on the water bath, and then made up to

\* It should not be forgotten that some of the carbon in the culture filtrates is represented by proteid or related matter (bacterial cells, residues from the yeast extract, etc.). If this, as is probable, remains inaccessible to *Acetobacter*, the gain of nitrogen per unit of available carbon would be considerably higher than it appears. The amount of available carbon cannot be readily ascertained, but if for each part of N in the medium we allow for three parts of protein-C, the gains of nitrogen per gm. of "non-protein carbon" in Series I, III and IV of Table 11 would be in the neighbourhood of 50-60 mgm.—a very high degree of economy.

300 c.c., to which were added 0.05%  $K_2HPO_4$ , 0.01%  $FeCl_3$ , 0.001%  $Na_2MoO_4$ , and 0.1%  $CaCO_3$ . Each lot of medium was divided into six portions of 50 c.c.; one of these was used for carbon determination, and the rest were placed in 250 c.c. Erlenmeyer flasks, sterilized, inoculated with *Az. chroococcum*, and incubated. Table 14 gives the results.

TABLE 14.  
*Influence of Access of Oxygen on Production of Food Substances for Azotobacter by Corynebacterium Vb.*

Culture Series.	Incubation, Days.	Total N in <i>Azotobacter</i> Cultures.	Gain of N, mgm.		
			Per Culture.	Per gm. Carbon in Culture.	Per gm. Cellulose Decomposed.
Paper in contact with atmosphere.	0	2.19 } 2.20	—	—	—
Each culture ≡ 0.100 gm. decomposed cellulose.	10	2.21 } 2.36	(0.16)	(7.0)	(1.6)
Total organic carbon at start :	14	2.46 } 2.41	(0.21)	(9.2)	(2.1)
25.2 } 22.8 mgm.		2.36 }			
20.5 }					
Paper submerged in solution.					
Each culture ≡ 0.205 gm. decomposed cellulose.	0	2.11 } 2.16	—	—	—
Total organic carbon at start :	10	2.22 } 3.30	1.14	22	5.5
53.5 } 52.3 mgm.	14	3.44 } 3.34	1.18	23	5.7
51.0 }		3.24 }			

The filtrate from the well-aerated Erlenmeyer flask cultures is seen to be very poor in soluble carbon compounds, and these are only inferior nutrients for *Azotobacter*; indeed, the gain of nitrogen is so slight as to be of questionable significance. The filtrate from cellulose decomposed under restricted aeration in round flasks contains a much larger amount of organic matter, which also permits a stronger nitrogen fixation per unit of carbon present. It seems clear that not only does restricted access of oxygen result in the formation of larger quantities of organic by-products, but these are also qualitatively better nutrients for *Azotobacter*.

The nitrogen fixation by *Azotobacter* in culture filtrates from the cellulose-decomposers is seen generally to be of the order of about 4 to 6 mgm. N per gm. of cellulose decomposed, i.e., about one-half of that which is found in associated cultures. Two explanations might be offered for the fact that more nitrogen is fixed when the two organisms work in association: *Azotobacter* might have access to intermediate hydrolysis products of the cellulose, or the oxygen tension in the medium might be lowered by the growth of the aerobic *Azotobacter* and the cellulose-decomposers thus be induced to form metabolic by-products in larger quantity and of higher value for *Azotobacter* than they would in pure culture. If the second possibility holds, one would expect the oxidation-reduction potential of the medium to be lower in associated cultures than in pure cultures of the cellulose-decomposers (cf. Vartiovaara, 1938, who observed only a slight decrease in the oxidation-reduction potential in cultures of cellulose-decomposing fungi, but very strong reduction in cultures of fungi + nitrogen-fixing clostridia). An attempt was made to find out if this is the case.

*Cor. Vb* was grown, alone or together with *Az. chroococcum*, in basal solution with 1.0% yeast extract,  $CaCO_3$  and strips of filter paper—(a) in a deep column of liquid, viz., 10 c.c. of medium in 1.2 cm. wide test tubes—and (b) a more shallow layer allowing better aeration: 5 c.c. of medium in test tubes 2 cm. wide. Cultures and sterile controls were incubated at 28–30°C.; at intervals, duplicate tubes were taken out and the oxidation-reduction potential (Eh) measured electrometrically, using a bright platinum foil electrode, with a 3.5 n KCl-HgCl-electrode as standard half-cell. (On oxidation-

reduction potentials in general and their application to bacteriological problems, see Hewitt, 1936.) After Eh-measurement, the pH-value of each tube was determined by means of a glass electrode. The results, averaged and corrected to pH 7.0, are shown graphically in Text-figure 1. The conventional factor of 0.070 volt per unit pH was used for the correction; it is to be remembered that in oxidation-reduction systems of unknown nature this factor has only an approximate meaning (Hewitt, 1936).

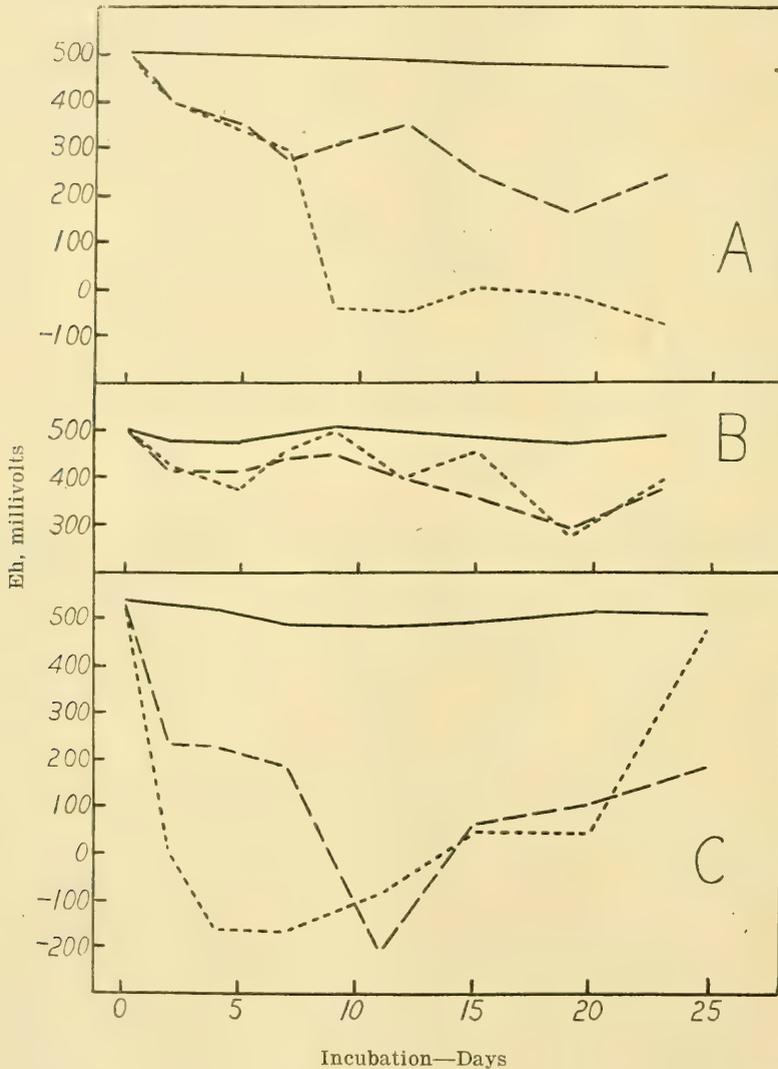


Fig. 1.—Oxidation-reduction potentials (Eh) in pure and combined cultures. A, filter paper in a deep layer of medium (10 c.c.). B, filter paper in a shallow layer of medium (5 c.c.). C, hemicellulose. Continuous lines: sterile medium; broken lines: *Corynebacterium Vb*; dotted lines: *Cor. Vb* + *Az. chroococcum*.

The graph shows that the Eh-values of the sterile medium remain practically stationary, and *Cor. Vb* alone causes only a moderate decrease. In the associated cultures in the deep layer of medium, *Azotobacter* started to make a good growth after one week; at the same time the Eh-values showed a sudden decline, and remained from then on at the level characteristic of most aerobic bacteria (Hewitt, 1936). In the

shallow layer of medium (wide tubes) the growth of *Azotobacter* was scant, and no effect on Eh was noticeable.

A similar experiment, shown in Figure 1c, was carried out in solution of 0.5% hemicellulose (crude xylan), in deep layers of medium only. The corynebacterium grows more rapidly in this medium than on cellulose, and the fall in Eh of pure cultures is quite pronounced, reaching a very low minimum after 11 days, but is much more rapid and persistent in the presence of *Azotobacter*.

Upon the whole, the experiments indicate clearly that under limited access of oxygen (deep layers of solution) *Azotobacter* is capable of creating conditions favourable for the production of organic compounds from the cellulose, and this is probably why nitrogen fixation is stronger in associated cultures than when the organisms exist in "metabiosis" (*Azotobacter* in culture filtrates). It is of course not excluded that intermediate products may also be used, but this seems unlikely, since reducing sugars can never be detected in pure cultures of the corynebacteria, even when deprived of oxygen, and since the nitrogen fixation is so slight in cellulosic material directly exposed to the air, where the conditions for interception by *Azotobacter* should be the best possible.

#### D. The Decomposition Products of Cellulose.

An attempt was made to identify the decomposition products in pure cultures of the cellulose-decomposers, especially *Cor. Vb*. The determination of the volatile products presented no difficulties. Ethyl alcohol and other neutral volatile compounds were not found; among acidic compounds, only formic and acetic acid in varying proportions were detected; a summary of the main results is given in Table 15. In cultures with ample supply of nitrogen (peptone) formic acid is the chief volatile product, which in *Cor. 3* accounts for no less than 60% of the carbon in the decomposed cellulose. Formic acid was also the only volatile product in other cultures of *Cor. Vb* with straw and glucose.

TABLE 15.  
*Decomposition Products of Cellulose.*

Experiment Number.	Loss of Cellulose, gm.	Decomposition Product Found.	% C in Decomposed Cellulose Accounted for.
I. <i>Corynebacterium Vb</i> , 15 gm. filter paper; solution of 2.5% yeast extract. Inc. 90 d. 28-30° C.	1.22	Total volatile acid (partly formic), 6.5 c.c. 1/n, containing 0.077 gm. C.	14.3
II. <i>Corynebacterium Vb</i> , 18 gm. filter paper; solution of 1% yeast extract, 0.5% peptone. Inc. 12 d. 28-30° C.	7.75	Volatile acids, formic and acetic, containing 0.710 gm. C.	20.3
III. <i>Corynebacterium Vb</i> , 6 gm. filter paper; solution of 1% yeast extract, 0.5% peptone. Inc. 20 d. 37° C.	4.38	Formic acid, 1.65 gm. . . . .	22.2
		Acetic acid, 0.341 gm. . . . .	7.0
		Lactic acid, 0.098 gm. . . . .	2.0
			} 31.2
IV. <i>Corynebacterium 3</i> , 5 gm. filter paper; solution of 1% yeast extract, 0.2% peptone. Inc. 24 d. 37° C.	1.84	Formic acid, 1.91 gm. . . . .	60.4
		(Acetic acid, nil) . . . . .	(0)
		Lactic acid, 0.050 gm. . . . .	2.5
			} 62.9

The non-volatile products, on the other hand, proved most difficult to determine, because of the necessity of adding yeast extract and peptone to the medium in order to obtain a vigorous decomposition. In Exp. I, Table 15, the calcium salts of the non-volatile acids other than lactic acid were precipitated with 80% alcohol according

to the method of Birkinshaw and Raistrick (1931). Most of the total carbon in the culture filtrate was found in this precipitate, as shown below:

Carbon represented by 1.22 gm. decomposed cellulose .. .. .	0.536 gm.
Total carbon found in culture filtrate .. .. .	0.427 gm.
<hr/>	
Loss (probably CO <sub>2</sub> ) .. .. .	0.109 gm.
Analysis of filtrate:	
Carbon recovered as volatile acids .. .. .	0.077 gm.
Carbon recovered as non-volatile acids (alcohol-precipitate) .. .. .	0.362 gm.
Carbon recovered as residual compounds (lactic acid?) .. .. .	0.072 gm.
<hr/>	
Total .. .. .	0.421 gm.
<hr/>	

The precipitate of calcium salts contained no compounds reducing Fehling's solution (ketonic and aldehydic acids absent), but decolourized KMnO<sub>4</sub> and gave slight reduction of ammoniacal AgNO<sub>3</sub>; oxalic and tartaric acids were not found; the iodoform test for citric acid was doubtful. The experiment thus suggests that most of the food for *Azotobacter* consists of unidentified organic acids; the calcium salts of these must be relatively soluble, since no precipitate was formed on addition of calcium acetate before alcohol was added.

In the solutions containing peptone the method of Birkinshaw and Raistrick (1931) proved unsuccessful, and gave precipitates consisting mainly of peptone or amino acids. It was found that the direct determination of lactic acid in the culture filtrates, using the method of oxidation to acetaldehyde with KMnO<sub>4</sub>, was vitiated by the presence of other compounds that also yielded aldehydes. Small quantities of lactic acid were found in ether-extracts of acidified dry residues of the filtrates (Table 15). Carbon determinations in culture filtrates from Exp. II and III, however, showed a greater content of soluble carbon than could be represented by the sum of the volatile acids, lactic acid, and peptone. Thus there must be other compounds present, but since no reduction of Fehling's solution was found, these could not include cellobiose, glucose, aldehydic or ketonic acids. The possible formation of gluconic acid was thought of, and therefore an attempt was made to isolate this compound from cultures of *Cor. Vb* by the method of Müller (1928): precipitation with lead subacetate in ammoniacal solution, decomposition with H<sub>2</sub>S-gas, conversion into Ca-salt, and crystallization from 30% alcohol. Only flocculent precipitates of a proteid-like appearance were found in the final stage, and in one case a precipitate resembling a mixture of proteids and calcium formate. Like the cellulose-decomposing bacteria of Khouvine (1923) and Simola (1931), the corynebacteria thus seem to produce compounds that cannot readily be identified. Finally it may be mentioned that a trace of reducing sugar was found in a culture of *Cor. Vb*, treated with toluene and incubated 4 weeks at 37°C., 1.74 gm. cellulose being decomposed; the sugar yielded an osazone resembling that of glucose (long needles, melting point 206°C.).

In general it appears that the formation of metabolic products varies greatly with the experimental conditions, and that the non-volatile compounds which represent the best sources of carbon for *Azotobacter*, are formed chiefly in media with a low nitrogen content, such as in Exp. I, Table 15. The associated cultures exist in such media poor in nitrogen, and therefore the metabolism of the cellulose-decomposers is under these conditions probably quite different from that in pure cultures with abundant supply of nitrogen. This is borne out by the fact that up to 14 mgm. N may be fixed per gm. of cellulose decomposed (Table 1); assuming that *Azotobacter* may fix 1 part of nitrogen per 20 parts of carbon consumed (the maximal efficiency observed according to Table 11), such a fixation would require the consumption of 280 mgm. carbon—i.e., nearly two-thirds of the cellulose-carbon must be converted into nutrients favourable for *Azotobacter*, and hence the production of compounds like carbon dioxide and formic acid must be very low.

*General Conclusions.*

Some conclusions of general interest may be drawn from these data. Firstly it appears that the fixation of some 10 mgm. nitrogen per gm. of cellulosic material decomposed, which has so frequently been observed in impure cultures or in soil, may be due to the activity of cellulose-decomposing corynebacteria in co-operation with *Azotobacter*. Secondly, it was found (Jensen, 1940a) that nitrogen fixation on the basis of cellulosic materials like straw, etc., only takes place in soil of high moisture content. This phenomenon finds a natural explanation in the fact that a limited access of oxygen is necessary for a copious formation of organic by-products by the corynebacteria; it is also a fact that exclusion of oxygen is necessary for development of the obligate anaerobic cellulose-decomposers as well as for production of soluble organic compounds by the true aerobic cellulose-decomposers (cellvibrios, fungi, etc.).

As to the agricultural significance of the association between *Azotobacter* and cellulose-decomposing corynebacteria, it would seem that arable soils under the climatic conditions obtaining in Australia would rarely offer a favourable environment, even if generally favourable for *Azotobacter*, as previously discussed (Jensen, 1940a). The process may be of high importance under conditions where prolonged partial exclusion of oxygen coincides with a favourable temperature, such as in compost or manure heaps, or irrigated land rich in organic matter of a wide C/N ratio. Cellulosic waste materials might therefore through the activity of these organisms be used as a profitable source of nitrogenous manure.

## SUMMARY.

Combinations of pure cultures of various species of *Azotobacter* and cellulose-decomposing corynebacteria can fix about 6 to 14 mgm. nitrogen per gm. of cellulose decomposed. Filter paper, grass and straw can be utilized with approximately the same efficiency, but the last material less rapidly. Hemicellulose, in the form of crude xylan, can also be utilized with a high efficiency.

Nitrogen fixation of this magnitude was observed only when the cellulosic material was submerged in liquid medium. Under strictly aerobic conditions (decomposing material in direct contact with the air), the fixation was less, or negligible (0 to 2 mgm. per gm.).

*Azotobacter* was able to grow in filtrates from cellulose-cultures of the corynebacteria, and to fix as much as 5.7 mgm. nitrogen at the expense of the decomposition products of each gm. of cellulose; most of the fixation took place by utilization of the non-volatile decomposition products. Under completely aerobic conditions the quantity of organic decomposition products of cellulose, as well as the value of these compounds as nutrients for *Azotobacter*, was less than under restricted access of oxygen.

The oxidation-reduction potential in combined cultures of *Azotobacter* and corynebacteria in cellulose-media reached a considerably lower level than in pure cultures of the corynebacteria, provided that a deep layer of liquid medium was used.

In pure cultures of the corynebacteria, the volatile decomposition products of cellulose consisted exclusively of formic and acetic acid in varying proportions, the formic acid accounting for as much as 60% of the carbon in the decomposed cellulose. Small amounts of lactic acid were found among the non-volatile products, besides certain not readily identifiable compounds, probably organic acids. Reducing sugars, ketonic acids and aldehydic acids were absent in normal cultures, but traces of glucose were detected in cultures treated with toluene.

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## PHYSIOLOGICAL STUDIES IN DROUGHT RESISTANCE. I. TECHNIQUE.

By ERIC ASHBY and VALERIE MAY.\*

*(From the Botany School, University of Sydney.)*

(Two Text-figures.)

[Read 28th May, 1941.]

*Introduction.*

Some ten years ago the study of drought resistance received a great impetus from the work of Maximov and his colleagues (1929, 1931). It was established that drought resistance was not usually concerned with conservation of water or with economy of transpiration, but rather with ability to endure wilting unharmed. There are indeed instances where a plant survives drought by virtue of its extensive root system, or its succulent water storage tissue; but the most common cause of xerophytism is a property of the protoplasm to withstand desiccation, analogous perhaps to the drought resisting properties of a resting seed. Zalenski (1904), Alexandrov (1922), Tumanov (1927), and others showed that for certain plants there is a close correlation between anatomical structure and drought resistance, but this xeromorphy is a consequence of dry conditions rather than the means of overcoming them.

All these researches gave a fresh orientation to work on drought resistance, and there has followed a steady flow of papers, especially from the U.S.S.R. and the U.S.A.; a critical summary of these will be presented in a later contribution to this series. One of the facts which emerge from this copious literature is that the current methods of measuring drought resistance are unsatisfactory. The wilting of the detached leaf, a criterion used by Paltridge and Mair in this country (1936), bears no relation to xerophytism. The percentage mortality after exposure to a hot, dry draught (Shirley, 1934) neglects the fact that actual death from drought is uncommon. An arrested development of the plant is the more usual response to drought, and no simple relation has yet been demonstrated between mortality rate and drought resistance in the sense understood by the agriculturist.

In 1931 one of the present writers (E.A.) carried out some preliminary experiments on a method of estimating drought resistance which does not involve the death of the plant, namely, by measuring the rate of growth immediately after a period of drought is over. A plant which succumbs to drought does not necessarily die, but it does not resume growth when the rain comes; resumption of growth is therefore an appropriate measure of drought resistance.

Studies are now in progress in this laboratory which apply this technique to the analysis of the effects of mineral fertilizers on drought resistance. The purpose of the present paper is to set out some preliminary data which illustrate the use of the new technique. The data refer to an experiment on the effect of nitrogen on the drought resistance of two varieties of oats, Algerian and Fulghum. Algerian, which is reputed to be drought resistant, is grown on the tablelands of New South Wales, and Fulghum is grown on the coast.

*Method.*

The plants were grown in sand cultures in a plant-house from March to June, 1939. Forty-eight unglazed earthenware pots, ten inches in diameter, were filled with washed river sand overlying a base of road metal and pot crocks for drainage. The pots were arranged in two blocks in the plant-house. Each block contained eight randomized treatments, and there were in each block three pots to each treatment. The plan of the experiment was as follows:

Two varieties (Algerian, A, and Fulghum, B).

Two levels of manuring (high nitrogen, +N, and low nitrogen, -N).

\* This paper was prepared when Miss Valerie May was a Linnean Macleay Fellow of the Society in Botany.

Two water treatments (normal watering, C, and drought, D).

Two blocks in the plant-house.

Three replicate pots in each treatment.

The use of pots ensured that any differences in drought resistance due to root development were eliminated. Errors due to variation of light and temperature through the plant-house were minimized by changing the position of the pots within blocks twice weekly. During the experiment temperature and humidity in the plant-house were recorded with a thermohydrograph; a summary of the readings is presented in Table 1,

TABLE 1.

Summary of Temperature and Humidity Readings in Plant-house and Details of Experiment on Drought Resistance.

Date.	Weekly Temp.		Weekly Humidity.		Height <sup>1</sup> Measured.	Fertilizer Applied.	Remarks.
	Min.	Max.	Min.	Max.			
Mar. 8 ..							Grain soaked in distilled water.
" 9 ..							Grain sown in pots, watered with tap water.
" 13-19	70	100	50	98			
" 20-26	60	96	58	100			
" 21					x	x <sup>5</sup>	1-2 leaves visible, height measured to tip of highest leaf.
" 23 ..							Plants reduced to 12 per pot. <sup>3</sup>
" 27-							
Apr. 2..	64	91	38	99			
Mar. 30 ..					x	x	3 leaves; manurial and varietal effects visible.
Apr. 3-9	68	98	50	100			All plants sprayed with nicotine and soap solution.
" 6 ..							All pots watered. DROUGHT BEGUN.
" 10-16	63	100	51	100			
" 11 ..					x		Dry weight samples. N-deficiency symptoms evident.
" 12 ..							Controls watered. <sup>3</sup>
" 17-23	56	97	51	100			
" 20 ..					x		Inflorescences and tillers appear in B+ND. <sup>4</sup>
" 22 ..					x		
" 24-30	54	94	34	99			
" 27 ..					x		Inflorescences in all treatments of B; none in A. <sup>4</sup>
May 1-7	59	95	59	100			Still adequate water in -ND plants (guttation).
" 4 ..					x		
" 8-15	56	99	55	100			
" 11 ..					x		Evidence of leaching in +NC.
" 12 ..							Dry weight samples taken.
" 13 ..						x	DROUGHT BROKEN. Nitrogen applied to all pots.
" 14 ..					x		Heights measured at frequent intervals till June 19 (for dates see Text-figure 1).
" 16-21	70	94	80	100	(x)		
" 18 ..					x		Tillering begun in all treatments; A later than B.
" 22-28	58	90	57	97	(x)		
" 24 ..						x	Nitrogen supplied to all pots.
" 29-							
June 4	60	84	75	96	(x)		
June 5-11	58	84	71	96	(x)		
" 12-18	62	90	78	100	(x)		
" 15 ..						x	Nitrogen supplied to all pots.
" 19-25	60	93	59	94			

(x) means that more than one measurement was taken in the week.

<sup>1</sup> This includes tillers present.

<sup>2</sup> Plants left of average size for each variety.

<sup>3</sup> Water was added whenever necessary after this date.

<sup>4</sup> B = Fulghum, A = Algerian; D = drought treatment; +N = high nitrogen.

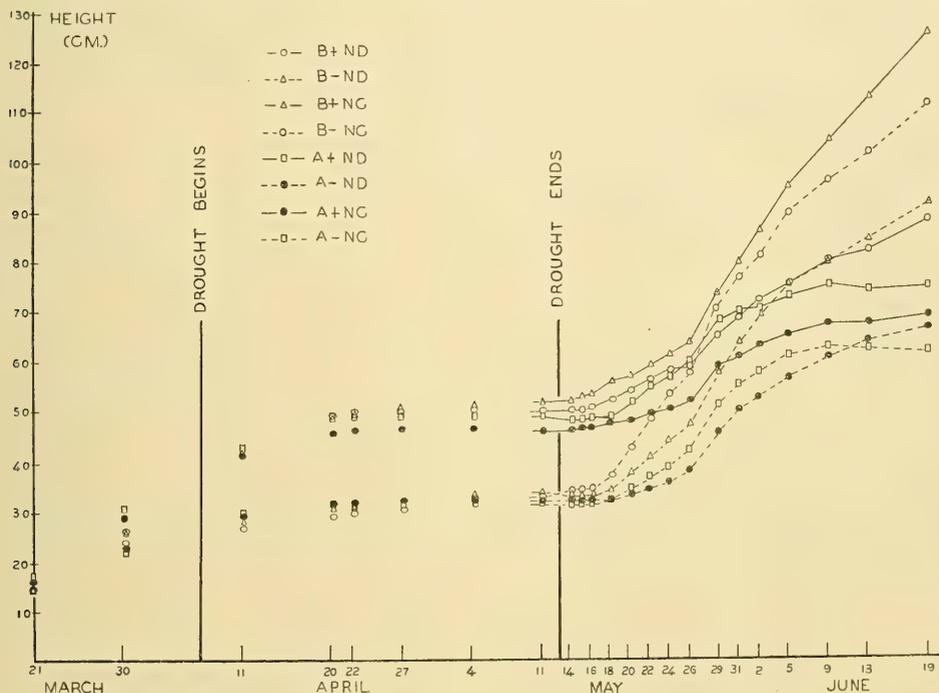
<sup>5</sup> The composition of the fertilizers was as follows:

	Gm. per Pot.						
	High Nitrogen.		Low Nitrogen.		13.v, 24.v, 15.vi		
	21.iii, 30.iii		21.iii	30.iii			
Nitrogen as Ca(NO <sub>3</sub> ) <sub>2</sub>	..	..	..	0.042	0.0013	0.0053	0.021
Potassium as KH <sub>2</sub> (PO <sub>3</sub> ) <sub>3</sub>	..	..	..	0.029	0.029	0.029	0.029
Magnesium as MgSO <sub>4</sub>	..	..	..	0.018	0.018	0.018	0.018
Calcium as CaSO <sub>4</sub>	..	..	..	0.000	0.058	0.052	0.030

together with details as to the procedure of the experiment. At the close of the experiment data were obtained on the water contents of, and rate of water loss from, plants under the different treatments. These data are too inconclusive to merit discussion at this stage.

#### Discussion.

The data on heights of plants are presented graphically in Text-figure 1. At the onset of the drought the plants fell into two classes in respect of size: those with adequate nitrogen and those starved of nitrogen. From 6th April to 14th May there was little growth in any of the plants, whether subjected to drought or not. It was



Text-fig. 1.—Height of plants from 21st March to 19th June. For explanation of symbols see text.

desirable to maintain the whole population at about the same "physiological age" during this period; this was accomplished by watering the controls with tap water and not with nitrogen. In the controls nitrogen was leached from the sand cultures; so that growth was retarded in the controls by temporary nitrogen deficiency, and in the treated plants also through drought. On 13th May, when all the plants were watered and treated with nitrogen, their heights still fell into "high nitrogen" and "low nitrogen" categories. Frequent readings of height were taken after this in order to trace the curves of recovery from drought. From an inspection of these curves (14th May to 19th June) the following comments can be made:

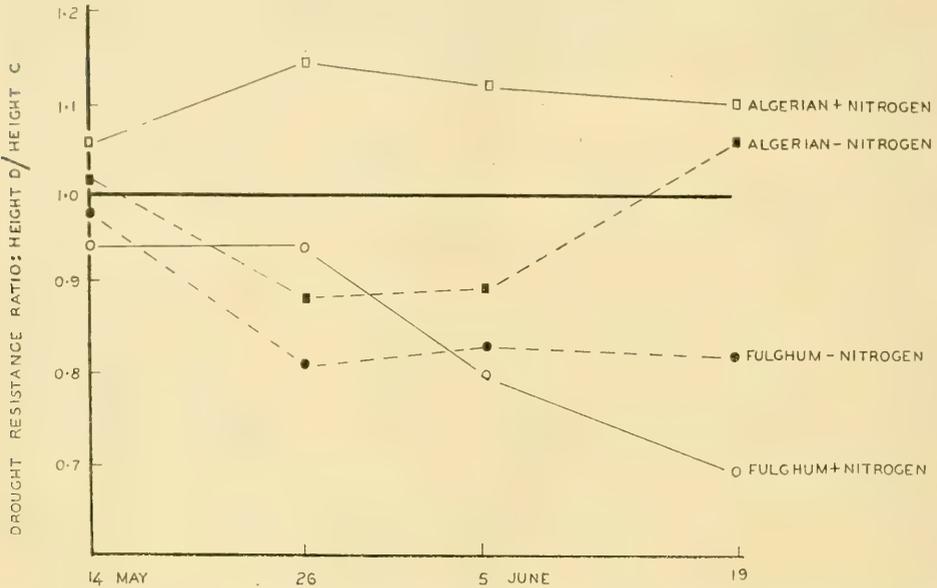
(a). Fulghum (controls) grew more rapidly and over a longer period than Algerian (controls).

(b). There is no striking difference between the recovery curves of drought and control Algerian oats, but there is a notable difference between the recovery curves of drought and control Fulghum; in other words Algerian has suffered from the drought less seriously than Fulghum.

(c). The "physiological maturity" of Algerian (fully manured and watered) as estimated from the shape of the growth curve, is reached early in June, whereas Fulghum is still growing rapidly in mid-June. The suggestion may be made, and it

is not inconsistent with the statistical analysis, that the superior drought resistance of Algerian in this experiment is related to its earlier physiological maturity, i.e., the higher the growth rate, the greater is the susceptibility to drought.

(d). Drought resistance should be measured not in terms of absolute recovery but in terms of recovery relative to the control. In Text-figure 2 the data for drought resistance are set out in this way.



Text-fig. 2.—Ratio of height of plant subjected to drought to that of control. Note that damage to Fulghum through drought increases with time, whereas in Algerian there is no evidence of damage due to drought.

(e). The deleterious effect of drought persists, and indeed increases, after the drought is over. Even five weeks after watering was resumed those plants of Fulghum which were subjected to drought were growing less rapidly than the controls.

A statistical analysis of the data yields further information. Details of the treatment are given in an appendix; in Table 2 the results of the analysis of growth after the drought are summarized. A further analysis into linear, quadratic and cubic components of the variance of real figures (not logarithms) revealed no features of biological interest beyond those already evident from the text-figures. The biological interpretation of the results set out in Table 2 is as follows:

TABLE 2.

Summary of significance of variables and interactions in the growth of Algerian and Fulghum oats, with high and low levels of nitrogen, after drought. Data calculated from the logarithms of readings of height. S=99 per cent. significance; s=95 per cent. significance.

	May.			June.			
	14	20	26	1	7	13	19
<i>Variables :</i>							
Variety .. .. .	s	S	S	S	S	S	S
Nitrogen .. .. .	S	S	S	S	s	s	s
Drought .. .. .	—	—	—	s	s	S	S
<i>First order interactions :</i>							
Variety × Nitrogen .. .. .	—	—	s	s	—	—	—
Variety × Drought .. .. .	—	s	s	s	S	S	S
Nitrogen × Drought .. .. .	—	—	s	—	—	—	—

(a). *Variety*: A differential growth rate between varieties is a common phenomenon. Its interest here is that the relatively vigorous growth of Fulghum after 14th May may be the immediate cause of its having a lower drought resistance than Algerian.

(b). *Nitrogen*: The experiment was so arranged that half the plants showed symptoms of nitrogen deficiency before the drought began, and all were given an adequate supply of nitrogen after the drought was over. The odds in favour of a significant effect were reduced by this late application of nitrogen, but on 19th June they still remain greater than 95:5. An initial mineral deficiency is not offset by a late application of fertilizer; this is a familiar fact in practical agriculture.

(c). *Drought*: It is noteworthy that the effect of drought on the subsequent behaviour of the plant is not significant until two weeks after watering is resumed; and that thereafter significance increases with time.

(d). *Variety*  $\times$  *Nitrogen*: There is a specific varietal response to nitrogen, in favour of Fulghum, analogous to that observed by Gregory and Crowther (1928, 1931) for barley.

(e). *Variety*  $\times$  *Drought*: The differential effect of drought on the two varieties is evident from Text-figure 2; the analysis shows that this difference is significant and continues to increase after drought is over. Algerian suffers less than Fulghum from drought, probably on account of its lower relative growth rate, and quite apart from any advantage conferred by the root system, a factor eliminated in this experiment.

(f). *Nitrogen*  $\times$  *Drought*: Since the subject of these studies is the effect of mineral elements on drought resistance it would be premature to discuss at this stage the influence of nitrogen. It is sufficient to point out that on one occasion (26th May) there was a significant interaction of nitrogen and drought resistance. The indication is that a high level of nitrogen (perhaps through its effect on the growth rate) renders the variety Fulghum more susceptible to the harmful effects of drought. A statistical analysis of the dry weight data (collected on 11th April and 12th May) confirms this.

In conclusion, it appears that the method of measuring drought resistance by rate of growth after drought has various advantages over the methods used hitherto. Frequent observations of shoot length are easy to take; recovery after drought is a feature of crop behaviour with which the agriculturist is concerned; the experiments require no elaborate apparatus, and they provide data which can be subjected to statistical analysis.

#### SUMMARY.

1. A method of studying drought resistance is described which involves the measurement of the rate at which growth is resumed and continued after drought.
2. The method is applied to an experiment on the effect of high and low nitrogen levels on the drought resistance of two varieties of oats (Algerian and Fulghum) in sand cultures.
3. Analysis of the data shows that there is a significant effect of drought on the recovery rate, depending upon variety and nitrogen level. The details of the analysis are set out in Table 2. The data indicate that drought resistance is an inverse function of the growth rate.

#### Acknowledgement.

The authors have pleasure in thanking Miss Helen Turner, statistician to the McMaster Laboratory of the Council for Scientific and Industrial Research, for her valuable help in the statistical analysis of the data.

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## APPENDIX.

*Statistical Treatment.*

Data of plant height during growth after drought were subjected to analysis of variance. Since it is desirable to work with observations at equal time intervals the only readings used were those for the following dates: 14th, 20th, 26th May, 1st, 7th, 13th, 19th June. The data for three of these occasions are interpolations but this does not affect the validity of the analysis.

Owing to damage to plants in one pot through accident, and in order to retain the symmetry of the analysis, the missing plot technique had to be applied. There were nine plants in each plot, and there was considerable variation between individuals owing to competition within the pot. Accordingly the unit selected for analysis was not the individual plant's height but the sum of the mean heights per pot in the three pots of each treatment. Variation within treatments was estimated from the data from different blocks.

The variance of plant height increases with time; it was necessary therefore to work with the logarithms of height and not with the original data. The results of the ordinary analysis of variance are summarized in Table 2 in the text. In addition an analysis using the long term experiment technique of Cochran (1939) was carried out and the interactions partitioned by the use of orthogonal functions, but the results of this analysis added nothing to the conclusions already drawn.

The data for dry weight collected on 11th April and 12th May were subjected to an ordinary analysis of variance; again a row of three pots was considered as a unit. The only significant effect on 11th April was nitrogen; on 12th May variety, nitrogen and the interaction of nitrogen and drought all reached significance.

## THE ECOLOGY OF THE CENTRAL COASTAL AREA OF NEW SOUTH WALES. IV.

FOREST TYPES ON SOILS FROM HAWKESBURY SANDSTONE AND WIANAMATTA SHALE.

By ILMA M. PIDGEON, M.Sc., Linnean Macleay Fellow of the Society in Botany.  
(From the Botany School, University of Sydney.)

(Five Text-figures.)

[Read 25th June, 1941.]

*Introduction.*

It is becoming apparent that the existing systems of ecological nomenclature cannot be satisfactorily applied to the classification of Australian forests. Formations and associations, as defined by Clements, can be recognized (Pidgeon, 1937), but beyond this stage the classification is unsuitable. This is exemplified by attempts to describe the sandstone forests of the central coastlands of New South Wales. Accordingly, the purpose of this paper is first, to indicate a working basis for the classification of forests occurring in the central coastlands, particularly on soils derived from Hawkesbury Sandstones and Wianamatta Shales, and secondly, to discuss the effect of climate and habitat on the distribution of *Eucalyptus* species, and finally to summarize the requirements of individual dominants.

Physiographically, the outstanding feature of the central coastlands is a much dissected Hawkesbury Sandstone plateau which weathers to an extremely poor sandy soil. The plateau extends over an area covered by a wide range of climatic conditions, and provides a variety of topographical habitats. The sandstone is covered by one association, viz., the Mixed *Eucalyptus* Forest Association (Pidgeon, 1937), the uniformity of which is attributable to edaphic conditions, and the many variants of which are determined by climatic and habitat variations. The plateau forms a semi-circle, and partly surrounds an undulating plain of Wianamatta Shales—the Cumberland Basin. This area is not only characterized by an entirely different series of soil types (heavy loams and clays), but it is a low rainfall basin, and is covered by a different type of forest, namely, the *E. hemiphloia*–*E. tereticornis* Association (Pidgeon, 1937). Outliers of these shales occur on the sandstone plateau under conditions of higher rainfall, both at high and low elevations, and here also the forests are entirely different—they are local expressions of several other associations, one of which is the *E. saligna*–*E. pilularis* Association (Pidgeon, 1937).

At the outset, there is thus one striking feature, namely, that on Hawkesbury Sandstone, notwithstanding the range of climate, the soil factor is sufficiently predominant to maintain the characteristics of one association throughout the whole area, whereas on Wianamatta Shale, climatic differences of the same order are responsible for the development of several different associations. There is one other noteworthy point, namely, that the dominants in the shale and sandstone forests are strictly segregated; very few species are common to both soil formations (Table 12). The soils are derived from the underlying formations *in situ*, and the boundaries are usually very sharp, but nevertheless the ecotone forests have definite characteristics.

The environmental variants of the central coastlands, such as climate and soil, have been discussed in detail in previous publications of this series. (Pidgeon, 1937, 1938, 1940).

In the classification of forests in this area, there are two sets of major difficulties involved, particularly with reference to sandstone forests:

- (i). The large number of tree species, most of which belong to the genus *Eucalyptus*, and which are remarkably sensitive indicators of climatic conditions, particularly of water balance.

- (ii). Immature physiography and soils, and consequently a mosaic of micro-climates and habitats.

The combination of these factors results in a bewildering variety of forest stands. In the sandstone forests, pure stands of any one species are not found over wide areas. Mixed stands from two up to as many as six species are typical, but the mixing of the species does not constitute the difficulty so much as the inconstancy of the stands; the species vary with every slight variation in habitat such as slope, aspect, etc. This variation in the mixtures of dominants is undoubtedly one of the most striking features of sandstone forests, and contrasts markedly with the pure stands of conifers, beech or oak, found in parts of U.S.A. and England. Therefore one cannot recognize consociations or consocieties as the typical units within the association, and none of the existing nomenclature of the successional analysis of vegetation provides a suitable term to describe these stands of sandstone forests.

Faciation and lociation are the only terms which are at all applicable, but even these are inadequate and unwieldy. It has been suggested (Pidgeon, 1940) that the only suitable method of classification within the association is by forest types,\* where "*forest type*" is defined as a forest stand which has, wherever it occurs, the same *floristic composition of dominants*, and which develops in essentially similar habitats. Minor variations in the environment occupied by the association cause this segregation into forest types, and although a forest type may not occupy a large area in any one locality, it constantly occurs in similar habitats. Each forest type occurs as a number of isolated forest stands with the same recurring floristic composition of the dominants. This floristic homogeneity is determined subjectively by observation, and ignores the frequency of the dominants. More detailed analysis of forest stands would doubtless reveal differences among them, both in relative frequency of dominants and in the subsidiary flora.

In the following pages an outline of the classification of forest types occurring on Hawkesbury Sandstones and Wianamatta Shales is given, and more particularly the effect of climate and habitat on the distribution of forest types and of individual species is discussed.

#### FORESTS ON SOILS DERIVED FROM HAWKESBURY SANDSTONE.

All the forests on Hawkesbury Sandstone belong to the one association—the Mixed *Eucalyptus* Forest. This association is limited to sandy soils, mostly derived from sandstones of the Hawkesbury Series, Newcastle Coal Measures and Upper Marine Series. The greatest extent of this association is in the central coastal area of New South Wales. Various features of the Hawkesbury Sandstone forests have been referred to in previous publications of this series, but the distribution of the dominants throughout the association has not yet been recorded, and apart from the succession studies which refer mainly to the coastal area, no details of habitat requirements of individual tree species have been published. Accordingly in this section, an attempt is made to summarize the general range of dominants throughout the association and the factors controlling this distribution, the effect of climate and habitat on the distribution of individual tree species, and the classification of forest types.

#### GENERAL RANGE OF DOMINANTS.

The Hawkesbury Sandstones cover an approximate area of 8,000 sq. miles; they extend from the coast up to a distance of more than 100 miles inland, and the altitude ranges from sea level to more than 3,000 ft. Over this area there is a wide range of climate—e.g., the mean rainfall varies from below 30 inches to more than 50 inches (see Pidgeon, 1937, Fig. 1); there is a difference of 10 Fahrenheit degrees between the mean temperatures on the coast at low elevations and inland on the high plateau. At high altitudes on the plateau the mean daily range is approximately twice that occurring on the coast; the winter temperatures at high altitudes are much lower, and frequently snow falls. The difference in length of frost-free period at high and low altitudes is ecologically the most important aspect of temperature.

\* Pryor (1939) has also successfully classified the vegetation of the Australian Capital Territory by this method.

With such a range of climate, it is not remarkable that many *Eucalyptus* species are restricted in their distribution to parts of the sandstone area; others are "tolerant" species and occur throughout the greater extent of the area—e.g., *E. haemastoma*, *E. micrantha*, *E. eugenioides* and *E. piperita*. This unrestricted extent of at least several dominants is of course one of the criteria by which an association is recognized. The general range of the dominants is indicated in Tables 1 and 3. From an inspection of Table 1 it is evident that there is an altitudinal range of species—e.g., *E. radiata*, *E. goniocalyx*, *E. maculosa* and *E. dives* are restricted to high altitudes, whilst *E. pilularis*, *E. eximia* and others are limited to low altitudes.

TABLE 1.  
Distribution of more important dominants of the mixed *Eucalyptus* Forest Association on sandstone at low coastal altitudes (about 500 ft.) and at high tableland altitudes (over 3000 ft.). For more complete list, see Table 3. 'x' denotes presence. The order of species in these tables is of no significance.

Species.	Altitudinal Distribution.	
	High (3000 ft.).	Low (500 ft.).
<i>E. Sieberiana</i> F. v. M.	x	x
<i>E. piperita</i> Sm.	x	x
<i>E. micrantha</i> DC.	x	x
<i>E. haemastoma</i> Sm.	x	x
<i>E. eugenioides</i> Sieb.	x	x
<i>E. gummiifera</i> Gaertn.		x
<i>E. punctata</i> DC.		x
<i>Angophora lanceolata</i> Cav.		x
<i>E. pilularis</i> Sm.		x
<i>E. eximia</i> Schau.		x
<i>E. umbra</i> R. T. Baker		x
<i>E. capitellata</i> Sm.		x
<i>E. botryoides</i> Sm.		x
<i>E. radiata</i> Sieb.	x	
<i>E. maculosa</i> R. T. Baker	x	
<i>E. oreades</i> R. T. Baker	x	
<i>E. Blaxlandi</i> Maiden and Cabbage	x	
<i>E. goniocalyx</i> F. v. M.	x	
<i>E. dives</i> Schau.	x	
<i>E. rubida</i> Deane and Maiden	x	

In some instances—e.g., *E. oreades*\* and *E. Blaxlandi*,\* altitudinal limitation may be merely a fortuitous floristic distribution, but in general, this is not the case. Nothing is known of the physiology of the various species of *Eucalyptus*, but it is highly probable that for many species limitation to high altitudes may be correlated with a more favourable water balance. Expressing this factor as  $\frac{\text{Precipitation}}{\text{Evaporation}}$  (P/E),† the indices for Katoomba (3,349 ft.) and Mt. Victoria (3,490 ft.) on the high plateau of the Blue Mts. are 1.6 and 1.3 respectively, whilst those of Sydney (138 ft.) and Riverview (71 ft.) on the coast

\* These two species occur only on the Blue Mts. and Moss Vale-Mittagong Tablelands, and on the lower slopes which link these two areas. Both species are typical of high altitudes, but *E. Blaxlandi* descends to 760 ft. at Blaxland, and *E. oreades* to 1,200 ft. at Springwood (both in the Blue Mountain area).

† Data on evaporation are not available except for Sydney, so the P/E index is obtained in the following manner. From percentage mean relative humidity and mean temperature, saturation deficit is obtained from tables; Prescott (1934) has shown that for Australia

$$\frac{\text{Evaporation}}{\text{Saturation deficit}} = 259,$$

$$\therefore \frac{P}{E} = \frac{\text{sat. d.} \times 259}{\text{temperature of } 53.8^\circ\text{F.}}, \text{ For example, Katoomba has a mean relative humidity of 71, and mean temperature of } 53.8^\circ\text{F., } \therefore \text{saturation deficit (from tables) = } 0.13; \text{ mean rainfall = } 55.1 \text{ inches,}$$

$$\therefore \frac{P}{E} = \frac{55.1}{259 \times 0.13} = 1.64.$$

This correction factor must be regarded as only approximate, e.g., for Sydney  $\frac{P}{E} = 1.21$ , but using  $\frac{\text{Evaporation}}{\text{sat. d.} \times 259}$ , it is 1.02.

are 1.02 and 0.89. Conversely, restriction to low altitudes does not necessarily mean that the species are limited to conditions of less favourable water balance (particularly is this not true of *E. pilularis*), but it may mean that they cannot survive the longer period of frosts typical of high altitudes. A scale of susceptibility to frosts, indicated by gradual disappearance at various altitudes, could be represented as in Table 2.

TABLE 2.  
Highest recorded altitudes for some of the extra-tableland dominants on sandstone.

Species.	Highest Recorded Altitude (Feet) in Central Coastlands.
<i>E. pilularis</i> .. .. .	1000
<i>E. eximia</i> .. .. .	1200
<i>E. punctata</i> .. .. .	2200
<i>A. lanceolata</i> .. .. .	2500
<i>E. gummifera</i> .. .. .	2800

The distribution of some species is apparently controlled by temperature; at least two species, namely *E. Sieberiana* and *E. goniocalyx*, provide evidence of a temperature range. *E. goniocalyx* is found in South Australia and in Victoria, and extends along the coast and tablelands of southern New South Wales, but in the central coastal area it is limited to the high tablelands, and thence continues intermittently at high elevations into northern New South Wales. *E. Sieberiana* extends from Tasmania throughout the coastlands of Victoria and southern New South Wales, and in the central

TABLE 3.  
Distribution of dominants of the Mixed Eucalyptus Forest Association in various regions of the sandstone plateau. For boundaries and climatic features of these sub-regions, see text. 'x' = presence, '.' = limited occurrence.

Species.	Regional Distribution.				
	Higher Tablelands. (iv).		Lower Tableland Slopes. (iii)	Coastal. (i)	Macdonald (ii)
	Blue Mts. 2000-3500 ft.	Wingecarribee 2000-2500 ft.	0-1800 ft.	0-1200 ft.	800-1000 ft.
<i>E. Sieberiana</i> F. v. M. . . . .	x	x	x	x	
<i>E. piperita</i> Sm. . . . .	x	x	x	x	
<i>E. micrantha</i> DC. . . . .	x	x	x	x	x
<i>E. haemastoma</i> Sm. . . . .	x	x	x	x	x
<i>E. eugenioides</i> Sieb. . . . .	x	x	x	x	x
<i>E. resinifera</i> Sm. . . . .			x	x	
<i>E. agglomerata</i> Maiden . . . . .					
<i>E. gummifera</i> Gaertn. . . . .	x		x	x	x
<i>E. punctata</i> DC. . . . .		x	x	x	x
<i>E. pilularis</i> Sm. . . . .				x	
<i>Angophora lanceolata</i> Cav. . . . .		x	x	x	x
<i>A. Bakeri</i> C. Hall . . . . .				x	x
<i>E. eximia</i> Schau. . . . .			x	x	x
<i>E. umbra</i> R. T. Baker . . . . .				x	
<i>E. botryoides</i> Sm. . . . .				x	
<i>E. capitellata</i> Sm. . . . .			x	x	x
<i>E. radiata</i> Sieb. . . . .	x	x			
<i>E. maculosa</i> R. T. Baker . . . . .	x	x			
<i>E. goniocalyx</i> F. v. M. . . . .	x				
<i>E. oreades</i> R. T. Baker . . . . .	x				
<i>E. Blaxlandi</i> Maiden and Cabbage . . . . .	x				
<i>E. dives</i> Schau. . . . .	x				
<i>E. rubida</i> Deane and Maiden . . . . .					
<i>E. notabilis</i> Maiden . . . . .					
<i>E. Consideniana</i> Maiden . . . . .					
<i>E. urceolaris</i> Maiden and Blakely . . . . .		x			
<i>E. frazinoides</i> Deane and Maiden . . . . .		x			
<i>Suncarpia laurifolia</i> Ten. . . . .			x	x	x

coastlands it is a dominant at high altitudes and in southern localities, but it gradually decreases in importance to the north of the area until it is represented only by a few scattered trees north of the Hawkesbury River. Of the more "tolerant" species, *E. haemastoma*, *E. micrantha*\* and *E. eugenioides* are widespread and not limited by rainfall or altitude, whereas *E. piperita* becomes scarce at low altitudes with a rainfall of approximately 30 inches, and may be said to be absent from regions receiving less than 30 inches.

The range of dominants throughout the association appears therefore to be governed by the broader aspects of climate, such as effective rainfall, temperature range and length of frost-free period, but the occurrence of any particular species within a restricted area is determined by local habitat conditions. For example, there is a definite spatial zonation from the tops of ridges to the bottoms of gorges; species which are typical of ridges (e.g., *E. haemastoma*) are rarely if ever found on sheltered slopes or gorges. Whether this restriction to less favourable habitats is due to competition or to inability to exist under better environmental conditions has not yet been investigated; for instance, it may be connected with the light factor. However, it has been established that the general restriction of *E. pilularis* to sheltered gorges in sandstone country is correlated with soil moisture conditions—this species grows equally well on the adjacent exposed shale ridges, because soil derived from shale has a greater water-retaining capacity. Small stands of *E. pilularis* are also found on the surface of the coastal sandstone plateau where the rainfall is about 55 inches.

It is possible to group the species occurring in any area according to their typical habitats on ridges and plateau surface, or on slopes and gullies. In the coastal region at low elevations, *E. haemastoma*, *E. micrantha*, *E. gummifera*, *E. punctata*, *E. Sieberiana*, *E. eugenioides* and *E. eximia* are typical of the plateau surface and upper slopes of gorges, whilst *E. piperita*, *Angophora lanceolata*, *E. pilularis* and *Syncarpia laurifolia* are gully types; on the higher tablelands *E. Sieberiana*, *E. piperita*, *E. maculosa* and *E. radiata* occur on the ridges, whilst *E. goniocalyx*, *E. oreades* and *E. Blaxlandi* are typical of more sheltered slopes. Other species have peculiar limitations, e.g., *E. umbra* and *E. botryoides* are confined to the coast not more than a few miles distant from the sea. Distribution of some species may be purely floristic, e.g., *E. urceolaris* has been recorded only in the Wingecarribee sub-region; it is closely related to the widespread *E. piperita*, and may represent a local strain of comparatively recent origin. The distribution of *E. eximia* presents an interesting problem. It occurs very sporadically throughout the coastal region, but is entirely absent from some sections; on the slopes of the tablelands it ascends only to a height of 1200 ft.

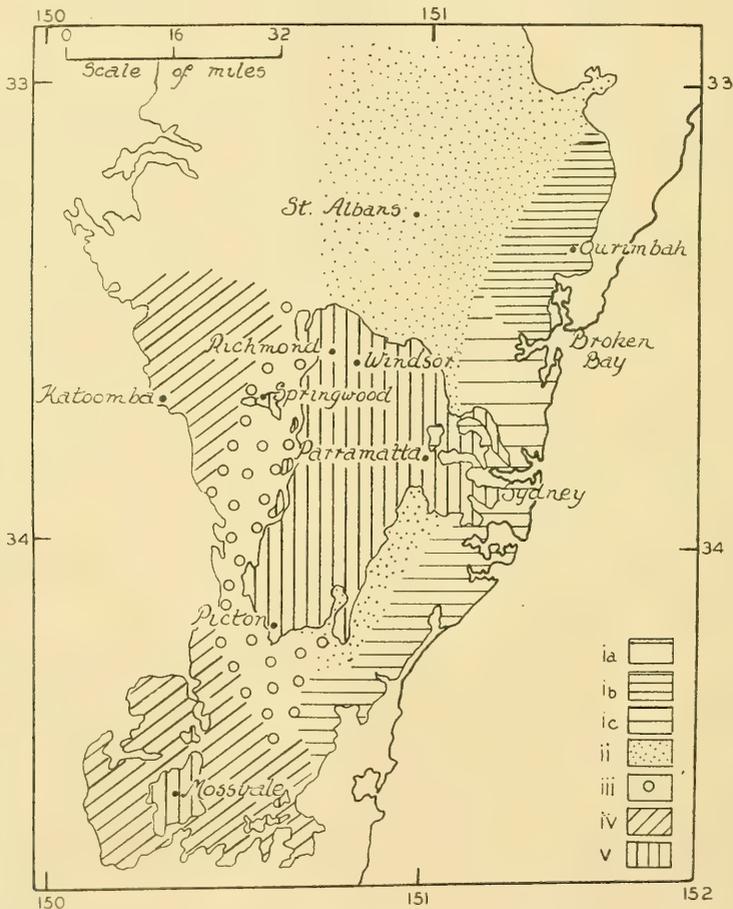
The distribution of the dominants outside the Mixed *Eucalyptus* Forest Association on sandstone is noteworthy. A few species are practically restricted to the central coastal area and to soils derived from Hawkesbury Sandstone or to similar sandy soils, e.g., *E. haemastoma*, *E. micrantha*, *E. eximia*, *E. oreades* and *E. Blaxlandi*. Others are very widely distributed coastal species extending from Victoria to Queensland, e.g., *E. pilularis* and *E. gummifera*, which are typical of well drained sandy or loam soils. *A. lanceolata* is widely distributed on poor sandy soils at low altitudes along the coast of New South Wales to Rockhampton in Queensland, and has also found its way to the north-west slopes of New South Wales. *E. piperita* is another species which is practically confined to sandy soils (but not necessarily those derived from Hawkesbury Sandstones). It extends only a short distance north and south of the central coast. *E. punctata* is distributed chiefly in the central coastal area on sandy soils, but extends to drier areas west of the Blue Mts. and in the Upper Hunter Valley. It has also been recorded in south Queensland. The distribution of *E. Sieberiana* and *E. goniocalyx*,

\* There appears to be some confusion with regard to the distribution of white gums. Blakely records *E. haemastoma* Sm. throughout the entire sandstone area, but does not record *E. micrantha* DC. in the Blue Mountains. He recognizes *E. haemastoma* var. *solerophylla* Blakely, as a small-fruited form endemic to the Blue Mountains. Although this variety has been recognized by the writer, there appears to be considerable doubt as to the restricted distribution of *E. micrantha*. Accordingly in this paper *E. micrantha* is regarded as having a distribution similar to that of *E. haemastoma*.

which are mainly tableland types, has already been mentioned. *E. radiata*, *E. dives* and *E. maculosa* are found on the tablelands and western slopes of New South Wales; the latter two extend into Victoria. These three species are all typical of sandy soils, but *E. maculosa* also occurs on granite formations. *E. rubida* has an extensive range from Tasmania through South Australia, Victoria, New South Wales and Queensland. In New South Wales it is a high tableland type, and prefers alluvial flats and soils derived from quartz porphyry and granite.

DISTRIBUTION AND HABITATS OF SPECIES, AND CLASSIFICATION OF FOREST TYPES.

The sandstone plateau may be divided into a number of regions\* (see Text-figure 1) which differ from one another physiographically and climatically, and consequently are characterized by different groups of forest types. Distribution and habitats of species, and classification of forest types are therefore discussed most conveniently in the various



Text-fig. 1.—Map of central coastlands showing regions and sub-regions of the sandstone plateau [(i) to (iv)] and Wianamatta Shale areas.

- (i). Coastal region: (a). Hornsby Plateau sub-region, (b). Ourimbah sub-region, (c). Nepean Ramp.
- (ii). Macdonald region.
- (iii). Lower Tableland Slopes region.
- (iv). Higher Tableland region: (a). Higher Blue Mountain Tableland (in vicinity of Katoomba), (b). Wingecarribee Tableland (in vicinity of Moss Vale).
- (v). Wianamatta Shale.

\* The writer is grateful to Dr. W. R. Browne, Department of Geology, Sydney University, for his assistance in naming these regions, also for suggesting the term Cumberland Basin.

regions. These are as follows (figures given for altitude and rainfall are only approximate):

- (i). The coastal region extending north and south of Sydney, and varying in elevation from sea level to 1200 ft. Mean rainfall is from 40 to more than 50 inches. There are three sub-regions: (a) Hornsby Plateau, (b) Ourimbah, (c) Nepean Ramp.
- (ii). The Macdonald region, which includes the country in the vicinity of the Macdonald River, especially the eastern watershed. Average elevation 800-1000 ft.; mean rainfall from less than 30 to less than 40 inches.
- (iii). The lower slopes of the tablelands, which include the sandstone valleys in the eastern section of the Blue Mountain Tableland. Elevation from sea level to 1800 ft., and mean rainfall 35 to 40 inches.
- (iv). The higher tableland region, which consists of two sub-regions:
  - (a). The higher Blue Mountain Tableland with an elevation of 2000 to 3500 ft. and mean rainfall 35 to 55 inches.
  - (b). The Wingecarribee Tableland, which is the area in the vicinity of the Wingecarribee River. This sub-region has sometimes been referred to as the Moss Vale Tableland. The elevation is from 2000 to 2500 ft. and the mean rainfall is from 30 to 40 inches. (Region iii links sub-regions *iva* and *ivb*.)

Little is known of the sandstone plateau in the vicinity of the Colo River, so discussion of the flora in this region must await further field work. It appears to carry the same type of forest as occurs over parts of region (ii). The outstanding characteristics of the forest flora in these regions are as follows:

*Region (i)*. A number of species is limited to this area, e.g., the strictly coastal forms, *E. botryoides* and *E. umbra*, and the low altitude, high rainfall species, namely *E. pilularis*. Dominants include *A. lanceolata*, *E. gummifera* (low to intermediate altitude types), and "tolerants" such as *E. haemastoma*, *E. micrantha*, *E. piperita* and *E. Sieberiana*.

*Region (ii)*. The composition of the forests differ somewhat from Region (i), because of decreased rainfall. No additional species are present, but trees which were relatively unimportant in region (i) assume dominance, e.g., *E. punctata*, *E. eximia* and *A. Bakeri*, whilst *E. piperita* rapidly becomes scarce and finally disappears. *E. gummifera* and *A. lanceolata* are also very rare in areas with rainfall of 30 inches.

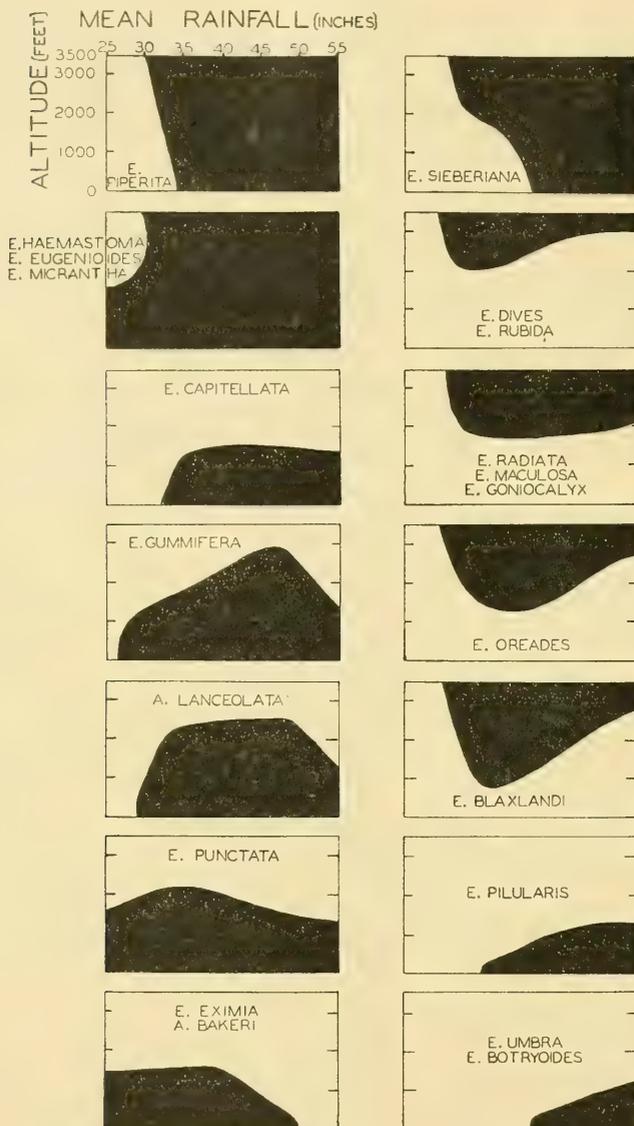
*Region (iii)*. Characterized by a mixture of low altitude species found in regions (i) and (ii).

*Region (iv)*. Species restricted to high altitudes typify this area, e.g., *E. radiata*, *E. maculosa*, *E. goniocalyx*, etc.

The distribution of the more important dominants on sandstone, as determined by altitude and rainfall, is shown in the diagrams, Text-figure 2. The most noteworthy point which emerges is the remarkable ecological specificity of the different species of *Eucalyptus*.

#### (i). Coastal Region.

In the coastal region the sandstones extend to the coastline only from south of Port Hacking to Broken Bay. North and south of this area the sandstone scarp flanks narrow coastal plains. The western boundary of this region is taken approximately at the 40 inch isohyet. The coastal region north of Sydney is rugged and presents a complicated pattern of ridges and gorges. It is cut into two sub-regions by the drowned estuary of the Hawkesbury River known as Broken Bay. The southern sub-region is the Hornsby Plateau and in this paper the sandstone area to the north of the Hawkesbury River is referred to as the Ourimbah sub-region. The coastal region south of Sydney (Nepean Ramp) is undulating with extensive drainage areas of upland swamps or moors; there are comparatively few gorges. Conditions for plant growth are more favourable here than on the Hornsby Plateau, where the youthful physiography has resulted in the exposure of a large amount of rock and in the



Text-fig. 2.—Diagrams showing, as blackened areas, climatic tolerance of dominants on soils derived from Hawkesbury Sandstone. There is a correlation between the two variables in the diagrams; for instance, no regions of high altitude and low rainfall fall into the area considered. Accordingly the shape of such a diagram as that for *E. haemastoma* is determined by the peculiarities of the climate, and not by any specificity of the tree species.

constant removal of soil from slopes. On the uplands of the Nepean Ramp the soil has developed comparatively rapidly—the continuous effect of seepage water has resulted in the rotting of the underlying rocks. In addition, the mean rainfall over parts of the Nepean Ramp exceeds 50 inches and mists are frequent. Consequently the forest types differ somewhat from those of the Hornsby Plateau, and are therefore discussed under a separate sub-region.

(a). *Hornsby Plateau Sub-region.*

Table 4 contains a list of the more important dominants occurring on the Hornsby Plateau. There are, in addition, a number of relatively unimportant trees of very sporadic

occurrence which are limited to sandstone. These are species such as *E. Bottii* Blakely, *E. pseudo-piperita* Maiden & Blakely, *E. Joyceae* Blakely, *E. penrithensis* Maiden, *E. squamosa* Deane & Maiden, *E. deformis* Blakely. A few other species are also found in this area, but they are not typical, e.g., *E. notabilis* Maiden, *E. pellita* F.v.M., etc.

TABLE 4.

Distribution of dominants on sandstone of the coastal region (i) and Macdonald region (ii). 'X' = most frequently occurring species, 'x' = presence, '.' = limited occurrence.

Species.	Distribution.		
	Coastal Region (i).		Macdonald Region (ii).
	Nepean Ramp.	Hornsby Plateau.	
<i>E. piperita</i>	X	X	.
<i>E. haemastoma</i>	x	X	x
<i>E. micrantha</i>	X	X	x
<i>E. gummiifera</i>	X	X	x
<i>E. pilularis</i>	x	X	.
<i>A. lanceolata</i>	x	X	x
<i>E. Sieberiana</i>	X	.	.
<i>E. eugenioides</i>	x	x	X
<i>E. punctata</i>	.	x	X
<i>E. eximia</i>	.	x	X
<i>E. umbra</i>	x	x	.
<i>E. botryoides</i>	x	x	.
<i>E. capitellata</i>	x	x	x
<i>A. Bakeri</i>	x	x	X
<i>A. intermedia</i>	.	.	x
<i>E. agglomerata</i>	.	.	.
<i>Syncarpia laurifolia</i>	.	x	x

The following notes contain a brief survey of the habitats of the dominants:

*Eucalyptus haemastoma* is probably the hardiest sandstone species, and often occupies exposed barren areas to the exclusion of other trees. Occasionally it forms mallee-like thickets. *E. micrantha* is a closely related species which flourishes particularly well in moist or semi-swamp situations on the uplands. *E. gummiifera* is a widespread and constant species which occurs over a wide range of habitats from ridges and valleys, and exhibits a variety of habits. These three species may be regarded as characteristic of the plateau surface. *E. piperita* is one of the most typical sandstone species and characterizes slopes. *Angophora lanceolata* is prominent and widespread; it assumes grotesque forms on rocky slopes, but fine specimens are found on lower gully slopes. *E. pilularis* and *Syncarpia laurifolia* are restricted, in this district, to sheltered gullies and slopes where there is a high soil moisture content. *E. punctata*\* is distributed sparsely over the plateau surface and upper gully slopes. *E. eximia* occurs very sporadically and is absent over extensive areas. Its preference for fairly dry habitats may be emphasized here. *E. eugenioides*† (*E. oblonga* and *E. scabra*) is widespread but sporadic in occurrence. Stringybarks tend to become more numerous on the patches of loam derived from intercalated shale beds and cappings which occur throughout the sandstone. *E. capitellata* is a typical sandstone stringybark of the ridges and uplands. *E. umbra* and *E. botryoides* occur occasionally rather than constantly, their usual habitats being on slopes near the sea. *E. Sieberiana* occurs in restricted areas on the plateau surface, but appears to be infrequent in dry areas. *Angophora intermedia* is only sparsely represented on sandstone (see p. 123) but is almost invariably associated

\* Blakely (1934) makes a distinction between this species and *E. Shiressii*, but for the purpose of the ecologist they are more satisfactorily regarded as ecological varieties.

† *E. eugenioides* Sieb. has been split into three species by Blakely, viz., *E. oblonga* Blakely (typical of sandstone), *E. globoidea* Blakely (deep shale), and *E. scabra* Dum-Cours (shaly-sandstone). These species are difficult to separate apart from their habitats and accordingly they are grouped under *E. eugenioides* in this paper.

with *E. punctata* and *Casuarina torulosa* on estuarine slopes just above the water level. *A. Bakeri* is sporadic in occurrence and often falls to the rank of a subdominant.

As previously stated, the dominants occur in mixed stands of at least two species. Table 5 has been compiled to illustrate how a classification according to forest types may be made. The extent of the stands listed in the table is usually very limited over any area, because of the broken physiography, but the types constantly recur in similar habitats. In general, it may be said that types 1-6 are characteristic of the ridges and

TABLE 5.

Some of the more important forest types occurring on the sandstone of the Hornsby Plateau sub-region. Types consisting of pure stands of one species not listed (these are rare).

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1. <i>E. haemastoma</i> — <i>E. micrantha</i> .
2. <i>E. haemastoma</i> — <i>E. gummifera</i> .
3. <i>E. haemastoma</i> — <i>E. capitellata</i> .
4. <i>E. micrantha</i> — <i>E. gummifera</i> .
5. <i>E. gummifera</i> — <i>E. capitellata</i> .
6. <i>E. gummifera</i> — <i>E. Sieberiana</i> .
7. <i>E. gummifera</i> — <i>E. piperita</i> .
8. <i>E. Sieberiana</i> — <i>E. gummifera</i> — <i>E. piperita</i> .
9. <i>E. piperita</i> — <i>A. lanceolata</i> — <i>E. gummifera</i> .
10. <i>E. piperita</i> — <i>A. lanceolata</i> — <i>E. Sieberiana</i> .
11. <i>E. piperita</i> — <i>A. lanceolata</i> .
12. <i>A. lanceolata</i> — <i>E. pilularis</i> .
13. <i>E. pilularis</i> — <i>E. piperita</i> — <i>A. lanceolata</i> .
14. <i>E. pilularis</i> — <i>Syncarpia laurifolia</i> .
15. <i>E. punctata</i> — <i>A. intermedia</i> .

---

uplands, 7-11 are typical of slopes and sheltered habitats on the uplands, whilst 12-14 are definite gully types, and 15 is practically restricted to estuarine slopes. The recognition of forest types does not take into account any quantitative estimate of the relative proportions of the various dominants, e.g., in type 2 (Table 5), *E. haemastoma* may be more abundant than *E. gummifera*, or *vice versa*, or they may be co-dominant. There are also many variants of these types, e.g., in the *E. piperita*-*A. lanceolata* type 11, there may be additional individuals of one or more species scattered throughout the stand, e.g., *E. umbra*, *E. eugenioides*, *E. punctata*. The actual composition of a few stands is given below:

<i>A. lanceolata</i>	a*	<i>A. lanceolata</i>	a	<i>A. lanceolata</i>	a
<i>E. piperita</i>	f*	<i>E. piperita</i>	a	<i>E. piperita</i>	a
<i>E. umbra</i>	o*	<i>E. Sieberiana</i>	r	<i>E. punctata</i>	a
<i>E. eugenioides</i>	r*	<i>E. gummifera</i>	r	<i>E. Sieberiana</i>	f
				<i>E. gummifera</i>	r

Stands which are probably mixtures of two types are also frequent, e.g., *E. haemastoma*-*E. gummifera*-*E. piperita* (types 2 and 7). Such types have not been listed in Table 3. Some of the mixed stands indicate successional changes, for example:

<i>E. gummifera</i>	a
<i>E. Sieberiana</i>	f
<i>E. haemastoma</i>	r
<i>A. lanceolata</i>	r

Here, *E. haemastoma* is probably a relict from a more xeric stand of forest, whereas the presence of *A. lanceolata* may indicate improvement of habitat. However, in interpreting any particular stand where successional change is indicated, other evidence must be taken into consideration, e.g., tree girth. In this example, the presence of very old trees of *E. haemastoma* with younger specimens of *A. lanceolata* would lend support to the idea of progressive succession.

(b). *Ourimbah Sub-region.*

These forests are much the same as those of the Hornsby Plateau, except that there are very few trees of *E. Sieberiana*, which is here at its northern limit, *E. piperita* is

\* a = abundant, f = frequent, o = occasional, r = rare.

less frequent but *E. micrantha*, *E. haemastoma*, *A. lanceolata* and *E. gummifera* are abundant. In addition, some *E. pellita* is found, often in association with *E. resinifera* in hollows below the ridges.

(c). *Nepean Ramp Sub-region.*

Table 4 summarizes the outstanding differences between the forests of this area and of the Hornsby Plateau. Because of fewer gullies in this sub-region, the *E. pilularis*, *E. piperita* and *A. lanceolata* forest types are less frequent than on the Hornsby Plateau. There is one interesting feature, however, namely, that stands of *E. pilularis*-*A. lanceolata* are not uncommon on the edge of the plateau overlooking the plain, at an elevation of several hundred feet. This relatively exposed habitat, which is unusual for *E. pilularis* when growing on Hawkesbury Sandstone, is compensated for by an increase of approximately 10 inches mean rainfall when compared with the corresponding topographic habitat on the Hornsby Plateau.

Another noteworthy feature in the Nepean Ramp is the absence of exposed and eroded ridges and consequently the comparative absence of the dry *E. haemastoma* types. *E. Sieberiana*, which in this area has not reached its northern limit, is particularly well represented on the swampy uplands, and frequently is associated with *E. micrantha* on the fringe of the swamps. Various combinations of forest types, including *E. micrantha*, *E. haemastoma*, *A. lanceolata*, *E. Sieberiana*, *E. gummifera*, *E. piperita* and stringybarks are found on the undulating plateau. *E. botryoides* is prominent on the cliffs and scarp overlooking the coastal plain. *E. eximia* is notably absent from this area but occurs further south in the Nowra-Jervis Bay area. The predominantly higher rainfall may account for its absence and also for the scarcity of *E. punctata*.

(ii). *Macdonald Region.*

This area is the westward extension of the Ourimbah and Hornsby Plateau sub-regions and is physiographically similar (although it attains higher elevations), but the rainfall is considerably lower and the temperature range greater. The division between this region and the damper more equable coastal region may be taken in the vicinity of the 40-inch isohyet. This region extends as a narrow strip from Parramatta northwards, but broadens considerably north and west of the Lower Hawkesbury River. Floristically the western margin of the Nepean Ramp (west of the 40-inch isohyet) belongs to this area, and also the small outliers of sandstone and exposures in creek cuttings in the Cumberland Basin.

With a mean rainfall of 30-35 inches, the outstanding differences between the forest types here and in regions *ia* and *ib* are (see Table 4): 1. The absence of *E. pilularis* and the infrequency of *E. piperita*, and 2. The increased importance of *E. punctata*, *E. eximia* and *A. Bakeri* and to a lesser extent of all stringybarks. *A. lanceolata*, *E. gummifera*, *E. haemastoma* and *E. micrantha* are still dominants, and *A. intermedia* and *E. paniculata* are locally important.\* With a rainfall of less than 30 inches, *A. lanceolata* and *E. gummifera* become rare, and may be altogether absent, whilst *E. punctata*, *A. Bakeri* and *E. eximia* are still the dominants over extensive areas.

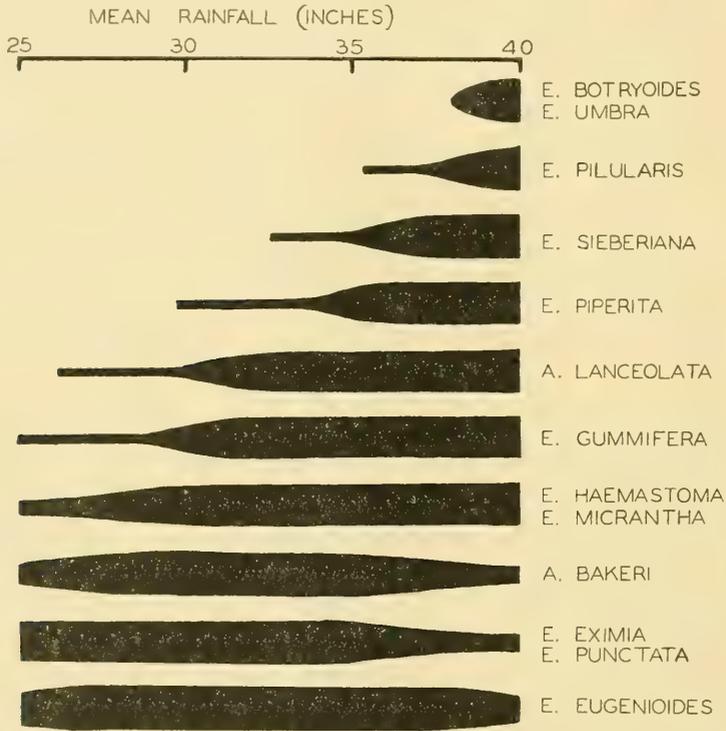
The effect of climate on the range of the dominants throughout the coastal and Macdonald regions is summarized in Text-figure 3.

(iii). *Lower Slopes of Tablelands.*

In this area are included the lower slopes and sandstone valleys in the eastern section of the Blue Mt. Tableland up to about Linden (1,700 ft.), the slopes ascending from the southern margin of the Cumberland Basin to the Wingecarribee Tableland about as far as Yerrinbool (1,500 ft.). This region has a fairly good rainfall, averaging 35-40 inches on the Blue Mt. slopes, but decreasing to about 30 inches on the southern slopes near Picton. As far as species are concerned, the lowest slopes of this area (up to about 800 ft.) are analogous to the eastern section of region (ii). On the lower slopes there are no extremes of temperature as on the tablelands, consequently the dominants are species typical of regions (i) and (ii), although two of the tableland species descend

\* The importance of these species is due to the prominence of shaly bands in the sandstone in this region. (See p. 134, ecotone forests.)

to these lower altitudes. These are *E. oreades*, which has been recorded at Springwood (1,200 ft.) and *E. Blaxlandi* (Blaxland 760 ft.); they are not, however, typical of this area. *E. botryoides*, *E. umbra* and *E. pilularis* are of course absent. The white gums, *E. haemastoma* and *E. micrantha*, are not so evident, probably because the topography is less rugged, whilst it is sufficiently dry for *E. punctata* and *E. eximia* to be well represented. In the sandstone gullies of the Blue Mts. *A. lanceolata*, *E. punctata* and *E. gummifera*, which are absent from the higher altitudes, are frequently occurring species. A list of the more important dominants of this region is given in Table 3.



Text-fig. 3.—Diagram showing effect of decreasing rainfall on distribution of dominants typical of the coastal and Macdonald regions of the sandstone plateau. -N.B.: with decreasing rainfall, i.e., increasing distance from the sea, the temperature range becomes greater.

(iv). Higher Tableland Region.

The probable correlation between P/E indices and the limitation of many species to high altitudes has been mentioned already. The floristic composition of the forests in the two sub-regions of the tablelands (see Table 6) are slightly different, for example, *E. punctata* is absent and *A. lanceolata* occurs only sporadically up to 2,500 ft. in the Blue Mountain sub-region, whilst *E. gummifera* is absent from the Wingecarribee sub-region. The high altitude species typical of the Blue Mts. such as *E. radiata*, *E. maculosa*, etc., although present in the Wingecarribee, are somewhat localized in their distribution. The absence of *A. lanceolata* and *E. punctata* from the Blue Mts. may be explained by the fact that these species have reached their maximum altitude at approximately 2,500 and 2,200 ft. respectively and are probably restricted from higher altitudes of the Blue Mt. Tableland by the shorter frost-free period. With regard to the less abundant distribution of high altitude species at Wingecarribee, this is most probably connected with P/E

TABLE 6.  
*Distribution of dominant species on the higher tableland sandstone region of the plateau. 'X' = most frequently occurring species, 'x' = presence, '.' = limited occurrence.*

Species.	Distribution.	
	Higher Tableland Region.	
	Wingecarribee.	Blue Mountains.
<i>E. Sieberiana</i>	X	X
<i>E. piperita</i>	X	X
<i>E. micrantha</i>	X	X
<i>E. haemastoma</i>	X	X
<i>E. radiata</i>	x	X
<i>E. maculosa</i>	x	X
<i>E. oreades</i>	x	X
<i>E. dives</i>	.	x
<i>E. Blaxlandi</i>	.	x
<i>E. goniocalyx</i>	.	x
<i>E. eugenioides</i>	x	x
<i>E. rubida</i>	.	.
<i>E. gummiifera</i>	.	x
<i>E. Consideriana</i>	.	.
<i>E. punctata</i>	X	.
<i>A. lanceolata</i>	X	.
<i>E. urceolaris</i>	x	.
<i>E. fraxinoides</i>	x	.
<i>E. agglomerata</i>	.	.

index. The Wingecarribee sub-region has a lower rainfall\* than the higher Blue Mt. Tableland, and although data are not available for P/E indices in this area, it is more than likely that they would be lower than those given for the Blue Mts. (see p. 115). No explanation can be given for the absence of *E. gummiifera* from the Wingecarribee sub-region; it is still present at Wentworth Falls (Blue Mts.) at an elevation of 2,800 ft. In these high plateaux a number of species typical of other associations occur sporadically—the western section of the Blue Mts. is in the nature of a meeting ground for the sandstone species and those typical of the forests on the cool western slopes.

(a). *Higher Blue Mountain Tableland.*

The rainfall in this sub-region decreases gradually to the north-west, so that from Katoomba (3,336 ft.), with a mean rainfall of 55 inches, it decreases at Mt. Victoria (3,424 ft.) to 37.5 inches. This is reflected to some extent in the forests; for example of the "peppermints", *E. piperita* prefers the moister eastern slopes whilst *E. dives* prefers the drier western section.

The species typical of the higher Blue Mt. Tableland are listed in Table 6. There is a topographical restriction of the various species, which, however, is not so well marked as in the coastal plateau, because in the central‡ and western sections of the Blue Mountains the rivers have cut through the sandstone of the Hawkesbury and Narrabeen Series, and have their valley floors either in the soft shales of the Coal Measures, Upper Marine Series, or in older rocks, e.g., granites. In these canyons and gorges there are different *Eucalyptus* forest associations, as well as patches of marginal sub-tropical rain-forest. However, Hawkesbury Sandstones form the surface of the plateau, and there is a variety of habitats from windswept cliffs to sheltered high valleys and slopes. *E. Sieberiana*, *E. piperita*, *E. maculosa* and

\* Mean rainfall.—Mittagong 32.7, Moss Vale 38.8, Sutton Forest 35.5, Bundanoon 42, whereas over the greater part of the Blue Mts. it is at least 45, and frequently more than 50 inches. This higher available moisture in the Blue Mts. is further emphasized by the following fact: the composition of the Hawkesbury Sandstones west of Lawson (Blue Mts.) appears to be somewhat different from much of the typical siliceous sandstone in that there is an increase in felspathic material, which increases the water-retaining capacity of the soil. This seems to be related to the nearness of granitic source of supply from the west.

‡ Most of the eastern section of the Blue Mts., in which sandstone extends to the base of the gorges, is included in region (iii).

*E. micrantha* are abundant on the tops and ridges of the plateau throughout a considerable area: *E. radiata* is common on the highest parts whilst *E. gummifera* occurs only at elevations below 3,000 ft. *E. oreades* and *E. goniocalyx* prefer the sheltered slopes, and in these habitats *E. viminalis* is sometimes found. The stringybarks *E. Blaxlandi* and *E. eugenioides* are abundant both on slopes and ridges. Among the less frequent species are *E. Consideriana*, and in the drier western section of the mountains, *E. dives* and *E. rubida*.

There are many unimportant species of sporadic occurrence which have not been listed; these include *E. notabilis* Maiden, *E. stellaris* Blakely, *E. petrophila* Blakely, *E. Bauerleni* F.v.M., *E. montana* Blakely and *E. squamosa*. With the exception of *E. squamosa* which is also found on the coastal region, these species are all practically restricted to sandstone of the Blue Mts., and may therefore be floristically peculiar to this area. There are also many other unimportant species which have been recorded as occurring sporadically in the Blue Mts., some of which occur on other soil formations or in other regions, e.g., *E. aggregata* Deane and Maiden, *E. mannifera* Mudie, *E. nigra* R. T. Baker, *E. elaeophora* F.v.M. and *E. agglomerata* Maiden.

The forest types of this sub-region are too numerous to list, but as an example of the variety encountered, the following are some of the types recorded in the Leura-Katoomba districts: *E. Sieberiana* (pure); *E. micrantha* (pure); *E. oreades* (pure); *E. Sieberiana*-*E. radiata*-*E. piperita*; *E. Sieberiana*-*E. piperita*-*E. maculosa*-*E. micrantha*; *E. goniocalyx*-*E. Blaxlandi*-*E. eugenioides*; *E. oreades*-*E. goniocalyx*; *E. oreades*-*E. piperita*-*E. Sieberiana*; *E. maculosa*-*E. radiata*-*E. oreades*.

(b). *Wingecarribee Sub-region.*

The most typical species occurring in this section are listed in Table 6. *E. Sieberiana*, *E. piperita*, *E. punctata*, *E. micrantha* and *E. eugenioides* are the most frequent dominants; *E. radiata* and *E. maculosa* are also common but somewhat localized in their distribution. Other dominants typical of the Blue Mts. such as *E. oreades*, *E. Blaxlandi* and *E. goniocalyx* are present, but not widespread. An important species which is floristically peculiar to this area is *E. urceolaris*. This plateau is also the only sandstone area where *E. fraxinoides* occurs; this species is at its northern limit here and extends south to the tablelands near the Victorian border. Of occasional occurrence are *E. dives* and *E. rubida*, whilst *E. Consideriana*, *E. Wilkinsoniana*, *E. agglomerata*, *E. aggregata* and *E. mannifera* occur very sporadically. A few unimportant species which are also found on other soils and in other associations in this region but which do not occur elsewhere on sandstone are *E. Callanii*, *E. vitrea* and *E. cinerea*.

DISTRIBUTION OF MALLEES.

The dwarf species of *Eucalyptus*, known as mallees, are typical of exposed areas, and are particularly characteristic of extensive areas of windswept plateau along the edges of cliffs in the higher Blue Mt. Tableland. In the coastal region, mallees occur sporadically and in small group societies, but do not form extensive areas of tree-scrub. The distribution of the various species of mallees, like that of the dominants, falls into two fairly well-defined groups characteristic of the low coastal region and the higher tablelands; several species, e.g., *E. stricta* and *E. multicaulis*, are not limited by altitude and occur throughout the association. The specific range is summarized in Table 7. In the coastal region *E. virgata*, *E. obtusiflora* and *E. multicaulis* are the most prominent mallees, but in the Blue Mts. *E. stricta* is the most frequent species.

FORESTS ON SOILS DERIVED FROM WIANAMATTA SHALES.

Most of the Wianamatta Shales occur in a basin-like area to the west of Sydney, referred to as the Cumberland Basin. The plains are gently undulating with low hills up to 500 ft. The physiography of this area has resulted in the preservation of these soft shales which, except for a few shallow outliers, have been eroded from the surrounding sandstone plateau. Three stages of the Wianamatta Shales are recognized. These are: 1. Upper stage, consisting mainly of sandstone with interbedded shales. 2. Middle stage, containing the calcareous ostracod sandstones. 3. Lower stage, consisting exclusively of shales. Over most of the Cumberland Basin the upper stage

TABLE 7.

Distribution of mallees in the various regions of the sandstone plateau. 'x' denotes presence.

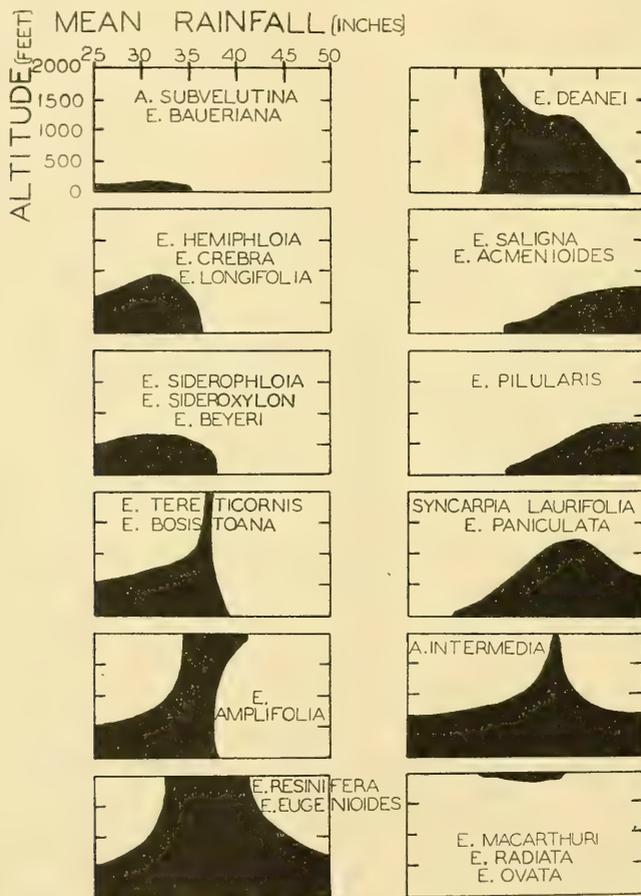
Species.	Distribution.				
	Coastal Region.			Higher Tableland Region.	
	Hornsby Plateau.	Ourimbah.	Nepean Ramp.	Blue Mountains.	Wingecarribee.
<i>E. virgata</i> Sieb. . . . .	x	x	x		
<i>E. obtusiflora</i> DC. . . . .	x	x	x		
<i>E. Camfieldi</i> Maiden . . . . .	x	x	x		
<i>E. multicaulis</i> Blakely . . . . .	x	x		x	
<i>E. deformis</i> Blakely . . . . .		x		x	
<i>E. pygmaea</i> Blakely . . . . .	x				
<i>E. stricta</i> Sieb. . . . .	x	x			
<i>E. apiculata</i> Baker and Smith . . . . .				x	x
<i>E. triflora</i> Blakely . . . . .				x	
<i>E. ligustrina</i> DC. . . . .				x	
<i>E. rigescans</i> Blakely . . . . .				x	
<i>E. aequans</i> Blakely . . . . .				x	
<i>E. tephrophloia</i> Blakely . . . . .				x	

has been eroded but parts of the middle stage have been preserved, and where the ostracod sandstones outcrop to any extent they have been utilized for vineyards. In the Parramatta-Windsor districts in the Cumberland Basin, the lower stage only remains, and the various shale outliers on the sandstone plateau are also formed entirely of these lower beds. Apart from the ostracod sandstones, which cover a relatively small area, the soils derived from the various shale horizons are therefore comparable. Small amounts of ostracod sandstones have little or no effect on the type of forest developed, but it is interesting to record that in the Kurrajong-Grose Vale districts on calcareous sandstones, remnants of "brush" or marginal rain-forest are found. The soil is probably not entirely responsible for this, because the area receives a high rainfall—approximately 50 inches, and is also relatively sheltered.

The Cumberland Basin corresponds approximately to a low rainfall area with a mean rainfall of less than 30 inches; the P/E index for Richmond, which is typical of the area, is 0.63 (cf. Sydney 1.02), whilst that of Parramatta on the eastern margin of the basin is 0.76. As well as being comparatively dry, this region is also hot with extremes of temperature—mean daily range at Richmond is 25 Fahrenheit degrees, whereas the range at Sydney is 14 Fahrenheit degrees. Shale soils under these climatic conditions are covered by the *E. hemiphloia*-*E. tereticornis* Association, but with an increase in mean rainfall up to approximately 38 inches this association is replaced by entirely different forests. The only Wianamatta Shale soils receiving this higher rainfall occur as outliers on the sandstone plateau. There are three distinct groups of outliers: (Text-fig. 1) (a) on the Hornsby Plateau, (b) on the lower slopes of the Blue Mts., (c) on the Wingecarribee Tableland in the vicinity of Moss Vale. In district (a) the *E. saligna*-*E. pilularis* forest types occur, and in district (b) forest types consisting of *E. Deanei*, *Syncarpia*, *E. paniculata* and *E. eugenioides* are present. All these forest types belong to the *E. saligna*-*E. pilularis* Association. In district (c) a different set of forest types consisting of *E. radiata*-*E. eugenioides*-*E. goniocalyx*, *E. Macarthuri*-*E. ovata*, and *E. pauciflora*-*E. stellulata* are present. These types are fragments of several different associations.

The most probable factor which determines the delimitation of these associations is P/E index. With an index of < 1 (approximately 0.6), the *E. hemiphloia*-*E. tereticornis* Association is present; with an index of approximately 1, the *E. saligna*-*E. pilularis* forest replaces the former. This association, however, does not occur at high altitudes, e.g., at Moss Vale, because both dominants are low altitude species, probably limited by length of frost-free period. Hence new forest types make their appearance, namely, *E. radiata*, *E. goniocalyx*, *E. Macarthuri*, *E. ovata*, *E. pauciflora*, etc. An attempt has been made to represent the climatic control of the distribution of

the dominants on shale soil in Text-figure 4. In Table 8 are listed all the important species occurring on the various outcrops of Wianamatta Shale in the central coastlands. There are a few species common to both the *E. saligna*-*E. pitularis* and *E. hemiphloia*-*E. tereticornis* Associations but the dominants from which these associations derive their names are segregated from one another; this justifies their separation as associations (Pidgeon, 1937); the forests of the cold tablelands have little in common with either of the other associations. In the following pages the various forest types and associations found on Wianamatta Shales are discussed in more detail. Apart from the *E. hemiphloia*-*E. tereticornis* Association, the other forest types are very limited and are recorded here only as an example of the dominating influence of climate on the development of different forest associations on the same geological formation.



Text-fig. 4.—Diagrams showing tolerance of dominants on soils derived from Wianamatta Shales.

#### *E. hemiphloia*-*E. tereticornis* Association.

As previously stated, this association is typical of soils derived from Wianamatta Shales with a rainfall of 30 inches or less. Other fragments of this association occur in dry areas along the coast of New South Wales, e.g., at Dapto (in the south of the central coastal area) and in the Upper Williams River (Fraser and Vickery, 1939).

Physiognomically, the *E. hemiphloia*-*E. tereticornis* Association has more affinity with woodland than typical coastal forest formation. The parkland appearance has been further emphasized by timber cutting for firewood (especially of *E. hemiphloia*) and clearing for cultivation.

TABLE 8.

List of more important dominants occurring on Wianamatta Shale soils in various sub-regions of the central coastlands. 'X' = most frequently occurring species, 'x' = presence, '.' = limited occurrence.

Species.	Distribution.			
	Cumberland Basin.	Hornsby Plateau.	Wingecarribee.	Lower Tableland Slopes.
<i>E. hemiphloia</i>	X			
<i>E. tereticornis</i>	X		.	
<i>E. siderophloia</i>	X			
<i>E. sideroxylon</i>	x			
<i>E. crebra</i>	X			
<i>E. Beyerii</i>	x			
<i>E. longifolia</i>	x			
<i>E. amplifolia</i>	X		x	
<i>Angophora intermedia</i>	X	x	.	.
<i>A. subvelutina</i>	X			
<i>E. eugenioides</i>	x	x	x	x
<i>E. resinifera</i>	.	x	.	x
<i>E. maculata</i>	.			
<i>E. Baueriana</i>	.			
<i>E. Rudderii</i>	.			
<i>E. Parramattensis</i>	.			
<i>E. Macarthurii</i>	.		X	
<i>E. ovata</i>	.		X	
<i>E. radiata</i>	.		X	
<i>E. goniocalyx</i>	.		X	
<i>E. stellulata</i>	.		.	
<i>E. pauciflora</i>	.		.	
<i>E. paniculata</i>	.	x		x
<i>E. saligna</i>	.	x		
<i>E. pilularis</i>	.	x		
<i>E. acmenioides</i>	.	x		
<i>Syncarpia laurifolia</i>	.	x		X
<i>E. Deanei</i>	.	.	.	X

TABLE 9.

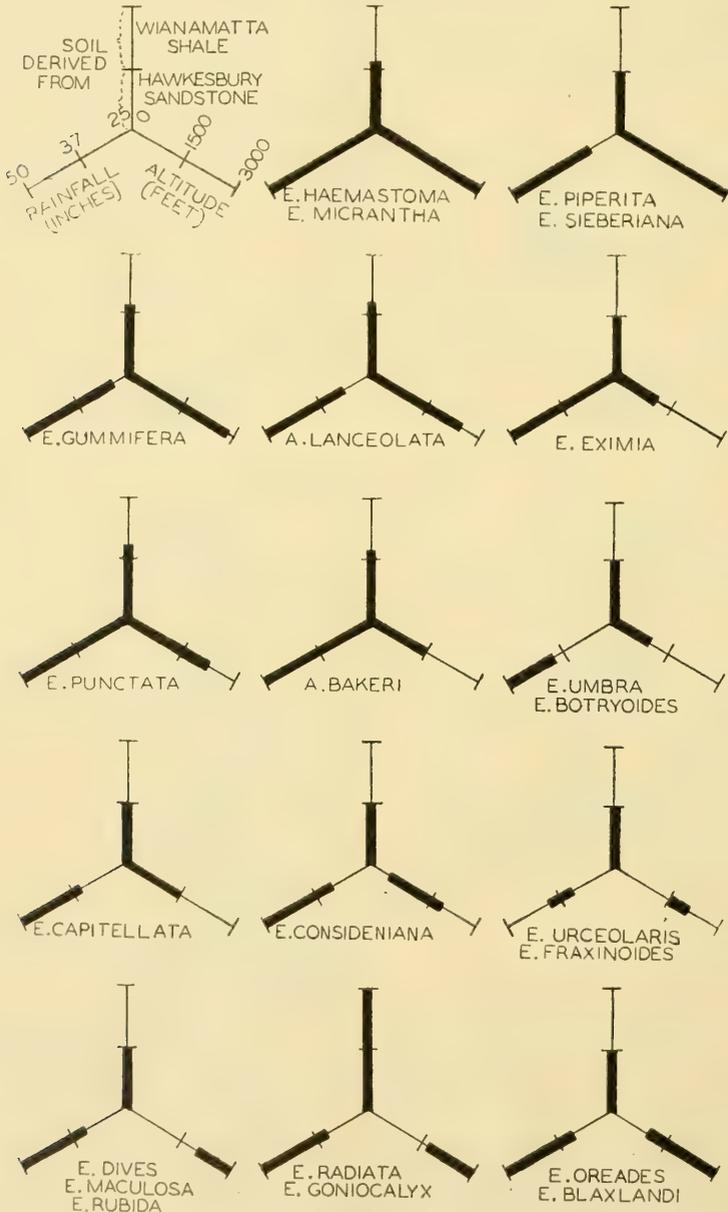
List of dominants in the *E. hemiphloia*-*E. tereticornis* Association. '\*' = most frequent species.

* <i>E. hemiphloia</i> F. v. M.	<i>E. resinifera</i> Sm.
* <i>E. tereticornis</i> Sm.	<i>E. paniculata</i> Sm.
* <i>E. amplifolia</i> Naudin.	<i>E. sparsifolia</i> Blakely.
* <i>E. siderophloia</i> Benth.	<i>E. Wilkinsoniana</i> R. T. Baker.
* <i>E. sideroxylon</i> (A. Cunn.).	<i>E. acervula</i> Sieb.
* <i>E. crebra</i> F. v. M.	<i>E. maculata</i> Hook.
* <i>E. Beyerii</i> R. T. Baker	<i>E. Parramattensis</i> C. Hall.
* <i>A. intermedia</i> DC.	<i>E. Bosistoana</i> F. v. M.
* <i>A. subvelutina</i> F. v. M.	<i>E. Baueriana</i> F. v. M.
* <i>E. eugenioides</i> Sieb.	<i>E. Rudderii</i> Maiden.
<i>E. longifolia</i> Linn. and Otto.	<i>Melaleuca</i> spp.
<i>Syncarpia laurifolia</i> Ten.	<i>Casuarina Cunninghamiana</i> (near fresh water).

The more important tree species of this association are listed in Table 9. The habitats available to these species are not so very diverse since the shale country is gently undulating; there are, however, extensive flats which are liable to flooding and waterlogging. Brief notes on the habitats of some of the more important species are given below:

*E. hemiphloia* and *E. tereticornis* are the most widespread species. They prefer well-drained soils of the slopes, but are not altogether absent from the flats. *E. amplifolia* is very similar to *E. tereticornis* and replaces it on swampy flats in the vicinity of creeks. The ironbarks *E. siderophloia*, *E. crebra* and less commonly *E. Beyerii*, *E. paniculata* and *E. sideroxylon*, occur on low ridges and hillsides, the soil often being lateritic gravel. *E. siderophloia* also extends to the flats. *E. paniculata* is more or less restricted to the margins of the Cumberland Basin,

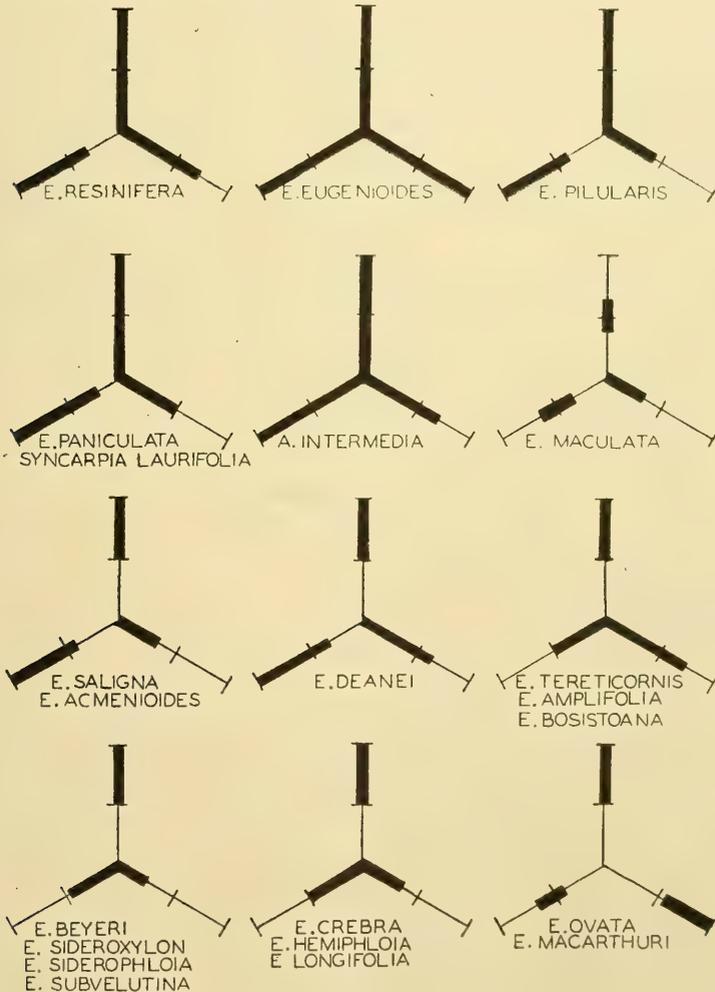
i.e., in the higher rainfall areas. *Angophora intermedia* is another widespread species, whilst *A. subvelutina* is limited to heavy soils on the flats. *E. eugenioides*, *E. resinifera*, other stringybarks and *E. longifolia* occur scattered throughout the whole area, usually on well-drained soils. There is a number of additional unimportant species of limited occurrence, e.g., *E. Baueriana* and *Casuarina Cunninghamiana*, which are restricted to creek banks, and *E. Bosistoana* and *E. Rudderi*. Small patches of *E. maculata* occur in isolated localities, usually on soil derived



Text-fig. 5a.—Diagrams showing edaphic and climatic tolerance of the more important species occurring on soils derived from Hawkesbury Sandstones and Wianamatta Shales. The distribution of species peculiar to edaphic ecotones is represented as in the diagram for *E. maculata*, and that of species peculiar to one particular soil type, but which also occur in ecotones, is represented as in the diagram for *A. lanceolata*.

from a mixture of sandstone and shale. The presence of subdominant strata of *Melaleuca* spp. (e.g., *M. styphelioides*, *M. linariifolia*) indicates occasional waterlogging of the soil.

The wider distribution of the more important dominants outside the *E. hemiphloia*-*E. tereticornis* Association is noteworthy. *E. hemiphloia* occurs in the drier parts of the central and northern coast of New South Wales and extends into Queensland. It is typical of heavy soils or light soils with clay sub-soil, rather low-lying and more or less subject to waterlogging. *E. tereticornis* is a coastal species extending from Victoria along the east coast of Australia. It has its best development on the flats on fairly rich soils. *E. amplifolia* extends further inland than *E. tereticornis*, but occurs only in New South Wales and Queensland. It is confined to shallow alluvial flats of heavy soils. *E. siderophloia* is chiefly coastal in its distribution and extends from the central coast of New South Wales to Rockhampton. It occurs on a variety of soils from sub-basaltic to poor sandy flats with hard clay sub-soil. *E. sideroxyton* extends from Victoria to Queensland and in New South Wales is more frequent on the western slopes where it favours Silurian slate ridges. It also occurs on the coast on poor sedimentary formations. *E. crebra* extends from the central coastlands of New South Wales to Queensland; it is not a coastal species, but flourishes under hot



Text-fig. 5b.—For explanatory details see Text-fig. 5a.

dry conditions. *E. Beyeri* is restricted to the shales of the Cumberland Basin. *E. paniculata* is a strictly coastal species extending along the coast of New South Wales and Queensland. It occurs mainly on shale and sandy-loams. *Angophora intermedia* and *A. subvelutina* extend from the central coast to Queensland. The former is widely distributed in the central and north-west slopes of New South Wales on alluvial and deep sandy soil, along flats and watercourses, and extending up hillsides. *A. subvelutina* is more coastal in distribution, and occurs on heavy, moderately rich soils, almost always near watercourses. *E. maculata* is distributed along the eastern coast of Australia on a wide range of soil types, but usually on moderately poor sandy-shales. In the central coastlands it frequently occurs on Narrabeen Shales. *E. longifolia* is chiefly distributed along the south and central coasts of New South Wales on deep alluvial soil.

No attempt is made to list all the forest types in the *E. hemiphloia*-*E. tereticornis* Association, but an indication of the variety of types found in one small area is given in Table 10. In addition to mixed stands, fairly pure stands of species such as *E. hemiphloia*, *E. crebra* and *E. siderophloia*, and co-dominant types such as *E. hemiphloia*-*E. siderophloia* and *E. tereticornis*-*E. hemiphloia* are of wide occurrence.

#### *E. saligna*-*E. pilularis* Association.

The *E. saligna*-*E. pilularis* Association is extensively distributed over the coastal plains of New South Wales, and in the central coastal area is typical of Narrabeen Shales and of some of the soils derived from the Upper Coal Measures. This paper is concerned only with its occurrence on the Wianamatta Shale outliers on the Hornsby Plateau, and on the lower slopes of the Blue Mts. On the Hornsby Plateau these outliers form two parallel divides, one of which separates the deep valleys of Middle Harbour and the Lane Cove River, and the other to the west links up with the shales of the Cumberland Basin (see Fig. 1).

TABLE 10.

Some forest types of the *E. hemiphloia*-*E. tereticornis* Association recorded in the Bankstown-Liverpool districts. Species in braces indicate those which may occur as subsidiary species in that particular forest type.

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<i>E. siderophloia</i> - <i>E. hemiphloia</i> ±	$\left\{ \begin{array}{l} E. tereticornis \\ Syncarpia laurifolia \end{array} \right\}$
<i>E. hemiphloia</i> - <i>E. tereticornis</i> .	
<i>E. hemiphloia</i> - <i>E. tereticornis</i> - <i>E. crebra</i> ±	$\left\{ \begin{array}{l} E. eugenioides \\ E. longifolia \\ E. siderophloia \end{array} \right\}$
<i>E. tereticornis</i> - <i>Angophora intermedia</i> .	
<i>A. intermedia</i> - <i>E. longifolia</i> - <i>E. tereticornis</i> ±	$\left\{ \begin{array}{l} E. eugenioides \\ E. sideroxylon \end{array} \right\}$
<i>E. paniculata</i> - <i>E. tereticornis</i> ±	$\left\{ \begin{array}{l} E. longifolia \\ E. siderophloia \end{array} \right\}$
<i>E. tereticornis</i> - <i>E. sideroxylon</i> - <i>E. crebra</i> .	
<i>E. crebra</i> - <i>E. siderophloia</i> .	
<i>A. subvelutina</i> - <i>E. amplifolia</i> .	

---

Since the shale outliers occupy ridges, they are for the most part fairly exposed, but there are shallow valleys and hollows which give protection. Whereas on sandstone these shallow valleys would result in a complete change in forest type from that on the ridge, because constancy of forest type is dependent on soil moisture conditions, and these vary with slope, on shale the same dominants (namely *E. saligna* and *E. pilularis*) occur in both habitats. This is explained by the fact that shale soils have a sufficiently high water-retaining capacity to enable the forest type to be independent of minor changes in environment. It is noteworthy, however, that with protection in the hollows, a number of mesophytic species occur in the sub-dominant strata.

Species which represent the association on Wianamatta Shale are: *E. saligna*, *E. pilularis*, *E. paniculata*, *E. acmenioides*, *E. resinifera*, *E. eugenioides*, *Angophora intermedia* and *Syncarpia laurifolia*. *E. saligna* and *E. acmenioides* occupy the moist habitats usually to the exclusion of other species, whilst *E. pilularis* and *E. paniculata*,

in addition to *E. saligna*, occur on the drier slopes. The forest types are mainly variants of *E. saligna*-*E. pilularis* and *E. pilularis*-*E. paniculata*-*Syncarpia* groupings.

On the shales to the east and north of Parramatta there is an ecotone in which *E. pilularis*, *E. saligna* and *E. tereticornis* are intermingled. The transition from the *E. saligna*-*E. pilularis* Association (rainfall 40 inches) to the *E. hemiphloia*-*E. tereticornis* Association (rainfall 30 inches) is illustrated by Table 11.

TABLE 11.  
Transect from Parramatta to Windsor, along the Windsor Road. (See Text-fig. 1.)

Approx. Mileage.	District.	Mean Rainfall. (Inches.)	Dominant Species.	Additional Notes.
0 4½	Parramatta to Baulkham Hills.	35	<i>E. paniculata.</i> <i>E. pilularis.</i> <i>E. saligna</i> (on flats near creeks). <i>A. intermedia.</i> <i>Syncarpia laurifolia.</i> <i>E. acenioides.</i> <i>E. punctata.</i> Various stringybarks.	<i>E. tereticornis</i> and <i>E. crebra</i> occur sporadically.
7 9	Seven Hills to Kellyville.	30 (approx.)	<i>A. intermedia.</i> <i>E. tereticornis.</i> <i>E. siderophloia.</i> <i>E. hemiphloia.</i> <i>E. crebra.</i> <i>E. eugenioides.</i> <i>E. saligna.</i>	<i>E. saligna</i> still abundant on flats. First appearance of <i>E. hemiphloia.</i>
9 13	Kellyville to Rouse Hill.	—	<i>E. crebra.</i> <i>E. siderophloia.</i> <i>E. tereticornis.</i> <i>E. amplifolia</i> <i>A. intermedia</i> } creeks.	<i>E. saligna</i> occasional on flats.
15	Riverstone turn-off.	—	<i>E. crebra.</i> <i>E. siderophloia.</i> <i>E. tereticornis.</i> <i>E. hemiphloia.</i> <i>E. amplifolia</i> <i>Casuarina</i> <i>Cunninghamiana</i> } creeks.	<i>E. saligna</i> disappears, <i>E. hemiphloia</i> abundant.
21	Windsor.	27	<i>E. tereticornis.</i> <i>E. hemiphloia.</i> <i>E. crebra.</i> <i>E. siderophloia.</i>	
28	Lower slopes Grose Vale road.	More than 35	<i>Syncarpia laurifolia.</i> <i>E. tereticornis.</i> <i>E. crebra</i> (on hills).	<i>E. hemiphloia</i> disappears; greater rainfall and well drained slopes.

On the lower slopes of the Blue Mts., e.g., at Springwood, there is a number of small scattered outliers of shale. Neither *E. saligna* nor *E. pilularis* occurs in these areas, but *E. Deanei* is present. This species appears to replace *E. saligna* at higher altitudes and inland from the coastal area. Other species which are present include *Syncarpia laurifolia*, *E. paniculata*, *E. eugenioides* and *E. resinifera*. These small stands of forest may be regarded as local variants of the *E. saligna*-*E. pilularis* Association.

*Forest Types on the Wingecarribee Tableland.*

The Wianamatta Shales in the Bundanoon-Moss Vale-Bowral area are characterized by an entirely different set of forest types, viz., *E. Macarthuri*-*E. ovata* on flats near watercourses; *E. radiata*-*E. goniocalyx*-*E. eugenioides* and *E. pauciflora*-*E. stellata* on well-drained areas. Additional species of minor importance include *E. viminalis*,

*E. amplifolia*, *Angophora intermedia*, *E. tereticornis* and *E. Bosistoana* (rare). So that, apart from *E. eugenioides* and *E. amplifolia*, and a few odd trees of *E. tereticornis*, *A. intermedia* and *E. Bosistoana*, this shale vegetation bears no relationship to the two preceding associations. The differences might be attributable to climate, which is of the cold tableland type with severe frosts.

The affinities of the various forest types are suggested as follows:

- (a). *E. radiata*-*E. goniocalyx*-*E. eugenioides* forest types: allied to the *E. viminalis*-*E. fastigata* Association (including *E. obliqua*). This is a wet sclerophyll type of forest characteristic of the southern tablelands of N.S.W.
- (b). *E. pauciflora*-*E. stellulata* type: a fragment of the association of the same name, also typical of southern tablelands at high elevations.
- (c). *E. amplifolia*, *E. tereticornis*, *E. Bosistoana*: scattered trees representing outliers of the *E. hemiphloia*-*E. tereticornis* Association.
- (d). *E. Macarthurii*-*E. ovata*: subclimax types controlled by drainage.

#### SANDSTONE AND SHALE ECOTONES.

Since there is every gradation between shale and sandstone around the outliers of shale, one would expect, and one does find transitional zones (ecotones). Most of the transitional forests have two features in common, first a mingling of dominants from both soil types, and secondly, a peculiarly characteristic undergrowth which can be distinguished from that typical of sandstone forests by the absence of a large number of sclerophyllous shrubs and an increase in the number of grasses and herbs. The actual composition of any stand of transitional forest is dependent on the depth of shale and on the soil moisture. A brief summary of some of the more frequent ecotone forests is recorded in the following notes:

##### *Ecotones between the E. saligna-E. pilularis and Mixed Eucalyptus Forest Association.*

These ecotones contain a predominance of stringybarks (*E. resinifera* and *E. eugenioides*), with *Syncarpia laurifolia*, *E. paniculata*, *E. pilularis* and *A. lanceolata*. Notable absentees are *E. saligna*, *E. piperita* and *E. haemastoma*. The composition of the stands varies according to the depth of shale. On thin cappings *A. lanceolata*, *E. gummifera* and *E. micrantha* may occur with scattered trees of *E. eugenioides*, *E. pilularis* and *Syncarpia*. On deeper shale transitions, *E. resinifera*, *E. eugenioides*, *E. pilularis*, *Syncarpia* and *E. paniculata* are the dominants.

##### *Ecotones between the E. hemiphloia-E. tereticornis and Mixed Eucalyptus Forest Associations.*

These ecotones are abundant and variable and since they occur in the vicinity of the 30 inch isohyet, the sandstone species are those typical of the drier areas. The constituent trees of ecotone forests in four localities are listed below:

Bankstown.	The Oaks: Camden.	Bargo.	Campbelltown-Appin.
<i>E. eugenioides</i> .	<i>Syncarpia laurifolia</i> .	<i>E. paniculata</i> .	<i>E. maculata</i> .
<i>A. intermedia</i> .	<i>A. lanceolata</i> .	<i>E. punctata</i> .	<i>E. eugenioides</i> .
<i>E. punctata</i> .	<i>E. punctata</i> .	<i>E. micrantha</i> .	<i>E. paniculata</i> .
<i>Syncarpia laurifolia</i> .	<i>A. intermedia</i> .	<i>E. eugenioides</i> .	<i>E. crebra</i> .
<i>E. paniculata</i> .	<i>E. resinifera</i> .		
	Various ironbarks and stringybarks.		

##### *Ecotone Forests on Soils derived from Shale Bands in Hawkesbury Sandstone.*

A number of relatively small lenticular shale beds are intercalated throughout the Hawkesbury Sandstone strata, and these weather to a slightly better soil than that derived from pure sandstone. These shale bands are particularly evident throughout parts of the Macdonald region, especially around the Upper Colo district, and on the loams derived from a mixture of these shales and sandstones occur species such as *E. paniculata*, *A. intermedia*, *Syncarpia*, and various stringybarks. These species are associated with other typical sandstone species such as *E. punctata*, *A. lanceolata*, and

*E. gummifera*. Similar shale bands of lesser extent occur throughout the coastal region, but here *A. intermedia* is less evident; it apparently prefers the drier areas. Where these shale beds are very thin they do not greatly improve the water-retaining capacity of the soil, and the forest may consist entirely of sandstone species such as *E. micrantha*, *A. lanceolata*, *E. eugenioides* and *E. gummifera*, but the stands are better developed than those on similar positions on pure sandstone soils.

CONCLUSIONS.

Any classification of vegetation is subjective, and must stand or fall by its accordance with current ideas on the structure of plant communities, and on its convenience to foresters and ecologists. The major difficulty in classifying the forests described in this paper is that many species of *Eucalyptus* are not only taxonomically but ecologically distinct. The data assembled in Text-figures 2, 3, and 4 illustrate how there is a group of Eucalypts adapted to every complex of conditions, and very few species are tolerant of a wide range of conditions. It is difficult, therefore, in an area with a great assortment of micro-climates, to avoid an unwieldy classification. Yet it is clear from the results of Scandinavian plant geographers that one must avoid the temptation to split up communities without good reason. Lindquist, for instance (1931), distinguishes thirteen different associations of an herbaceous plant *Asperula*, according to the species associated with it; and Osvald (1923), following the same course, discovers 164 separate associations in a stretch of moorland only forty square miles in area. On the criteria used by these workers hundreds of associations could be described among the forests around Sydney. Each of the *Angophora lanceolata* forest

TABLE 12.

Table showing specific effect of soil on species distribution in the central coastlands. 'x' = presence, 'x'' = presence in Wingecarribee sub-region only, '·' = limited occurrence.

Species.	Distribution on Soils Derived from			Species.	Distribution on Soils Derived from		
	Hawkesbury Sandstone.	Wianamatta Shale.	Ecotones.		Hawkesbury Sandstone.	Wianamatta Shale.	Ecotones.
<i>E. Sieberiana</i> .. .. .	x			<i>Syncarpia laurifolia</i> ..	x	·	x
<i>E. piperita</i> .. .. .	x			<i>E. paniculata</i> .. .. .		x	x
<i>E. micrantha</i> .. .. .	x			<i>E. agglomerata</i> .. .. .			·
<i>E. haemastoma</i> .. .. .	x			<i>A. intermedia</i> .. .. .		x	x
<i>E. gummifera</i> .. .. .	x			<i>A. subvelutina</i> .. .. .		x	
<i>E. eximia</i> .. .. .	x			<i>E. Wilkinsoniana</i> .. ..			·
<i>E. punctata</i> .. .. .	x		x	<i>E. acervula</i> .. .. .			·
<i>A. lanceolata</i> .. .. .	x		x	<i>E. sparsifolia</i> .. .. .		x	·
<i>A. Bakeri</i> .. .. .	x		x	<i>E. saligna</i> .. .. .		x	
<i>E. umbra</i> .. .. .	x			<i>E. acmenioides</i> .. .. .		x	
<i>E. botryoides</i> .. .. .	x			<i>E. hemiphloia</i> .. .. .		x	
<i>E. capitellata</i> .. .. .	x			<i>E. tereticornis</i> .. .. .		x	
<i>E. eugenioides</i> .. .. .	x	x	x	<i>E. amphifolia</i> .. .. .		x	
<i>E. resinifera</i> .. .. .	x		x	<i>E. longifolia</i> .. .. .		x	
<i>E. Blaxlandi</i> .. .. .	x			<i>E. crebra</i> .. .. .		x	
<i>E. maculosa</i> .. .. .	x			<i>E. Beyerii</i> .. .. .		x	
<i>E. rubida</i> .. .. .	x			<i>E. sideroxyylon</i> .. .. .		x	
<i>E. oreades</i> .. .. .	x			<i>E. Macarthuri</i> .. .. .		x'	
<i>E. dives</i> .. .. .	x			<i>E. ovata</i> .. .. .		x'	
<i>E. notabilis</i> .. .. .	x			<i>E. stellulata</i> .. .. .		x'	
<i>E. Consideriana</i> .. .. .	x			<i>E. pauciflora</i> .. .. .		x'	
<i>E. urceolaris</i> .. .. .	x'			<i>E. maculata</i> .. .. .			
<i>E. fraxinoides</i> .. .. .	x'			<i>E. Baueriana</i> .. .. .		x	
<i>E. pilularis</i> .. .. .	x		x	<i>E. Rudderi</i> .. .. .			
<i>E. radiata</i> .. .. .	x	x'		<i>E. Parramattensis</i> .. ..		·	
<i>E. goniocalyx</i> .. .. .	x	x'					

types in Table 5 and on page 122, for instance, would be a separate association, and one could doubtless discover a dozen more of them.

To avoid the manifest disadvantages of this procedure, the writer has described all forests on sandstone as Mixed *Eucalyptus* Forest. There are indeed striking contrasts among these forests, but as reference to Table 3 shows, there is so much overlap that *no species are peculiar to any one variant* of the Mixed *Eucalyptus* Forest. On the shale, however, there is a sufficiently clear distinction between the common species in the Cumberland Basin, on the Hornsby Plateau and on the Wingecarribee Tableland (Table 8) to justify the classification into two well represented associations: the *E. hemiphloia*-*E. tereticornis* Association, and the *E. saligna*-*E. pilularis* Association, with fragments of two other associations: the *E. viminalis*-*E. fastigata* Association and the *E. pauciflora*-*E. stellulata* Association.

There is a striking difference both in regard to floristics and physiognomy between the sandstone and shale forests, irrespective of the climate. Table 12 provides evidence for this specific effect of soil on species distribution. In sandstone gullies on the Hornsby Plateau where the water balance in the soil is comparable to that on the outliers of shale, one does not find typical *E. saligna*-*E. pilularis* shale forest; only *E. pilularis* is common to both habitats. It is apparent, therefore, that the restriction of certain species to certain soils is determined by some factor other than soil moisture. The distribution of species over the sandstone and shale regions is determined primarily by rainfall and altitude, the former through its effect on the P/E, and the latter through its effect on the temperature range and the length of the frost-free period. The edaphic and climatic tolerance of the more important species is summarized by Text-figure 5.

Further analysis of the forest vegetation in the central coastal area of New South Wales must await studies in the comparative physiology of species of *Eucalyptus*. The factors which restrict *E. haemastoma* to poor sandstone soils, *E. hemiphloia* to dry shale soils, *E. dives* to high altitudes, and *E. botryoides* to situations near the sea, will doubtless be difficult to analyse; but until the physiological data are available, any views as to the cause of the distribution of forest types must remain mere speculation.

#### SUMMARY.

A brief account is given of the distribution of forest types on the soils derived from Hawkesbury Sandstone and Wianamatta Shale in the central coastal area of New South Wales.

For reasons discussed in the body of the paper, forests on sandstone are classified as variants of one association: the Mixed *Eucalyptus* Forest; and forests on shale fall into several distinct associations: *E. hemiphloia*-*E. tereticornis*, *E. saligna*-*E. pilularis*, *E. viminalis*-*E. fastigata*, and *E. pauciflora*-*E. stellulata* Associations.

Data are given which illustrate the remarkable specificity of species of *Eucalyptus* to ecological conditions, in particular to rainfall, altitude, and soil type. The bearing of this phenomenon upon the problem of classifying the forests is discussed.

#### Acknowledgement.

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## THE DIPTERA OF THE TERRITORY OF NEW GUINEA. XII.

FAMILY TIPULIDAE. PART IV.\*

By CHARLES P. ALEXANDER.

(Communicated by F. H. Taylor, F.R.E.S., F.Z.S.)

(Eleven Text-figures.)

[Read 25th June, 1941.]

In the present instalment I am considering a further series collected by Mr. Frank H. Taylor, chiefly at Aitape and Wewak. Types of the novelties will be returned to Mr. Taylor and will be preserved in the collection of the School of Public Health and Tropical Medicine of the University of Sydney. As before, I herewith express my deepest thanks to Director Harvey Sutton, of the School of Public Health, and to my colleague, Mr. Frank H. Taylor, who has added so materially to our knowledge of the Diptera of New Guinea.

## LIMONIINAE.

## LIMONIINI.

## LIMONIA (LIMONIA) UMBRATA PERREDUCTA, n. subsp.

♂.—Length about 4.4–5 mm.; wing 4.5–5 mm.

♀.—Length about 5 mm.; wing 4.5 mm.

Similar to the typical form but with the apex of each gonapophysis of the male terminalia reduced to a single conical or peg-like point instead of the bilobed blade of typical *umbrata*. In the holotype, the dark wing pattern is paler and less conspicuous than in the other specimens.

Holotype, ♂, Wewak, 25th October, 1936. Allotopotype, ♀, 21st November, 1936. Paratype, ♂, Aitape, 8th January, 1937 (F. H. Taylor).

The species *umbrata* (de Meijere) is widespread not only in the tropics of the Oriental Region but also in the Neotropics (Cuba, Mexico, Brazil), to which latter region it evidently has been transported by human means.

## LIMONIA (LAOSA) INNUBA, n. sp.

General colouration brownish-yellow; antennae with scape and pedicel black, the flagellum yellowish-brown; halteres yellow, the knob brownish-black at apex; legs yellow, the terminal tarsal segments darkened; wings whitish-hyaline on basal half, weakly infumated on outer portion; a darker brown pattern, including a major area beyond cord; certain of cells variegated by whitish areas; Rs strongly arcuated; cell 2nd A wide; abdominal tergites obscure-yellow, the caudal borders broadly black; sternites more uniformly yellow.

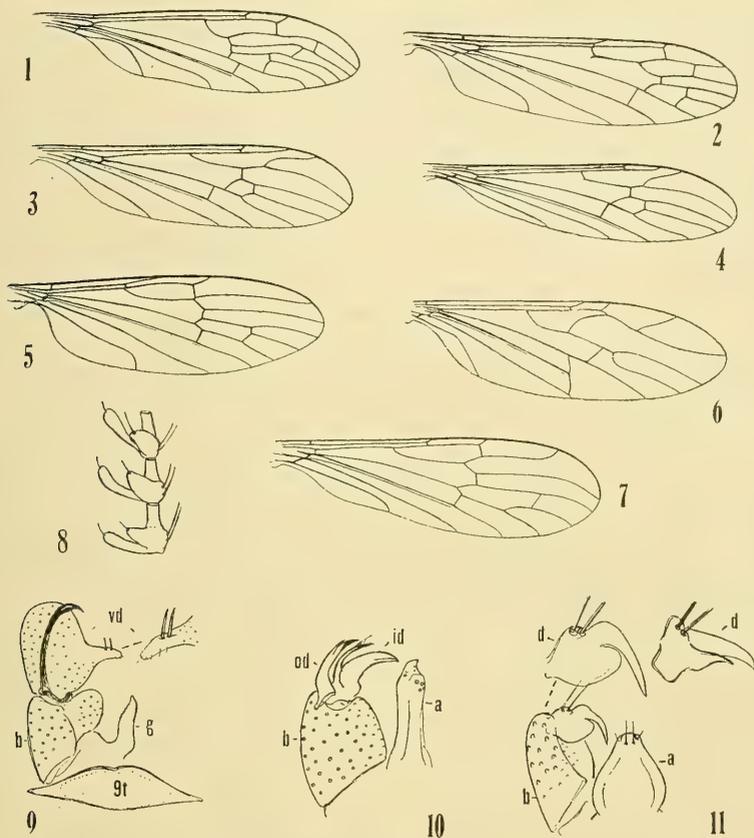
♀.—Length about 10 mm.; wing 10 mm.

Rostrum black, shiny; palpi brownish-black. Antennae with scape and pedicel black, flagellum pale yellowish-brown; terminal flagellar segment elongate, exceeding the penultimate. Anterior vertex narrow, grey, as are the posterior orbits; remainder of dorsum of head darker grey.

Pronotum obscure brownish-yellow. Mesonotum almost uniformly brownish-yellow, the praescutum without distinct stripes, the humeral region a trifle darker; scutal lobes slightly darker; scutellum and mediotergite more pruinose. Pleura obscure brownish-yellow, the anepisternum a little darker. Halteres yellow, the apex of knob brownish-black. Legs with the coxae yellow, the fore pair more infuscated; trochanters yellow; remainder of legs yellow, the outer tarsal segments infuscated. Wings (Fig. 1) with the ground colour of basal half whitish-hyaline, of the distal portion weakly infuscated; a slightly darker brown pattern, as follows: at arculus; a narrow oblique band crossing

\* Continued from These PROCEEDINGS, lxi, 1936, 322.

the basal fourth of wing, extending from vein R to the margin at end of vein 2nd A; small isolated spots at origin of Rs and end of vein 1st A; a large darkened area beginning at cord and including more than one-half of the remainder of wing to shortly beyond the level of the outer supernumerary cross-vein in cell  $R_3$ , variegated by linear whitish lines in cell  $R_3$  before the cross-vein, in basal third of cell  $R_5$  and in the



Text-figs. 1-11.

1.—*Limonia (Laosa) innuba*, n. sp., venation. 2.—*L. (Rhipidia) diploclada*, n. sp., venation. 3.—*Helius (Rhampholimnobia) diffusus*, n. sp., venation. 4.—*H. (R.) nimbus*, n. sp., venation. 5.—*Teucholabis (Teucholabis) delandi*, n. sp., venation. 6.—*Trentepöhlia (Trentepöhlia) delectabilis*, n. sp., venation. 7.—*Riedelomyia papuensis*, n. sp., venation. 8.—*Limonia (Rhipidia) diploclada*, n. sp., three flagellar segments. 9.—*L. (R.) diploclada*, n. sp., male terminalia. 10.—*Teucholabis (Teucholabis) delandi*, n. sp., male terminalia. 11.—*Riedelomyia papuensis*, n. sp., male terminalia.

*a*, aedeagus; *b*, basistyle; *d*, dististyle; *g*, gonapophysis; *id*, inner dististyle; *od*, outer dististyle; *t*, tergite; *vd*, ventral dististyle.

basal portions of cells 1st  $M_2$  and 2nd  $M_2$ , respectively; vaguer and less clearly defined areas lying more distally in cells  $R_2$  and  $R_5$ ; veins pale, a trifle darker in the clouded areas. Venation: Rs strongly arcuated; branches of Rs sinuous, cell  $R_3$  widest on basal portion, narrowest at midlength; cell  $R_5$  narrowest on basal third, widest at midlength; both veins deflected strongly caudad on outer portions, so cell  $R_2$  at margin is unusually wide; supernumerary cross-veins in cells  $R_3$  and  $R_5$  relatively faint; cell 1st  $M_2$  widened at distal end, with m-cu at near one-third its length; cell 2nd A wide.

Abdominal tergites obscure-yellow, the caudal margins broadly black, especially on segments two to four, narrower on segments five and six, the subterminal segments uniformly blackened; sternites obscure-yellow, the second segment more brownish; subgenital shield reddish-brown, darker basally; cerci slender, simple and acute at tips.

Holotype, ♀, Vanimo, 21st December, 1936 (F. H. Taylor).

The nearest relative of this very distinct fly is *Limonia (Laosa) bipartita* Alexander, of San Cristoval Island, Western Polynesia (*Proc. California Acad. Sci.*, (4) xxii, 1936, 5, fig. 2), which differs in the yellow rostrum, pale antennal scape and pedicel, and in the distinct wing pattern.

LIMONIA (LAOSA) FALCATA Alexander.

PROC. LINN. SOC. N.S.W., lx, 1935, 55, fig. 3.

The unique type, a ♂, was from Rabaul, New Britain. A second ♂: Aitape, 26th December, 1936 (F. H. Taylor).

LIMONIA (LIBNOTES) MOPSA Alexander.

*Philipp. J. Sci.*, liv, 1934, 450, pl. 1, fig. 11.

The types were from Bogadjim (Stephansort), Astrolabe Bay, New Guinea. Three further specimens: Wewak, 26th January, 1937; Aitape, 27th December, 1936 (F. H. Taylor).

LIMONIA (DICRANOMYIA) MISERA (Riedel).

*Dicranomyia misera* Riedel, *Ann. Mus. Nat. Hung.*, xviii, 1921, 131, fig. 1.

The types were from Madang (Friedrich Wilhelmshafen, New Guinea), collected by Biró. One ♀, Aitape, 26th December, 1936 (F. H. Taylor). In this specimen, m-cu is at or just before the fork of M.

LIMONIA (RHIPIDIA) DIPLOCLADA, n. sp.

Allied to *plurinervis*; mesonotum grey, the praescutum with a black median stripe; antennal flagellum bipectinate, the branches unequal; legs black, the femoral bases restrictedly yellow; wings greyish, cells C and Sc brownish-black; sparse brown seams and clouds, including the centres of cells  $R_2$  and 2nd  $R_3$ ; a supernumerary cross-vein in cell  $R_3$  at near two-thirds the length; abdomen brownish-grey, the caudal margins of the segments narrowly pale; terminalia yellow; male terminalia with rostral spines two, equal.

♂.—Length about 5 mm.; wing, 6 mm.

Rostrum and palpi black. Antennae black; flagellar segments bipectinate, the branches slightly unequal, one being a little shorter and more flattened than the other which is slightly expanded at outer end (Fig. 8). Head brownish-black; anterior vertex reduced to a linear strip.

Pronotum brownish-black above, more greyish laterally. Mesonotal praescutum grey with a black median stripe that is narrowly split behind; posterior sclerites of notum grey-pruinose, sparsely variegated with brown. Pleura grey. Halteres short, yellow, the knobs infuscated. Legs with the coxae darkened basally, yellow at tips; trochanters yellow; femora black, the bases narrowly yellow, most extensively so on the posterior legs where more than the basal third is included; remainder of legs black. Wings (Fig. 2) greyish; cells C and Sc brownish-black; stigma light brown, lying before vein  $R_2$ ; narrow brown seams along cord and outer end of cell 1st  $M_2$ ; pale grey areas in centres of cells  $R_2$  and 2nd  $R_3$ ; veins brown, darker in the infuscated areas. Venation: Sc relatively long,  $Sc_1$  ending about opposite one-fifth the length of Rs,  $Sc_2$  about opposite the origin of the latter vein; Rs angulated and strongly spurred at origin; supernumerary cross-vein in cell  $R_3$  at near two-thirds the length of cell; m-cu about one-third its length before fork of M.

Abdomen brownish-grey, the caudal margins of segments narrowly pale; terminalia yellow. Male terminalia (Fig. 9) with the tergite, 9t, transverse, the lateral portions produced into narrow points, the caudal margin very slightly emarginate. Ventral dististyle, *vd*, relatively small, fleshy, subequal in extent to the basistyle *b*; rostral prolongation with two equal spines, placed at near midlength of the prolongation. Margin of gonapophysis, *g*, microscopically serrulate.

Holotype, ♂, Wewak, 18th February, 1937 (J. R. Rigby).

The nearest ally of the present fly is *Limonia (Rhipidia) plurinervis* (Riedel), of New Guinea, which has a unipectinate antenna and differs further in slight details of

colouration of the body and wings. It seems very possible that these two species are derivatives of the subgenus *Idioglochina* Alexander rather than of *Rhipidia*, but until intermediate forms are discovered, it seems advisable to refer them to this latter group to where they would run by means of existing keys to the Tipulidae.

HELIUS (RHAMPHOLIMNOBIA) DIFFUSUS, n. sp.

General colouration of mesonotum yellow, with a conspicuous dark brown lateral stripe, extending from behind the humeral region of praescutum along the dorsopleural membrane to the base of abdomen; rostrum relatively short, black; halteres yellow; legs yellow, the femora with the extreme tips and a narrow subterminal ring dark brown; tibiae yellow, the tips narrowly dark brown; wings whitish-subhyaline, the prearcular and narrow costal regions yellow; a diffuse, relatively sparse, pale brown, reticulated pattern; m-cu before fork of M; abdominal tergites dark brown, with broad, obscure-yellow, posterior borders; sternites yellow, with a dark spot on either side of the basal ring.

♀.—Length about 6 mm.; wing, 5 mm.

Rostrum black, relatively short, a little exceeding the remainder of head; palpi black. Antennae with scape and pedicel black, flagellum brown; flagellar segments oval. Head brownish-grey.

Pronotum dark. Mesothorax yellow, with a conspicuous, dark brown, lateral stripe extending from behind the humeral region of praescutum along the dorsopleural membrane, passing through the base of halteres to the abdomen; scutal lobes and mediotergite less conspicuously darkened. Halteres pale yellow. Legs with the coxae and trochanters yellow; femora yellow, with the extreme tip and a slightly wider subterminal ring dark brown, the two dark annuli enclosing a wider yellow ring; tibiae yellow, the tips narrowly but conspicuously dark brown; tarsi yellow, the terminal segments darkened. Wings (Fig. 3) whitish-subhyaline, the costal border and prearcular field conspicuously light yellow; a relatively heavy, reticulated, pale brown pattern, much paler and more diffuse than in *papuanus* but distributed much the same, the reticulations more sparse than in *reticulata*. Venation: m-cu more than one-half its length before fork of M.

Abdomen bicoloured, the tergites dark brown with broad, obscure-yellow posterior borders, the latter a little less extensive than the darkened portions; sternites yellow, with a dark spot on either side of basal ring; genital segment and the very long valves of ovipositor yellow.

Holotype, ♀, Aitape, 1st November, 1937 (F. H. Taylor).

*Helius* (*Rhampholimnobia*) *diffusus* is most similar to *H. (R.) papuanus* Alexander, in the relatively short rostrum and general arrangement of the wing-pattern, differing conspicuously in the pattern of the body and legs. It is becoming increasingly difficult to separate the members of the two subgeneric groups *Rhampholimnobia* Alexander and *Eurhamphidia* Alexander although it is still possible to define them on venation. Both appear to be dominant groups of the genus in the Papuan subregion.

HELIUS (RHAMPHOLIMNOBIA) NIMBUS, n. sp.

General colouration black, the caudal borders of the abdominal sternites light grey; antennae short, only a little longer than the relatively short rostrum; knobs of halteres weakly darkened; legs black, the extreme bases of tibiae whitened, the tarsi chiefly yellow; wings with a brownish tinge, very restrictedly patterned with dark brown; costal fringe (♂) long and conspicuous; m-cu at or shortly before fork of M.

♂.—Length about 4.5–5 mm.; wing, 4.5–5 mm.

♀.—Length about 6–6.5 mm.; wing, 4.8–5.2 mm.

Rostrum slightly more than one-half longer than remainder of head, black; palpi black. Antennae short, only a little longer than the rostrum; flagellar segments oval, the verticils secund, considerably longer than the segments. Head dull black.

Thorax almost uniformly black, the surface subnitidous; median area of scutum more pruinose. Halteres with stem whitish, the large knobs weakly darkened. Legs with the coxae and trochanters black; femora light brown basally, passing into black; tibiae black, the extreme bases narrowly but evidently white; tarsi light brown, paling

to yellow on and beyond the basitarsi; terminal segments slightly darker. Wings (Fig. 4) with a brownish tinge, very restrictedly patterned with dark brown, including the stigma, a spot at origin of Rs, cord and outer end of cell 1st  $M_2$ ; a dusky marginal seam the entire width of cell  $R_3$ ; prearcular field weakly infumated; cells C and Sc a trifle more yellowish than the remainder of ground; veins brownish-black. Costal fringe (♂) long and conspicuous. Venation: Basal section of Rs relatively long, weakly angulated to short-spurred at origin; second section of Rs subequal to or a little longer than r-m; m-cu at or shortly before fork of M; cell 1st  $M_2$  small, its inner end pointed.

Abdomen black, the caudal margins of the sternites light grey, in cases more or less interrupted at the midline; terminalia obscure-yellow, the basistyles darkened on apical halves. Male terminalia with both dististyles elongate, the outer with two short blackened teeth at apex, the inner subequal in length, provided with long coarse setae.

Holotype, ♂, Aitape, 26th December, 1936. Allotype, ♀, Wewak, 23rd November, 1936. Paratopotypes, 1 ♂, 1 ♀, with holotype, 26th December, 1936-14th January, 1937 (F. H. Taylor).

*Helius (Rhamphotimnobia) nimbus* is quite distinct from the other species of the subgenus so far made known. It is closest to *H. (R.) brevinasus* Alexander and *H. (R.) papuanus* Alexander, but is readily told by the colouration of the body, legs and wings.

#### GONOMYIA (IDIOCERA) PUNCTIPENNIS (Edwards).

GONOMYIA (PTILOSTENA) PUNCTIPENNIS Edwards, *Treubia*, vii, 1926, 140.

One male, Wewak, 14th November, 1936 (Dr. C. M. Deland). The species is widespread in the Austromalayan Islands. The present specimen has the middle dististyle of the terminalia longer than in Philippine material, being about three-fourths as long as the outer dististyle, yet certainly appears to be conspecific. In Edwards's figure of the male terminalia, the aedeagus appears as a simple straight rod but in the present material and others that I have seen, the organ, as seen in profile, appears of rather peculiar structure. It terminates in a long spinous point, on the ventral face with two protuberances, the more basal one at near midlength, blackened and sharp-edged, the outer protuberance subacute in profile and uniformly pale.

#### TEUCHOLABIS (TEUCHOLABIS) DELANDI, n. sp.

General colouration orange-yellow, the praescutum with three black stripes, the lateral pair with their cephalic ends outcurved to the margin; scutellum and mediotergite broadly blackened; head silvery-grey; halteres black; femora yellow, the outer third of fore femora, outer two-thirds of mid-femora, and all of posterior femora black; tibiae and basitarsi obscure-yellow, the tips narrowly blackened; wings yellowish-subhyaline, the stigma and a marginal radial seam dark brown; a paler brown seam along cord; cell 1st  $M_2$  long, subequal to cell 2nd  $M_2$ ; abdomen orange throughout.

♂.—Length about 6 mm.; wing, 6-6.2 mm.

♀.—Length about 6-6.5 mm.; wing, 5.5 mm.

Rostrum and palpi black, the former shorter than the remainder of head. Antennae black throughout; flagellar segments oval, the verticils exceeding the segments in length. Head light silvery-grey.

Pronotum orange. Mesonotal praescutum orange, patterned with black; median stripe not reaching the suture behind; lateral stripes at their cephalic ends deflected strongly laterad to margin of sclerite, the posterior ends crossing the suture on to the scutal lobes; scutellum and most of mediotergite extensively blackened, the remainder of mesonotum yellow. Pleura yellow, the ventral sternopleurite a little more reddish. Halteres black, the extreme base of stem yellow. Legs with the coxae and trochanters yellow; fore femora yellow, with a little more than the outer third black; middle femora with nearly the outer two-thirds black; posterior femora uniformly blackened, excepting the extreme bases which are yellow; tibiae and basitarsi obscure-yellow, the tips narrowly and weakly blackened; remainder of tarsi black. Wings (Fig. 5) yellowish-subhyaline; stigma and a narrow marginal seam in outer radial field dark brown, the latter ending at vein  $R_3$ ; a much paler brown seam along cord, in cases this scarcely evident; veins dark brown, more yellowish in the prearcular region. Costal fringe (♂)

relatively long. Venation:  $Sc_1$  ending shortly before midlength of Rs,  $Sc_2$  some distance from its tip, shortly beyond origin of Rs; cell 1st  $M_2$  long and narrow, subequal in length to cell 2nd  $M_2$ ; m-cu its own length or less beyond fork of M. In the paratype, the right wing has cell  $M_2$  open by the atrophy of m, the left wing being normal.

Abdomen uniformly orange throughout. Male terminalia (Fig. 10) with the basistyle obtusely rounded at apex. Outer dististyle, *od*, small, terminating in an acute spine, the outer margin before apex with a more slender appressed spine. Inner dististyle, *id*, appearing as a flattened curved blade, at base on outer margin with a long curved rod that is about two-thirds as long as the blade itself, beyond midlength bearing two long, closely approximated setae.

Holotype, ♂, Wewak, 16th November, 1936 (Deland and Taylor). Allotopotype, ♀, with type. Paratopotypes, 1 ♂, 1 ♀, 26th November, 1936. Paratype, 1 ♀, Vanimo, 14th December, 1936 (F. H. Taylor).

I am very pleased to name this species in honour of the collector of part of the type series, Dr. C. M. Deland. The fly is generally similar to *Teucholabis* (*Teucholabis*) *exclusa* (Walker), of north-western New Guinea, differing especially in the light grey head, pattern of praescutum, colouration of the legs and wings, and in the uniformly orange abdomen.

#### TRENTEPOHLIA (TRENTEPOHLIA) DELECTABILIS, n. sp.

General colouration of mesonotum yellow, patterned with black, including a  $\cap$ -shaped area on either side of the posterior half of praescutum; pleura chiefly black, variegated with paler; halteres and legs yellow; wings whitish, heavily patterned with brown, arranged chiefly as three crossbands that are more or less interconnected and broken by whitish droplets; Rs and petiole of cell  $R_3$  arcuated; abdomen black, the caudal margins of the segments grey.

♀.—Length about 5.5 mm.; wing, 4.5 mm.

Rostrum and palpi black. Antennae with scape brownish-black; succeeding segments pale testaceous-brown, passing into darker brown. Head ochreous, darker behind.

Pronotum brownish-black. Mesonotal praescutum with the ground colour yellow, on either side of posterior half with a  $\cap$ -shaped brown marking encircling the usual yellow lateral stripes; median region of praescutum on posterior half less clearly darkened; scutum obscure-yellow, each lobe conspicuously patterned with dark brown; scutellum brownish-black, the central portion very narrowly and indistinctly paler; mediotergite pale on cephalic half, the posterior portion dark brown. Pleura chiefly brownish-black, variegated with paler, more testaceous, including the dorsopleural membrane and portions of the mesopleura, before and behind the mesepisternum. Halteres pale yellow. Legs with the coxae brownish-black; trochanters obscure-yellow; remainder of legs pale yellow, only the terminal tarsal segments dark brown. Wings (Fig. 6) whitish, heavily patterned with brown, forming three major crossbands, the basal two interconnected in cell M; basal band extending to vein Cu, thence greatly narrowed across cells Cu, 1st A and 2nd A, variegated by two ground droplets on and beneath vein M; second band extending from C to vein M, abruptly narrowed on m-cu and isolated as a seam along basal section of  $M_{1+2}$ , in cells R and  $R_1$  variegated by two ground droplets; third band most extensive, involving the broad apex, variegated by droplets in cells  $R_2$ , base of  $R_5$  and near outer end of cell  $M_2$ ; more yellowish spots at wing-tip in cells  $R_3$  and  $R_4$ ; prearcular field abruptly white; veins very pale in the ground areas, brown in the dark fields. Venation: Rs strongly arcuated, shorter than the petiole of cell  $R_5$ , the latter likewise strongly arcuated;  $R_5$  less arched than  $M_{1+2}$ , the fork of cell  $R_5$  thus asymmetrical.

Abdomen black, the caudal margins of the segments grey; genital shield and valves of ovipositor horn-yellow.

Holotype, ♀, Aitape, 1st January, 1937 (F. H. Taylor).

*Trentepohlia* (*Trentepohlia*) *delectabilis* is generally similar to Oriental species, such as *T. (T.) festivipennis* Edwards, *T. (T.) ornatipennis* Brunetti, and *T. (T.) venustipennis* Edwards, yet differs conspicuously from all in the pattern of the thorax and wings.

## RIEDELOMYIA PAPUENSIS, n. sp.

General colouration of mesonotum light brown, unmarked or virtually so; antennae virtually unmodified, at most with the basal two flagellar segments united into a fusion-segment but strongly constricted so the antennae appear to be 16-segmented; basal two flagellar segments light yellow, the remainder dark brown; pronotum and lateral pretergites china-white; legs yellow, the tips of femora narrowly white, preceded by a brown subterminal ring; wings with a faint greyish tinge, the prearcular and costal portions more whitened; a conspicuous brown pattern involving many of the veins, including a marginal series on all longitudinal veins; cell 1st  $M_2$  very long, exceeding in length any of the veins beyond it;  $R_s$  and  $R_1$  subequal in length; male terminalia with the dististyle single, terminating in spinous points.

♂.—Length about 3.5–4 mm.; wing, 4–4.2 mm.

♀.—Length about 5.5–6 mm.; wing, 4.5–4.8 mm.

Rostrum and palpi brown. Antennae 15 or 16 segmented, the flagellar segments not united into a conical fusion-segment as in the previously described species; scape and pedicel pale, more silvery above; basal two segments of flagellum light yellow, the remaining segments abruptly brown; the basal two flagellar segments although strongly separated by a constriction appear to be fused in both sexes, the suture between them not or but feebly indicated; all flagellar segments oval, with conspicuous verticils. Head silvery, more darkened on median portion.

Pronotum china-white above, darkened on sides, the colour continued laterad along pretergites to wing-root. Mesonotal praescutum, scutum and scutellum almost uniformly light brown, the centres of the scutal lobes a trifle darker; mediotergite a little darker brown. Pleura brownish-testaceous. Halteres dark brown. Legs with the coxae yellow, the fore and middle pair a little darkened basally; femora yellow, the tips narrowly whitened, preceded by poorly delimited subterminal brown rings; tibiae and tarsi pale yellow, the terminal tarsal segments darker. Wings (Fig. 7) with a faint greyish tinge, the prearcular and costal portions more whitened; a conspicuous brown pattern, including clouds at arculus, origin of  $R_s$ , fork of  $Sc$ , cord, outer end of cell 1st  $M_2$  and at ends of all longitudinal veins, the largest at  $R_4$ ; veins yellow, darker in the clouded areas. Venation: Veins  $C$ ,  $Sc$  and  $R$  closely approximated;  $R_s$  and  $R_1$  subequal;  $R_3$  atrophied;  $R_2$  longer than  $R_{1+2}$ ; cell 1st  $M_2$  very long, exceeding any of the veins beyond it.

Abdominal tergites dark brown; sternites paler except on lateral portions; terminalia obscure-yellow. Male terminalia (Fig. 11) of simple structure, the basistyle,  $b$ , obtuse at apex, provided with long coarse setae. Dististyle,  $d$ , apparently single but deeply divided; the dististyles of the two sides are slightly different, as shown. Aedeagus,  $a$ , broad, simple, narrowed outwardly; at and near apex with a few setae.

Holotype, ♂, Aitape, 26th December, 1936 (F. H. Taylor). Allotype, ♀, Wewak, 23rd November, 1936. Paratypes, 5 ♂, ♀, with the allotype, 18th–29th November, 1936 (F. H. Taylor); 1 ♂, January, 1937 (C. M. Deland).

The still poorly understood genus *Riedelomyia* Alexander has been known only from three previously described species, *R. niveiapicalis* (Brunetti), of south-western India; *R. gratiosa* Alexander, of Cochin State, India; and *R. teucholabina* (Alexander) of Fiji. These species have been discussed in detail in another paper by the present writer (*Philipp. J. Sci.*, 35, 1928, 481–484). The present fly shows the minimum development of the fusion-segment of the antennal flagellum, which, at most, feebly involves only the basal two segments. In its venation, especially the elongate cell 1st  $M_2$ , the present fly comes closest to *R. teucholabina*, differing most evidently in the structure and colouration of the antennae, the thoracic colouration, and in the details of venation, as the subequal  $R_s$  and  $R_1$ , in *teucholabina* the latter vein being markedly longer. The male terminalia is of simple structure and appears definitely Eriopterine in its fundamental features.

## STYRINGOMYIA DIDYMA Grimshaw.

*Styringomyia didyma* Grimshaw, *Fauna Hawaiiensis, Diptera*, iii, pt. 1, 1901, 10.

*Idiophlebia pallida* Grünberg, *Zool. Anzeig.*, xxvi, 1903, 527.

Very widespread in the Pacific and Austromalayan regions. 1 ♂, Aitape, 26th December, 1936 (F. H. Taylor).

## SEROLOGICAL STUDIES OF THE ROOT-NODULE BACTERIA.

### I. STRAINS OF RHIZOBIUM MELILOTI.

By J. M. VINCENT, School of Agriculture, University of Sydney.

[Read 25th June, 1941.]

#### Introduction.

Although a number of studies of the serological relationships of the root-nodule bacteria (*Rhizobium* spp.) have been undertaken (cit. Fred, Baldwin and McCoy, 1932), papers on this subject are comparatively rare in the more recent literature. Yet the earlier work gave some promising results both in confirming species differentiation and, more especially, in distinguishing strains of the one species, e.g., Stevens (1925) working with strains of *Rhizobium meliloti*.

Whilst several of the early workers included a variety of serological techniques, precipitation, complement fixation and agglutination, the latter was most used and is probably still the most convenient since the reaction is readily observed and a serum of adequately high titre can be obtained with little difficulty. Little has been done, however, in bringing to the study of *Rhizobium*, techniques which have given so much information in respect of pathogens, as, for example, the serological differentiation obtained within the Salmonella group by White and Kauffmann (Savage and White, 1925; White, 1926, and citations Topley and Wilson, 1936). Bushnell and Sarles (1939) point out the need for improved techniques and use three types of antigen: whole-cell, heated and saline extracted. Still, their results do not give a very clear picture of the antigenic constitution of the organisms with which they were working (from soybean and lupine), and they have made no differential flagellar and somatic analysis.

It seems likely that the serological reactions of the rhizobia will find more application as a means of differentiation between strains when we understand better the detail of the antigenic constitution of the cells, and attempt the correlation of this with other features of importance in the organisms' behaviour. Two simple points of technique merit further attention, viz.: (i) distinction between flagellar (*H*) and somatic (*O*) agglutination, and (ii) the application of serum absorption tests. So far as one is aware these refinements have not yet been reported with respect to *Rhizobium* although the keys to some of the tabulated results (Vogel and Zipfel, 1921; Wright, 1925) indicate that, at times, floccules characteristic of flagellar agglutination have been observed even though their significance has not been appreciated. The fact that readings were usually recorded after 24 hours would militate against distinction between *H* and *O* since, after that time, in the presence of both types, the agglutinated mass would be compacted.

This paper reports results when these techniques are applied to a number of strains of *Rh. meliloti* obtained from widespread areas and from various species of *Medicago*. Detailed attention has first been directed towards six organisms, for which antisera have been developed, in order to determine for these a minimal antigenic constitution—flagellar distinguished from somatic. These sera have then been used to study the serological relationships of 42 other strains.

#### METHODS.

*Organisms used for the Development of Antisera.*—These were selected to provide a variety of host species and to be representative of widely separated localities. Details are:

Collection No.	Host Plant.	Locality.
47	<i>Medicago sativa</i>	Bathurst, N.S.W.
74	<i>M. sativa</i>	Roseworthy, S. Aust.
27	<i>M. hispida</i> var. <i>denticulata</i>	Merrylands, N.S.W.
62	<i>M. hispida</i> var. <i>denticulata</i>	Roseworthy, S. Aust.
102	<i>M. arabica</i>	Dandenong, Vict.
66	<i>M. minima</i>	Tailem Bend, S. Aust.

All cultures were obtained from nodules during the latter half of 1939 by repeated single colony picking. They were further tested by plating on yeast mannitol agar containing congo red, growth on litmus milk and by streaking on potato slopes. In all cases these tests of purity were satisfactory and nodules were produced on inoculated lucerne plants.

*Inoculating Antigen.*—Growth from a yeast mannitol agar slope was rubbed off into about 5 ml. yeast mannitol solution (calcium carbonate omitted) and the suspension used to inoculate a slope of the same solid medium made up in a 4 oz. medicine bottle (flat). Slope cultures were incubated at 28°C., inclined so that a thin moist layer of inoculum covered the whole agar surface.

The suspension used for inoculating the animal contained about 500 million cells per ml. and was prepared by rubbing off the surface growth with sterile beads into sterile 0.85% saline. Younger (2-day) were mixed with older (5-day) growths to ensure a fair proportion of actively motile cells in the inoculum. Motility was checked by microscopic examination. The freshly prepared untreated suspension was inoculated intravenously into the ear of a rabbit in four increasing daily doses: 1 ml., 2 ml., 3 ml. and 3.5 ml.

*Testing for "Normal" Antibodies.*—A small sample of blood was collected from the ear of each animal before inoculation and the serum tested after separation against the organism used for that animal. In all cases the pre-inoculation serum failed to cause agglutination at a final dilution of 1/20.

*Collection of Blood and Preparation of Serum.*—Seven days after the completion of the course of injections, the presence of antibodies in the serum was checked using a small sample from the ear. Since these proved to be reasonably high, the principal yield of blood was obtained by bleeding out after a further three or four days. The serum was separated from the clot after a short incubation (1 hour at 37°C.) and standing over-night in a refrigerator. For storage, phenol was added to a final concentration of 0.5% and the serum kept in a refrigerator.

*Dilution of Serum for Titrations.*—The serum was diluted with 0.85% saline, usually starting at an initial dilution of 1/25 (= 1/50 after the addition of testing antigen in equal volume) and increasing four times at each dilution. This, whilst not giving a very accurate titre, covered the range quickly and was convenient for the purposes of this investigation where highly quantitative results would have no particular significance.

*Agglutinating Antigen.*—The organisms were grown on bottle slopes as in the case of the inoculating antigen; the shallow layer of liquid favoured the rapid development of an actively motile culture. As would be expected, cultures with few motile cells frequently gave poor, or no, *H* agglutination whereas the same strain taken earlier in development, when motile cells were abundant, provided a strong flocculent reaction. Two- to three-day cultures, grown at 28°C., were generally satisfactory although, in a few cases, 24- to 36-hour growths were markedly superior. Two types of agglutinating suspension were used:

- (i) *Whole antigen*; mostly without any treatment although sometimes formalized to a concentration of 0.2% formalin. Whether untreated or formalized this antigen is capable of giving the two types of agglutination, viz., (a) typically flagellar, and (b) somatic.
- (ii) *Heated antigen*; steamed for 30 minutes. The longer heating used by Bushnell and Sarles (1939) is not necessary to suppress *H*, and had a slight—though not marked—lowering effect on the *O* titre.

Because of the clumping tendency in *Rhizobium*, it was found advisable to give the suspension a light spinning (1,000 r.p.m. for 5 minutes) and to use the evenly turbid supernatant. In almost every case this treatment sufficed to give a stable suspension although some preparations gave a degree of "self-agglutination" in saline controls. This could yet be distinguished from typical agglutination, except perhaps causing one to be doubtful about the highest probably-agglutinating dilution. Greater stability in the one or two very badly "self-agglutinating" strains was obtained by using 0.5% instead of 0.85% saline for dilutions and preparation of suspension. In all cases saline-suspension controls were set up for comparison.

*Effect of Centrifugation on Antigen Suspension.*—In the course of absorption experiments, it was found that antigen reconstituted with saline from material concentrated by centrifuging and removing the supernatant (very slightly turbid) gave weak or no *H*-agglutination. The following case serves as an example:

Organism.	Treatment.	Dilutions of Serum 27.				
		1/25.	1/100.	1/400.	1/1,600.	1/6,400.
27	Untreated ..	H+	H+	H+	H+	H+
	Centrifuged ..	+	+	+	+	+
74	Untreated ..	H	H	H	H	H
	Centrifuged ..	(h)	(h)	—	—	—

H = full flocculent, (h) = very slightly flocculent, + = finely granular, — = no reaction.

A similar result was obtained in absorption when centrifuged material failed to remove completely antibodies to *H*. Centrifugation itself did not destroy the *H* antigen since a centrifuged preparation re-suspended in its own supernatant showed no loss of *H* agglutinability. Microscopic examination of the supernatant showed some motile organisms, but these seemed too few to account fully for the differences recorded above.

*The Agglutination Test.*—Equal parts of diluted serum and test antigen were mixed in Dreyer tubes and incubated at 53°C. in a water bath. Readings were taken after a shorter and longer period. Sometimes it was advantageous to include a one-hour or earlier observation for best recognition of *H* agglutination. Somatic agglutination was well developed after 2 hours, and, whilst a longer period served to confirm the results, it seldom added more than one further dilution step to the titre.

The two types of agglutination were sharply defined and perfectly normal. The flagellar was more rapid (usually evident within 15 minutes), markedly flocculent and, when without *O*, showed only partial clearing of the suspension. The somatic was very finely granular and gave typical complete clearing.

All readings were made by means of a reading box with oblique illumination and using a simple magnifying lens.

*Absorption.*—Preliminary trials indicated the need for a massive absorbing dose for satisfactory reduction of titre by the homologous organism. With the heavy dosage needed, the development of adequate supplies of antigen—at the same time young enough to contain a fair proportion of motile cells—presented a problem. Growth on slopes of moist medium proved superior to that in shallow liquid layers both for yield and motility. Attempts to concentrate absorbing antigen by centrifugation, removal of supernatant and making up to reduced volume with fresh saline showed that whilst absorption of *O* was thereby improved, it was impossible to remove the last of the *H*. For example, progressive exposure of serum 27 to doses of antigen concentrated in this way to  $10 \times 10^9$  per ml. gave removal of *O* but a slight amount of *H* persisted at a dilution of 1/800 even after  $50 \times 10^9$  cells had been applied per ml. of serum at 1/50.

It was found most practical to remove the *H* and *O* antibodies separately by means of the appropriate treatment. The *H* was best removed by using heavy (but not centrifuged) suspensions in the order of  $3 \times 10^9$  cells per ml. of serum at a dilution of 1/50 or 1/100. Where this did not suffice for complete removal of *H*, the once-exposed supernatant was given a second treatment with the same suspension and the supernatant from this exposure tested with a few drops of concentrated testing antigen. The treatment for *H* did not usually suffice for complete exhaustion of *O* although the absorption effect could be seen in a lowering of titre and slowing down of reaction. The *O* antibodies were best removed by heavier doses ( $10 \times 10^9$  cells per ml. of serum at 1/50 or 1/100), using concentrated material prepared from sedimented cells.

The effect of three temperatures, 50°C., 37°C. and approximately 2°C., was compared. There was some indication that the highest temperature militated against complete absorption of *H* antibodies although the *O* were all removed after 2 hours. The refrigerator temperature was satisfactory provided exposure was prolonged overnight, and 37°C. was effective after 8 hours.

*The Absorption Test.*—The serum (usually at a dilution of 1/50) was mixed with the absorbing antigen and allowed to stand for the required time. The cells were then sedimented by centrifugation and the clear supernatant used to provide final dilutions—usually 1/100, 1/400 and 1/1,600. Control sera treated with (a) saline, and (b) homologous organism were used to check the testing antigen and conditions of absorption. In some cases it was useful to test the treated serum with the absorbing, as well as with the homologous organism, for removal of the particular antibodies with which the absorbing antigen was able to react.

## RESULTS.

*Cross-Agglutination Relationships of Six Strains studied in Detail.*

Results of repeated tests of the six organisms used for the development of antisera are set out in Table 1. In each case the figure given takes account of at least two completely separate determinations carried out with a period of several months intervening. Agreement has been good both between duplicate tests and where the position of antigen and antiserum is reversed.

TABLE 1.  
*Cross-Agglutination Relationships of Six Strains.*

Testing Antigen.	H-Reaction.						Sera.						O-Reaction.					
	47	74	27	62	102	66	47	74	27	62	102	66	47	74	27	62	102	66
47 .. ..	3	1	1	1	2	2	4	—	3	3	1	—	—	—	—	—	—	—
74 .. ..	1	4	4	3	4	4	—	3	—	—	—	—	—	—	—	—	—	1
27 .. ..	1	4	4	4	4	4	2	—	4	4	—	—	—	—	—	—	—	—
62 .. ..	1	4	4	4	3	4	2	—	4	4	—	—	—	—	—	—	—	—
102 .. ..	1	4	4	3	4	4	1	—	—	—	—	—	—	—	—	—	—	4
66* .. ..	—	4	4	3	4	4	—	—	—	—	—	—	—	—	—	—	—	4

\* Antigen of 66, possibly due to its heavy gum production, gave some trouble with its H agglutinations.

Key: — = no reaction observed at 1/50 (final concentration of serum).

1 = positive reaction at 1/50 or 1/100; 2 = positive reaction at 1/200 or 1/400.

3 = positive reaction at 1/800 or 1/1,600; 4 = positive reaction at 1/3,200 or higher.

*Flagellar Antigens.*—74, 27, 62, 102 and 66 cross react to a high titre and 47 reacts with the others only to a low titre. It is not possible on the basis of this evidence to be more specific regarding H. agglutinogens; the present data do not justify the assumption that those of 74, 27, 62, 102 and 66 are identical. Absorption experiments are necessary to determine this point.

*Somatic Antigens.*—A consideration of these may be facilitated by a rearrangement of the O results and the use of symbols (Roman numerals) to represent a minimal antigenic constitution which can be deduced at this stage. These points are included in Table 2.

TABLE 2.  
*Somatic Cross Reactions.*

	27	62	47	102	74	66	Minimal Antigenic Constitution.
27 vs.	4	4	2	—	—	—	I
62 vs.		4	2	—	—	—	I
47 vs.			4	1	—	—	I, III
102 vs.				4	—	—	III
74 vs.					3	1	II
66 vs.						4	II

Key: Numbers 1-4 and (—) as in Table 1.

Strains 27 and 62 have at least one common antigen (I) which is lacking in 102, 74 and 66. Strain 47 shares an antigen with 27 and 62 but must have at least one other not possessed by these but shared with 102. We may therefore assign to 47 the formula: I, III. Strains 74 and 66 share a common antigen not possessed by the others (II).

*Low Titre Cross-Agglutinations.*—It will have been noted that, in a number of cases, cross-agglutinations, both flagellar and somatic, together or separately, have been obtained only to a low titre (1/50 to 1/200). At the same time these agglutinations are quite definite and have all been carefully checked against saline controls of the suspension. There have been similar records by other workers, e.g., Vogel and Zipfel (1921) and Stevens (1925), but these workers have disregarded positive results at low titres or interpreted them as being due to "normal antibodies" contained in the sera of animals before inoculation. One feels that these results, because of the definite nature of the reaction observed and the uniform failure of the pre-inoculation sera to react at concentrations as high as 1/20, should be considered in drawing a picture of the antigenic constitution of the organism. It might be noted here that tests of eleven more sera from uninoculated rabbits were negative against the organisms being used for inoculation.

*Absorption Tests of Antigenic Identity.*

*Absorption of Flagellar Antigens.*—The kind of result obtained in numerous tests is illustrated in Table 3, which summarizes the absorptions between strain 27 and four other strains. The results are based on at least duplicate tests and where the absorption after one exposure was incomplete, a second exposure was given.

TABLE 3.  
*Absorptions of Flagellar Antibodies between 27 and 47, 74, 62, 102.*

Serum.	Absorbed.	Tested.	Result.			Absorption.
			1/100.	1/400.	1/1,600.	
27	Saline	27	H+	H+	H+	Positive.
27	27	27	+	+-	-	
27	47	27	H+	H+	H+	Negative.
47	Saline.	47	H+	H+	H+	
47	47	47	(h)+	+	+-	Negative.
47	27	47	H+	H+	H+	
27	74	27	+	+	+	Positive.
74	Saline.	74	H+	H+	H	
74	74	74	+-	-	-	Positive.
74	27	74	+	+	-	
27	62	27	+	-	-	Positive.
62	Saline.	62	H+	H+	H+	
62	62	62	-	-	-	Positive.
62	27	62	+	-	-	
27	102	27	+	-	-	Positive.
102	Saline.	102	H+	H+	H+	
102	102	102	(h)+	(h)+	-	Positive.
102	27	102	(h)+	(h)+	-	

Key: H = full flocculent, (h) = very slightly flocculent, += granular, -- = no reaction, +- = slightly granular.

It is evident from these tests that 27, 62, 74 and 102 have qualitatively identical flagellar antigens whilst 47 has an antigen not possessed by the others and these have an antigen not possessed by 47. On this basis one can assign to 47 a minimal flagellar constitution of *Ab* and to the other four, *bC*.

Other cross absorption tests are confirmatory and results are summarized in Table 4. For simplicity any records of *O* agglutination are omitted.



TABLE 4.  
Flagellar Absorptions between 47, 74, 62 and 102.

Test Dilutions.	Serum Absorbed and Testing Antigen.											
	47			74			62			102		
	1 100	1 400	1 1,600	1 100	1 400	1 1,600	1 100	1 400	1 1,600	1 100	1 400	1 1,600
Absorbed by—												
Saline .. .. .	H	H	H	H	H	h	H	H	H	H	H	H
47 .. .. .	h	—	—	H	H	h	H	H	H	H	H	H
74 .. .. .	H	H	h	—	—	—	—	—	—	—	—	—
62 .. .. .	H	H	h	—	—	—	—	—	—	h	—	—
102 .. .. .	H	H	—	—	—	—	—	—	—	h	—	—

Key: H=full flocculent, h=slight flocculent, —=no reaction.

*Results with Strain 66.*—Absorption tests with this strain have presented difficulties due to (i) gum production by the organism giving a very viscous serum after absorption, and (ii) a tendency for the testing antigen of strain 66 to give poor H agglutination, apparently due in part to loss of motility by the culture and in part to the gummy nature of the suspension. However, in a number of cases the difficulties were overcome and these satisfactory cases show identity with the *bC* strains:

Serum.	Absorbed.	Tested.	Result.		
			1/100.	1/400.	1/1,600.
74	66	74	(h)+	+	—
66	74	66	+	+	—
62	66	62	+	+	—
66	62	66	+	+	+
47	66	47	H+	H+	H+
66	47	66	H+	H+	H+

Key: As in Table 4.

*Absorption of Somatic Antigens.*—As noted above in connection with O cross-agglutinations, the six organisms provide a diverse collection of antigens. They may, however, be grouped thus:

(a) 27, 62 and 47, (b) 47 and 102, (c) 66 and 74.

The cross-absorptions within these groups are summarized in Table 5.

*Interpretation of Results for Somatic Antigens.*—Group (a): Cross-agglutination behaviour has already led to a formulation of I for 27 and 62 and I, III for 47. It would not be expected then that either 27 or 62 would absorb completely the serum of 47 and this was borne out by the results. Since the sera of 27 and 62 were not exhausted by 47, an additional antigen—not necessarily the same—will have to be postulated for these latter. Because 27 and 62 cross-absorb completely they can be written as I, IV.

Group (b): The addition of an extra antigen (V) to 102 will explain results.

Group (c): Since neither can absorb out the other each will require an extra antigen; 74 may then be written as II, VI and 66 as II, VII.

*Agglutination Reactions of Other Cultures of Rhizobium meliloti against Sera of Five Different Strains.*

In order to obtain a first picture of the antigenic relationships of a larger group of organisms their reactions were determined with the sera of strains 47, 74, 27, 102 and 66. Previous detailed investigation has shown that each of these has a different antigenic constitution. All tests have been carried out at least twice against four dilutions of each serum. Flagellar and somatic agglutination have been distinguished; in some cases heated and unheated suspensions were used, although it was easy to distinguish

TABLE 5.  
Somatic Cross-absorption Tests.

Test Dilutions.	Serum Absorbed and Testing Antigen.																	
	27			62			47			102			66			74		
	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	100	400	1,600	100	400	1,600	100	400	1,600	100	400	1,600	100	400	1,600	100	400	1,600
Absorbed by— Saline .. .. .	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-
27 } 62 } (a) 47 } 102 } (b)	-	-	-	-	-	-	+	+	+									
	+*	-	-	-	-	-	+	+	+									
	+	+	+	+	+	+	±	-	-	+	+	+						
							+	+	±	-	-	-						
66 } 74 } (c)													±†	±†	-	+	+	-
													+	+	-	-	-	-

Key : + = granular agglutination, ± = slightly granular, - = no reaction.

\* 27 abs. 62 and tested 62 gave a similar reaction at 1/100, an indication of incomplete absorption by 62 of its own antibody in serum 27.

† This reaction is very slow and slight compared with the others recorded for the same serum and its significance is doubtful.

each type even when present together and, except for confirmatory purposes, the use of heated antigen was discontinued.

In all but few cases the agreement between duplicates was good; in the case of disagreement one returned to cultures kept as reserve stocks for checking. In a few cases even young cultures failed to give an *H* reaction but, except for strain 101, when these were harvested at a time when active motility was observed good floccules were obtained with either one of the *H* groups.

For convenience the results are summarized in Table 6. The flagellar and somatic reactions are recorded separately and, in the case of the former, it is sufficient to indicate reactions with 47 and the remaining four, which have similar *H* antibodies, as a group exemplified by serum 27.

TABLE 6.  
Agglutination Relationships of Various Strains of *Rhizobium meliloti*.

Collection No.	Host Plant.	Source.	Reactions with Test Sera.						
			Flagellar.				Somatic.		
			47	27	47	74	27	102	66
27*	M.H.D.	Merrylands, N.S.W. .. .. .	1	4	2	-	4	-	-
62*	M.H.D.	Roseworthy, S.A. .. .. .	1	4	2	-	4	-	-
7†		Wisconsin (No. 101) .. .. .	2	4	2	-	4	-	-
45	M.H.D.	Dandenong, Vic. .. .. .	1	4	2	-	4	-	-
124‡	M.H.D.	Sydney, N.S.W. (J/M.d-U1) .. .. .	1	4	2	-	4	-	-
24	M.S.	Leeton, N.S.W. .. .. .	1	4	2	-	4	-	-
85	M.H.D.	Temora, N.S.W. .. .. .	±	4	3	-	4	-	-
72	M.H.D.	Meningie, S.A. .. .. .	1	4	3	-	4	-	-
125‡	M.H.D.	Vaucluse, N.S.W. (J/M.d-V) .. .. .	1	4	3	-	4	-	-
31	M.A.	Manildra, N.S.W. .. .. .	±	4	3	-	4	-	-
63	M.M.	Orange, N.S.W. .. .. .	1	4	3	-	4	-	-

Key to species : M.A. = *Medicago arabica*, M.C. = *Medicago coerulea*, M.F. = *Medicago falcata*, M.G. = *Medicago gaeletula*, M.H.D. = *Medicago hispida* var. *denticulata*, M.L. = *Medicago lupulina*, M.M. = *Medicago minima*, M.Mu. = *Medicago murex*, M.O. = *Medicago orbicularis*, M.S. = *Medicago sativa*, M.Sc. = *Medicago scutellata*, M.T. = *Medicago truncatula*.

Key to reactions : 4 = positive at 1/3,200 or higher, 3 = positive at 1/800, 2 = positive at 1/200, 1 = positive at 1/50, ± = inconsistent at 1/50, - = negative at 1/50.

\* = Included from earlier section for comparison.

† = Supplied from another collection such as : 7 from Dept. of Agricultural Bacteriology, University of Wisconsin, their number being 101 ; 12 from N.S.W. Dept. of Agric. originally from U.S.A.

‡ = Supplied by Dr. H. L. Jensen, host plant and locality known ; Jensen's number given thus (J/M.d-V) for No. 125.

TABLE 6.—Continued.  
*Agglutination Relationships of Various Strains of Rhizobium meliloti.*—Continued.

Collection No.	Host Plant.	Source.	Reactions with Test Sera.						
			Flagellar.				Somatic.		
			47	27	47	74	27	102	66
97	M.H.D.	Narrandera, N.S.W.	—	4	4	—	4	—	—
49	M.A.	Myrning, Vic.	1	4	2	—	2	—	—
92	M.M.	Balranald, N.S.W.	1	4	3	—	2	—	—
75	M.H.D.	Bega, N.S.W.	1	4	3	—	2	—	—
123†	M.L.	Canberra, A.C.T. (J/M.L-34)	—	3	4	—	2	—	—
79	M.M.	Euston, N.S.W.	1	4	2	—	—	—	—
74*	M.S.	Roseworthy, S.A.	1	4	—	3	—	—	1
134†	M.S.	Canberra, A.C.T. (J/M-h-10)	1	4	—	3	—	—	±
102*	M.A.	Dandenong, Vic.	1	4	1	—	—	4	—
26	M.S.	Leeton, N.S.W.	1	4	1	—	—	4	1
126†	M.A.	Canberra, A.C.T. (J/M.A-31)	—	4	—	—	—	3	—
89	M.H.D.	Hay, N.S.W.	1	4	—	—	—	—	1
133†	M.Mu.	Canberra, A.C.T. (J/M.Mu-2)	—	4	4	—	4	—	1
112	M.S.	Wagga Wagga, N.S.W.	1	4	4	—	4	2	2
8†		Wisconsin (Nitragin P.)	1	4	1	2	2	2	3
12†		Dept. Agric., N.S.W. (U.S.A.)	1	4	3	2	2	2	3
14†		Dept. Agric., W.A.	1	4	2	2	2	2	3
15		Dept. Agric., N.S.W. (Wyang)	1	4	—	—	—	—	—
40	M.S.	Manildra, N.S.W.	1	4	±	—	—	—	—
122†	M.S.	Lawes, Q. (J/M.S-C3)	—	3	—	—	—	—	—
51	M.S.	Blandford, N.S.W.	1	4	—	—	—	—	—
53	M.H.D.	Pinnaroo, S.A.	±	4	—	—	—	—	—
76	M.H.D.	Myrning, Vic.	1	4	—	—	—	—	—
127†	M.G.	Canberra, A.C.T. (J/M.G-1)	1	4	—	—	—	—	—
129†	M.M.	Canberra, A.C.T. (J/M.M-164)	1	4	—	—	—	—	—
130†	M.O.	Canberra, A.C.T. (J/M.O-35)	1	4	—	—	—	—	—
132†	M.T.	Canberra, A.C.T. (J/M.Tr-90)	—	4	—	—	—	—	—
135†	M.C.	Canberra, A.C.T. (J/M.C-1-3)	1	4	—	—	—	—	—
47*	M.S.	Bathurst, N.S.W.	3	1	4	—	3	1	—
131†	M.Sc.	Canberra, A.C.T. (J/M.Sc-12)	3	1	2	—	3	—	—
25	M.S.	Leeton, N.S.W.	3	1	2	—	2	—	—
59	M.S.	Scone, N.S.W.	3	2	2	—	—	—	—
10†		Wisconsin (No. 109 G)	4	2	±	—	—	—	—
11†		Wisconsin (No. 107-1 G)	4	2	±	—	—	—	—
123†	M.F.	Lawes, Q. (J/M.F-C1)	4	1	—	—	—	—	—
101	M.S.	Wingen, N.S.W.	—	—	—	—	—	—	—

Key to species of host plant: M.A.=*Medicago arabica*, M.C.=*Medicago coerulea*, M.F.=*Medicago falcata*, M.G.=*Medicago gaeula*, M.H.D.=*Medicago hispida* var. *denticulata*, M.L.=*Medicago lupulina*, M.M.=*Medicago minima*, M.Mu.=*Medicago murex*, M.O.=*Medicago orbicularis*, M.S.=*Medicago sativa*, M.Sc.=*Medicago scutellata*, M.T.=*Medicago truncatula*.

Key to reactions: 4 = positive at 1/3,200 or higher, 3 = positive at 1/800, 2 = positive at 1/200, 1 = positive at 1/50, ± = inconsistent at 1/50, — = negative at 1/50.

\* = Included from earlier section for comparison.

† = Supplied from another collection such as: 7 from Dept. of Agricultural Bacteriology, University of Wisconsin, their number being 101; 12 from N.S.W. Dept. of Agric. originally from U.S.A.

‡ = Supplied by Dr. H. L. Jensen, host plant and locality known; Jensen's number given thus (J/M.d-V) for No. 125.

On the basis of flagellar agglutination all but one of the forty-two strains examined fell into either of these two groups: (i) reacting weakly with serum 47 but strongly with 74, 27, 102 and 66 (35 out of 42 strains); (ii) reacting strongly with 47 but weakly with the sera of the other four (6 out of 42 strains). Strain 101, although successfully

re-tested for nodulation and re-isolated from these nodules, failed to give either an *H* or *O* with any of the five sera.

The somatic antigens give more division within this *H*-grouping. Within group (i) a proportionately large number (14/35) react with 47 and 27 (comparable with behaviour of 27 and 62), whilst two others react with either 66 (No. 133) or 102 and 66 (No. 112), in addition. One reacts strongly with serum 47, one with 74, two strongly with 102 and one, only slightly, with 66. Three organisms (8, 12 and 14) have an interestingly wide reactivity. The large group failing to react with any of the five sera for *O* indicates that even with the large number of antigens already postulated, the variety in somatic constitution is by no means exhausted. Within the group (ii), three out of six show little *O* reaction, 59 reacts with 47 only, and the remaining two strains show some similarity in reaction to strain 47 with which they are grouped in the table.

These results do not reveal any marked grouping according to locality; note, for example, the variety of areas supplying strains to the first and largest group. There is, however, some grouping possible on a host basis: three-quarters of those isolated from M.H.D. fall into the "27, 62" group and only one in eleven of those isolated from lucerne.

#### General Discussion.

The results presented in this paper emphasize the heterogeneous nature of strains of *Rhizobium meliloti*. The extent of such divergence is apparent from a separate consideration of the somatic and flagellar antigens and it will be interesting if it proves possible to connect one or other of these antigenic surfaces with characteristics of strain behaviour. For the present one has concentrated on the antigenic properties, but it is hoped to make collateral study of other characters a subject for further investigation.

It seems probable that the present division of the strains studied (Table 6) into groups showing some similarities in their behaviour with the five test sera, reveals only part of the serological constitution. Its full understanding requires a detailed investigation of the kind reported herein for six strains only. As a step in this direction, sera are now available for eleven organisms selected from those of Table 6; from these, more precise information should be forthcoming.

#### SUMMARY.

A detailed serological analysis of six strains of *Rh. meliloti* requires the postulation of at least three flagellar and seven somatic antigens. Only two of the six strains appear to be identical and the antigens are shared as follows:

Strain.	H.	O.
47	<i>Ab</i>	I, III
74	<i>bC</i>	II, VI
27	<i>bC</i>	I, IV
62		
102	<i>bC</i>	III, V
66	<i>bC</i>	II, VII

Tests of forty-two other strains against antisera of the five different strains above showed:

Wider grouping is possible on an *H* basis than on an *O*, the latter is more strain specific.

A fair proportion of the organisms possessed none of the *O* antigens postulated above.

A large proportion gave reactions very similar to strains 27 and 62 and this group contained about three-quarters of those isolated from *Medicago hispida* var. *denticulata* growing in widely scattered areas.

#### Acknowledgements.

The author's best thanks are due to Dr. H. R. Carne and Mr. Pulsford, of the School of Veterinary Science, University of Sydney, for animals, facilities and generous assistance, to Mr. W. Hurry for technical help throughout the course of the investigation and to Mr. A. W. Mitchell for assistance in the early stages. The investigation has been

assisted by a grant from the Commonwealth Research Fund, and continually by the goodwill and encouragement of Dr. W. L. Waterhouse of the School of Agriculture, University of Sydney.

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THE SYNONYMY, HOSTS, AND TYPE MATERIAL OF *GUNTHERIA BIPYGALIS*  
(GUNTHER) (ACARINA: TROMBIDIIDAE).

By CARL E. M. GUNTHER, M.D., B.S., D.T.M. (Sydney), Field Medical Officer,  
Bulolo Gold Dredging Limited, Bulolo, Territory of New Guinea.

[Read 28th May, 1941.]

Genus *GUNTHERIA* Womersley.

Womersley, 1939; Gunther, 1940.

*Neoschöngastia* Ewing, 1929; Gunther, 1939, 1939a, 1939b.

*GUNTHERIA BIPYGALIS* (Gunther).

*Neoschöngastia callipygea* Gunther [*nomen nudum*], 1938.

*Neoschöngastia kallipygos* Derrick et al. [*nomen nudum*], 1939.

*Neoschöngastia kallipygos* Gunther, 1939, 1939a, 1939b; Womersley, 1939.

*Neoschöngastia bipygalis* Gunther, 1939a.

*Guntheria kallipygos* (Gunther, 1939); Womersley, 1939.

*Guntheria bipygalis* (Gunther, 1939), Gunther, 1940, 1940a.

*Territory of New Guinea*: Brown's rat, little rat (*Rattus browni* Alston, 1877); the brown bush rat (*R. ringens* Peters and Doria, 1881); the brown scrub rat (*R. mordax* (*sensu lato*) Thomas, 1904); Monckton's scale-tailed rat (*Melomys moncktoni* Thomas, 1904); Stalker's scale-tailed rat (*M. stalker* Thomas, 1904); the rufous scale-tailed rat (*M. rubex* Thomas, 1922); arboreal "mouse" (*Melomys* sp.); Cockerell's bandicoot (*Echymipera cockerelli* Ramsay, 1877); Raffray's bandicoot (*Peroryctes raffrayana* A. Milne-Edwards, 1878).

*Queensland*: The giant brindled bandicoot (*Isoodon torosus* Ramsay, 1877); the spiny-haired rat (*Rattus culmorum youngi* Thomas, 1926).

TYPE.—*Ovum*: South Australian Museum. *Larva*: School of Public Health and Tropical Medicine, University of Sydney. PARATYPES.—*Ova*: School of Public Health and Tropical Medicine, University of Sydney. *Larvae*: South Australian Museum; Australian Museum; British Museum; Rocky Mountain Laboratory; Natal Museum; King Edward VII College of Medicine; Public Health Laboratory, Rabaul.

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## AN ERYTHRAEID MITE FROM NEW GUINEA (ACARINA: ERYTHRAEIDAE).

By CARL E. M. GUNTHER, M.D., B.S., D.T.M. (Sydney), Field Medical Officer,  
Bulolo Gold Dredging Limited, Bulolo, Territory of New Guinea.

(Four Text-figures.)

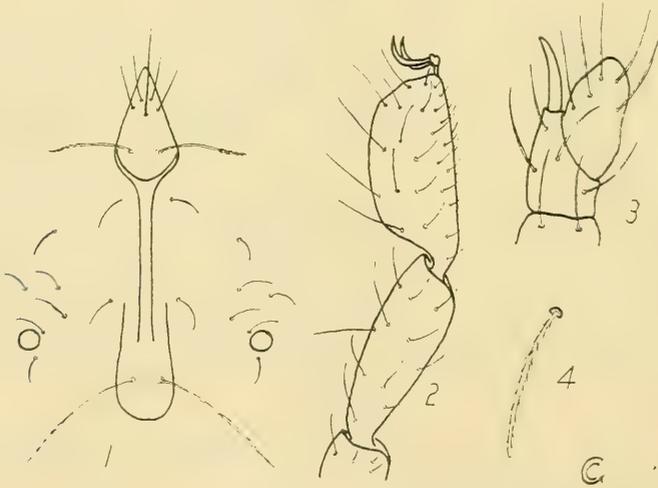
[Read 28th May, 1941.]

## Genus BELAUSTIUM Oudemans 1897.

*Tijdschr. Ent.*, xl, 119.

## BELAUSTIUM NOVAEGUINENSIS, n. sp. Figs. 1, 2, 3, 4.

Body oval; L, 667 $\mu$ ; W, 333 $\mu$ . Colour light red. Moderately well clothed with stout, almost straight, bluntly-pointed setae bearing very fine short branches; dorsal setae 20 $\mu$  to 25 $\mu$  long. No dorsal pits. Anus on the ventral surface, towards the posterior pole; lined on both margins by curved setae; a single duct opening into the middle of each lateral wall. Palpi not expanded. Palpal claw curved, bluntly pointed. Appendiculum tapering. Legs slender: i, 458 $\mu$ ; ii, 292 $\mu$ ; iii, 330 $\mu$ ; iv, 445 $\mu$ . Last two segments of each leg simple. Tarsi expanded; tarsus i 87 $\mu$  long, 28 $\mu$  wide. Sixth segment of leg i 84 $\mu$  long. Two tarsal claws, no pulvillus. Crista incomplete posteriorly; a long sharp



Figs. 1-4.—*Belaustium novaeguinaensis*, n. sp. 1, Scutum and sensillary area. 2, Terminal segments of leg i. 3, Terminal segments of appendiculum. 4, Body seta.

nasus extending forward 37.5 $\mu$  from the anterior pseudostigmata. Only the narrow, rounded posterior end of the scutum from the anterior pseudostigmata. Only the narrow, rounded posterior end of the scutum can be discerned. Anterior sensillary area well defined, 28 $\mu$  wide, and bearing two pseudostigmata 12.5 $\mu$  apart; posterior area not outlined, but occupied by two pseudostigmata 12.5 $\mu$  apart. Distance between the two pairs of pseudostigmata 103 $\mu$ . Pseudostigmatic organs filiform, with a few very fine short branches distally; anterior, 38 $\mu$ ; posterior, 62.5 $\mu$ . Nasus with a central straight seta 39 $\mu$  long, and four finer setae 20 $\mu$  long. Eyes single, sessile, just forward of the posterior sensillary area.

A single specimen found entangled in the scrotal hairs of a wallaby (*Macropus* sp.) from the Watut valley, Territory of New Guinea.

Type specimen lodged with the Australian Museum, Sydney.

TWO NEW TROMBIDIID LARVAE FROM NEW GUINEA  
(ACARINA: TROMBIDIIDAE).

By CARL E. M. GUNTHER, M.D., B.S., D.T.M. (Sydney), Field Medical Officer,  
Bulolo Gold Dredging Limited, Bulolo, Territory of New Guinea.

(Five Text-figures.)

[Read 25th June, 1941.]

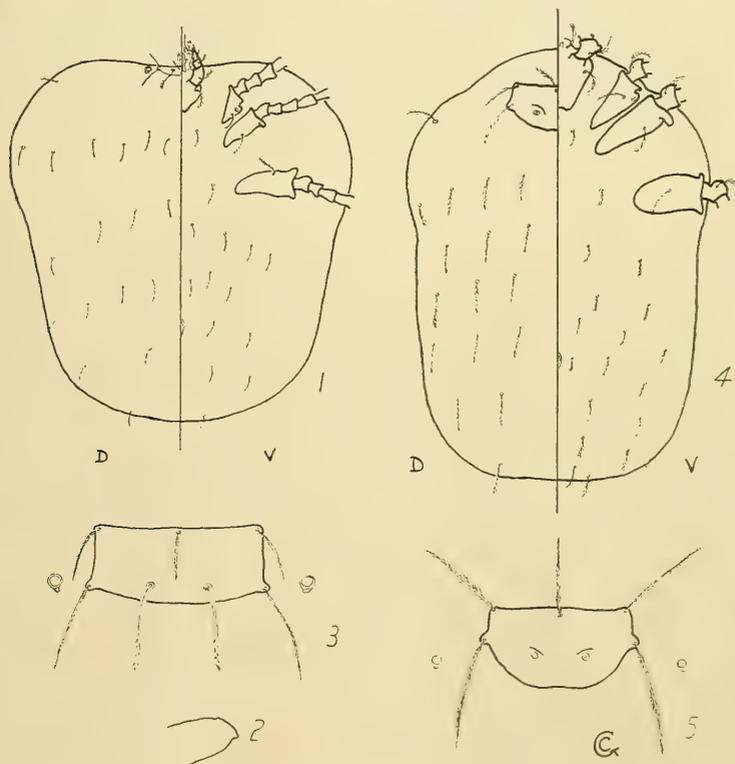
The following new larvae of the subfamily Trombiculinae have been taken in New Guinea:

Genus TROMBICULA Berlese 1905.

*Redia*, ii, fasc. 2, 155.

TROMBICULA ROBUSTA, n. sp. Figs. 1, 2, 3.

Body hump-backed, with broad rounded shoulders, and rounded posteriorly; widest opposite coxae iii. The cephalothorax set well back on the ventral surface, with only the chelicerae and part of the palpi showing from the dorsal aspect. Striations strong and coarse. Pitting on maxilla, scutum, and coxae. Colour blood red. Only well-engorged specimens taken; L,\* 688 $\mu$ ; W, 655 $\mu$ ; largest seen, 820 $\mu$   $\times$  833 $\mu$ . Maxillary



Figs. 1-3.—*Trombicula robusta*, n. sp. 1, Composite dorsal and ventral diagram. (This figure is drawn to one-half the scale of Fig. 4.) 2, Cheliceral teeth. 3, Scutum.

Figs. 4, 5.—*Neoschöngastia shieldsi*, n. sp. 4, Composite dorsal and ventral diagram. 5, Scutum.

\* As in previous papers, L = length, W = width, AL = anterolateral, AM = Anteromedian, and PL = posterolateral.

setae short, fine, curved, with a few fine branches. Chelicerae straight, stout, abruptly pointed; dorsoapical tooth minute, subterminal; ventral tooth minute, terminal. A short nude seta on each cheliceral sheath. Palpi stout, rounded, with a long branched seta on ii; a coarse many-branched seta on iii; on iv, two nude setae near the base, and one with very short branches half-way. Appendiculum very small, rounded, with eight setae: one long nude seta, one short stout spur, one very long, straight, coarse seta with long branches, and five other branched setae. Palpal claws trifurcate, the middle element long, stout, and bluntly pointed; the dorsal element similar but smaller; the ventral element vestigial. Scutum set on the forward face of the body, only visible in profile in most specimens (hence its description and length are not accurate); L, 37.5 $\mu$ ; W, 87.5 $\mu$ . Anterior margin sinuate, concave; anterior corners rounded; lateral margins convex; posterior margin sinuate, convex in its middle four-sixths; posterior corners angular, projecting laterally. Scutal setae 5: stout, tapered, with very short spine-like branches. The AL in the anterior corners, just in front of the AM; the PL in the posterior corners. AM, 25 $\mu$ ; AL, 28 $\mu$ ; PL, 47 $\mu$ . Pseudostigmata level with the PL setae; 27 $\mu$  apart. Pseudostigmatic organs filiform, with a few fine branches on the distal two-fifths; L, 41 $\mu$ . Ocular shield present. Eyes double, the anterior much the larger and set with its posterior margin opposite the pseudostigmata. Body setae 64: short, curved, with very short spine-like branches. Dorsum: setae 36, arranged in rows as follows: 2, 12, 8, 8, 4, 2. Venter: setae 28, arranged in rows as follows: 2, 2, 8, 6, 4, 4, 2; the anus is just behind row 5. Legs short; i, 292 $\mu$ ; ii, 278 $\mu$ ; iii, 333 $\mu$ . Leg setae long, straight, with fine branches on all sides. Coxal setae single, short, fine, curved, with fine branches along the convex side. Sixth segments not unduly expanded or constricted. All tarsi tapering; that of leg iii very long and slender. A short spur on tarsi i and ii; on iii, a long straight seta with very short spine-like branches.

Principal hosts: *Pitta* (*Pitta mackloti* Temminck, 1834), colonies on legs; Baiune. Bird (*Microeca* sp.), colonies on legs; Bulolo, T.N.G.

#### Genus NEOSCHÖNGASTIA Ewing '1929.

A Manual of External Parasites, 187.

#### NEOSCHÖNGASTIA SHIELDSI, n. sp. Figs. 4, 5.

Body ovoid, with a suggestion of indentations at the level of coxae ii, and behind coxae iii; widest opposite coxae iii. Striations fine and indefinite. Pitting on maxilla, scutum, and coxae. Colour cream. Only well-engorged specimens taken; L, 416 $\mu$ ; W, 291 $\mu$ ; largest seen, 444 $\mu$   $\times$  333 $\mu$ . Maxillary setae long, curved, with long branches. Chelicerae straight and stout; dorsoapical tooth small and blunt; ventral tooth apparently missing. A coarse, slightly curved seta with branches on the convex side on each cheliceral sheath. Palpi angular, wide at segment ii, with a sharp tubercle on the angle. On ii, one long coarse seta with many long branches; three branched setae on iii, two at the base and one towards the apex; on iv, one nude and one branched seta near the base. Appendiculum very small and bluntly pointed, bearing one short spur, one curved nude seta, and at least three branched setae. Palpal claw bifurcate, the dorsal element slender, slightly curved and bluntly pointed; the ventral element similar, but slightly shorter. Scutum straight before, convex behind, twice as wide as long. Anterior margin sinuate; anterior corners rounded, slightly projecting; lateral margins short, sinuate; posterior margin strongly salient, rounded, smoothly indented in its middle sixth; posterior corners angular and projecting; L, 39 $\mu$ ; W, 75 $\mu$ . A small oblique ridge in front of each pseudostigma. Scutal setae 5: almost straight, moderately stout, with long branches on all sides; the AL in the anterior corners, 45 $\mu$  long; the AM 37.5 $\mu$  long, set back from the anterior margin; the PL in the posterior corners, 56 $\mu$  long. Pseudostigmata two-thirds of the way back, behind the PL setae, 24 $\mu$  apart. Pseudostigmatic organs missing in all specimens. Ocular shield not visible. Eyes double, the posterior small and almost invisible, the anterior about 25 $\mu$  from the scutum with its front edge level with the pseudostigmata. Body setae 70: those of the dorsum coarse, almost straight, with long branches on all sides; those of the anterior portion of the venter very short, straight, with relatively long branches on all sides; those of the posterior portion of the venter intermediate in size. Dorsum: setae 34, arranged in

rows as follows: 2, 8, 6, 6, 6, 4, 2. Venter: setae 36, arranged in rows as follows: 2, 2, 4, 4, 6, 6, 4, 4, 4. The anus is at the level of row 6. Legs: i, 170 $\mu$ ; ii, 125 $\mu$ ; iii, 210 $\mu$ . Leg setae short, straight, and slender, with fine branches. Coxal setae single, with branches on the convex side only. A long stout curved seta on each second segment, with many long branches. Sixth segments not unduly constricted or expanded. Tarsi i and ii short and stumpy; iii long and slender. A short spur on tarsi i and ii; no spur or long nude seta on iii.

Casual host: The rufous scale-tailed rat (*Melomys rubex* Thomas, 1922), eight specimens inside ear; Bulolo, T.N.G.

Although the pseudostigmatic organs are missing from all specimens, the general features of the species and the scutal appearance convince the writer that there is little doubt that it belongs to the genus *Neoschöngastia*, in which it is provisionally placed.

The type specimens of the above species, described as new, will be deposited in the collection of the School of Public Health and Tropical Medicine, University of Sydney. Paratypes at the Australian Museum, Sydney.



## STUDIES IN SILURIAN BRACHIOPODA.

## I. DESCRIPTION OF A NEW GENUS AND SPECIES.

By JOAN JOHNSTON, B.Sc.\*

(Plate vii; two Text-figures.)

[Read 25th June, 1941.]

*Introduction.*

The object of this paper is to discuss and study the variation within a species of Silurian Brachiopoda described as new, and for which a new genus is also proposed.

The specimens comprise a set of some three hundred brachiopods collected from a limestone band within the Yass Beds, near Cliftonwood, Yass River. Previously, no description nor figure has been published but the form was referred by Shearsby (1912, pp. 112, 113) to Dun's species *Meristina* (?) *australis* (Dun, 1904, p. 318). It is evident that this was a misinterpretation, as the two species have very few common characters and are now placed in different families.

Collection was restricted to a single zone, from a band of impure limestone 1-2 feet thick. Weathered specimens were picked out or sifted from the soil over an area of some 9-10 feet in the direction of dip. A large proportion of these were adult stages, with relatively few of the immature and young, so that most of the discussion deals with characters as developed in the adult.

*Methods of Investigation.*

Various methods were used to determine the details of internal and external characters of the shell.

The complete set of specimens was subjected to measurement of length, breadth, thickness, height (or length) of dorsal valve, length of hinge line and umbonal angle. Each of the linear measurements was correct to one-tenth of a millimetre and the angular measurement to a half-degree. The percentages of length to breadth, length of dorsal valve to length, thickness to length and length of hinge line to breadth were calculated. Graphs were plotted to show the amount of variation within the group.

The nature of the internal characters was revealed by the construction of serial sections and in the production of internal and external moulds.

A few specimens were selected for the preparation of serial sections. As far as possible average forms were used, but consideration was given to good preservation and absence of chipping in the shell. The treatment, preliminary to grinding, was essentially that of Muir-Wood (1934) for some Mesozoic brachiopods, with slight modifications.

The selected specimen was heated to red heat over a Bunsen flame for about ten to fifteen minutes, care being taken to introduce the heat gradually and so avoid splitting and flaking of the outer shell layers. Heating was always continued until the specimen appeared to have been sufficiently calcined to contrast the detail of the internal structures against the matrix. It was then allowed to cool in the air, without plunging into water, and when *completely* cold, an application of a solution of one part of amyl acetate in four parts of collodion was made. When this was dry a further coating of the solution was applied and the process was repeated until a bright pink skin was formed, completely enclosing the specimen. Usually four or five coats sufficed. When thoroughly

\* This work was carried out during the tenure of a Science Research Scholarship and while the writer was part-holder of the Deas-Thomson Scholarship for Geology in the University of Sydney.

dry, the specimen was mounted in plaster of Paris on a grinding tray. The writer found it necessary to mount the specimen as soon as possible after the previous process to avoid disintegration.

Finally the grinding tray was securely attached to the calibrated grinding instrument (similar to that of Caldwell, 1935). Transverse and longitudinal sections at right angles to, and parallel to the plane of symmetry were constructed by grinding off known thicknesses of the shell. The exposed section, showing the shelly structures partly calcined and appearing white against the darkened matrix as a result of the heating process, was drawn at frequent intervals, always with any change in the internal features. A camera lucida enabled the production of enlarged diagrams.

Internal and external moulds were prepared for the examination of muscle scars, pallial markings and external ornamentation. This was accomplished by heating the specimens to redness and carefully scraping off the softened shell with a sharp needle under the binocular microscope (cf. Ulrich and Cooper, 1938).

Genus *SPIRINELLA*, n. gen.

*Meristina* Shearsby 1912, *Rep. Aust. Ass. Adv. Sci.*, Sydney, 1911, xiii, 112-113.

non *Meristina* Hall 1867, *20th Rep. N.Y. State Cabinet*, 1867, 157, fig. (*vide* Schuchert and Le Vene, 1929).

non *Meristina* (?) Dun 1904, *Rec. Geol. Surv. N.S.W.*, vii (4), 318.

*Diagnosis*.—Relatively smooth Spiriferids; outline transversely semi-oval to semi-circular. Ventral interarea anacline, moderate in size, divided medially by a triangular delthyrium; cardinal margin submegathyrid. Well developed blunt teeth of the ventral valve fit into corresponding sockets of the dorsal. Apical plates inclined, divergent; median septum absent. Brachial supports in the form of two opposed spires of seven to eight volutions, directed postero-laterally, not united at any part by a jugum. Slight sulcus in ventral valve with a corresponding fold on the dorsal. Anterior commissure uniplicate but only slightly deflected by the sinus of ventral valve.

Ornamentation of only very fine radiating striae superimposed on fine concentric growth lines.

Shell substance fibrous and impunctate.

Genotype.—*Spirinella caecistriata*, n. sp., Yass Beds, Cliftonwood, near Yass, N.S.W.

*SPIRINELLA CAECISTRIATA*, n. sp.

(*caecus*, obscure; *striatus*, striated.)

*Meristina* (?) *australis* Shearsby 1912 (*nomen nudum*), *Rep. Aust. Ass. Adv. Sci.*, Sydney, 1911, xiii, 112-113.

non *Meristina* (?) *australis* Dun 1904, *Rec. Geol. Surv. N.S.W.*, vii (4), 318.

non *Atrypoides australis* (Dun) Mitchell and Dun 1920, *Proc. Linn. Soc. N.S.W.*, xlv, 272.

Shell small, biconvex; outline transversely semi-oval to semi-circular; generally wider than long, length about nine-tenths of breadth. Ventral valve larger and always slightly more convex than the dorsal. Ventral umbo incurved, dorsal much smaller; umbonal angle 104°-105° (average). Cardinal margin submegathyrid; hinge line equal to about nine-tenths of greatest breadth of the shell; cardinal extremities rounded. Ventral interarea anacline, moderate, curved, medially divided by a fairly wide delthyrium. Deltidial plates disjunct, as two dorsally projecting divergent ridges on either side of the delthyrium. Apical plates well developed, inclined. Cardinalia as for genus. Median septum and jugal structures absent. Muscle and pallial markings not completely determined.

Folding of the shell restricted to a slight sulcus in the ventral valve and corresponding fold in the dorsal, producing a slightly uniplicate anterior commissure; lateral commissure not flexed. Surface ornamented by very fine radiating striae, about 15-16 per mm. (average) and hardly visible to the naked eye, superimposed on fine concentric growth lines; in the posterior portion 3-4 per mm., but 9-10 to the space of one millimetre near the anterior margin.

Shell substance fibrous and impunctate.

Holotype; specimen No. F39376, and two paratypes, Nos. F39378 and F39379, in the Australian Museum, Sydney.

Only the external features observed. Shell rather strongly biconvex; convexity of ventral valve greater than that of the dorsal. Ventral valve with a rounded umbo, incurved; umbo of dorsal valve not prominent. Ventral interarea slightly curved; features of delthyrium covered by matrix. Sulcus of ventral valve not well defined; corresponding fold on dorsal valve giving slight sinus in anterior margin (uniplicate); anterior and lateral commissures closely fitting, not crenulated, but a little distorted in the specimen.

Most of the outer lamellar layer has been removed but the portion preserved shows growth lines and faint indications of radiating striae. The presence of pallial markings as radiating ridges on the internal mould is revealed in the pedicle valve, where portion of the fibrous shelly layer has been removed.

The following table gives measurements of the holotype, and for specimens *A*, *B* and *C*, sectioned for Text-fig. 2, also the average of all specimens collected.

	<i>Holotype</i>	<i>A</i>	<i>B</i>	<i>C</i>	<i>Average</i>
Length in mm. . . . .	16.6	16.5	17.8	16.1	13.8
Breadth in mm. . . . .	17.5	17.2	18.5	18.9	15.8
Thickness in mm. . . . .	11.0	11.7	12.3	12.1	9.6
Length of dorsal valve in mm.	13.2	13.0	14.4	14.4	11.5
Hinge-line in mm. . . . .	15.5	—	16.1	16.1	14.1
Umbonal angle in degrees . .	104	100.5	106.5	103	104.1
Per cent. length to breadth . .	95.5	95.9	96.2	85.2	87.0
Per cent. length of d.v. to length	79.5	78.8	80.9	89.5	82.2
Per cent. hinge-line to breadth	88.6	—	87.0	84.7	89.6
Per cent. thickness to length . .	68.3	71.0	69.1	75.2	68.6

Topotype material is in the Australian Museum Collection, Nos. F38810 and F38811, and in the collection of the Geological Department, University of Sydney, No. 7556.

*Horizon and locality.*—Limestone band of upper portion of the Yass Beds, from the outcrop near Cliftonwood, Yass River, about three-quarters of a mile below Railway Bridge in Por. 14, opp. Por. 103, Ph. Yass, Co. King. Silurian.

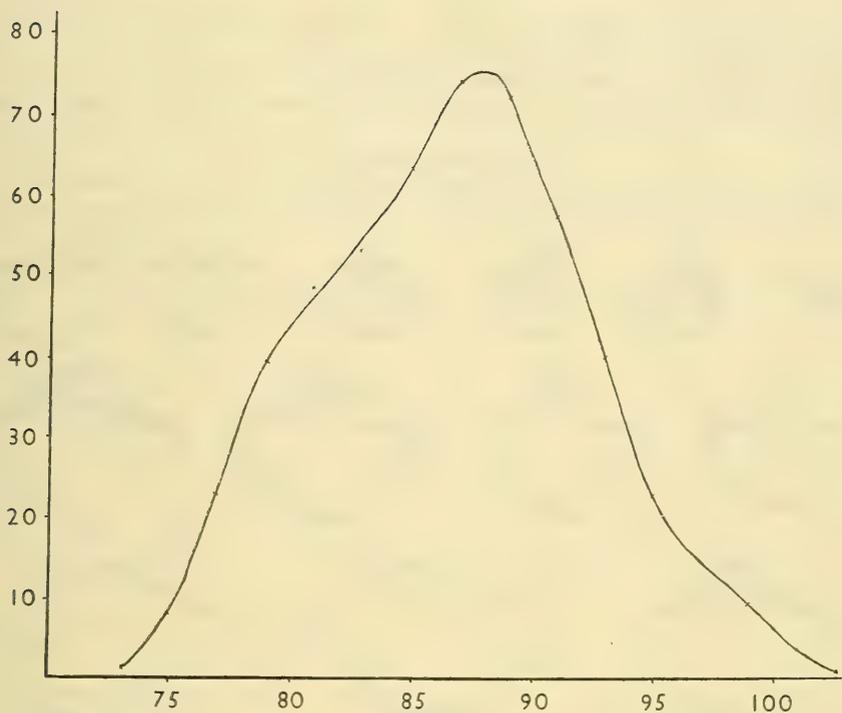
#### DISCUSSION.

##### *External Characters.*

Normal shells are transversely oval in outline, with the length approximately nine-tenths of the breadth and the maximum thickness occurring in the median plane, being usually rather greater than half (about three-fifths) the breadth. Graphs were plotted showing (*a*) percentage length to breadth, (*b*) percentage thickness to length, (*c*) percentage length of dorsal valve to length and (*d*) percentage length of hinge line to breadth, against the number of specimens with the respective percentages. In the graph (Text-fig. 1) the percentage length to breadth is plotted at intervals of two on the percentage scale for some 280 specimens and thus indicates the variation in the ratio of length to breadth. Since these graphs have the nature of simple curves, it is considered that a single species is present.

The maximum breadth is always attained anteriorly to the cardinal margin, at varying distances from the latter but never more than one-third of the length of the dorsal valve, in average forms being at about one-quarter of this distance (i.e., from hinge line to anterior margin). The umbones are both rounded, that of the ventral valve being incurved and much more prominent and higher than that of the dorsal. Measurements of the umbonal angle (Muir-Wood, 1935; apical angle North, 1920) give an average of 104° but a large percentage of the specimens have values from 98–112° although some are as low as 90° and others as high as 124°.

The ventral interarea (Buckman, 1919; Muir-Wood, 1935; Schuchert and Cooper, 1931, 1932; cardinal area North, 1920) anacline, of moderate size, is slightly concave, although always straight in horizontal section, and divided medially by a triangular delthyrium. In the majority of specimens the area is completely concealed by adhering matrix and thus can only be determined in section. The delthyrial angle (St. Joseph, 1935; North, 1920) varies from 45° to 60° and the delthyrium is partially closed by two deltidial plates. In none of the specimens examined was there any interarea present on the dorsal valve.



Text-fig. 1.—Curve representing the distribution of individuals according to their percentage length to breadth ratio.

*Deltidial Plates.*—The presence of deltidial plates (*deltidium discretum* Miloradovitch, 1937; *deltidium* George, 1932) was revealed by the transverse sections, although their position could be observed in the preparation of internal moulds. Their nature is too delicate in contrast to the hard limestone matrix in which they are embedded to permit the removal of the latter.

For the greater part of their length (i.e., equivalent to the lateral edge of the delthyrium) they are discrete, but are united just below the ventral umbo. They have the form of two thin “more or less triangular plates, but the triangles are included within the delthyrium apically, rather than cardinally, as generally occurs in the terebratuloids and rhynchonelloids. The plates project above the surface of the cardinal area at a marked angle”. (George, 1932, p. 526, for *Phricodothyris*.)

In this case the angle is about  $120^{\circ}$ – $135^{\circ}$  while if extended dorsally, the two plates would converge at  $60^{\circ}$ – $90^{\circ}$ . Transverse sections 4–9 (Text-fig. 2) just at the apex of the dorsal umbo, indicate that the extent is at least half-way from the ventral interarea to the dorsal umbo, and that they are continuous with the apical lamellae, but are inclined at a blunt angle to these latter.

*Folding and Ornamentation.*—The median ventral sulcus and corresponding dorsal fold are only poorly defined even in the specimens with greatest depression and elevation in the respective valves, although they are developed to some extent in all specimens examined, while a certain amount of deflection dorsally (sinus) occurs in the anterior commissure (uniplicate) as well as a corresponding deflection in the growth lines as they cross the sulcus.

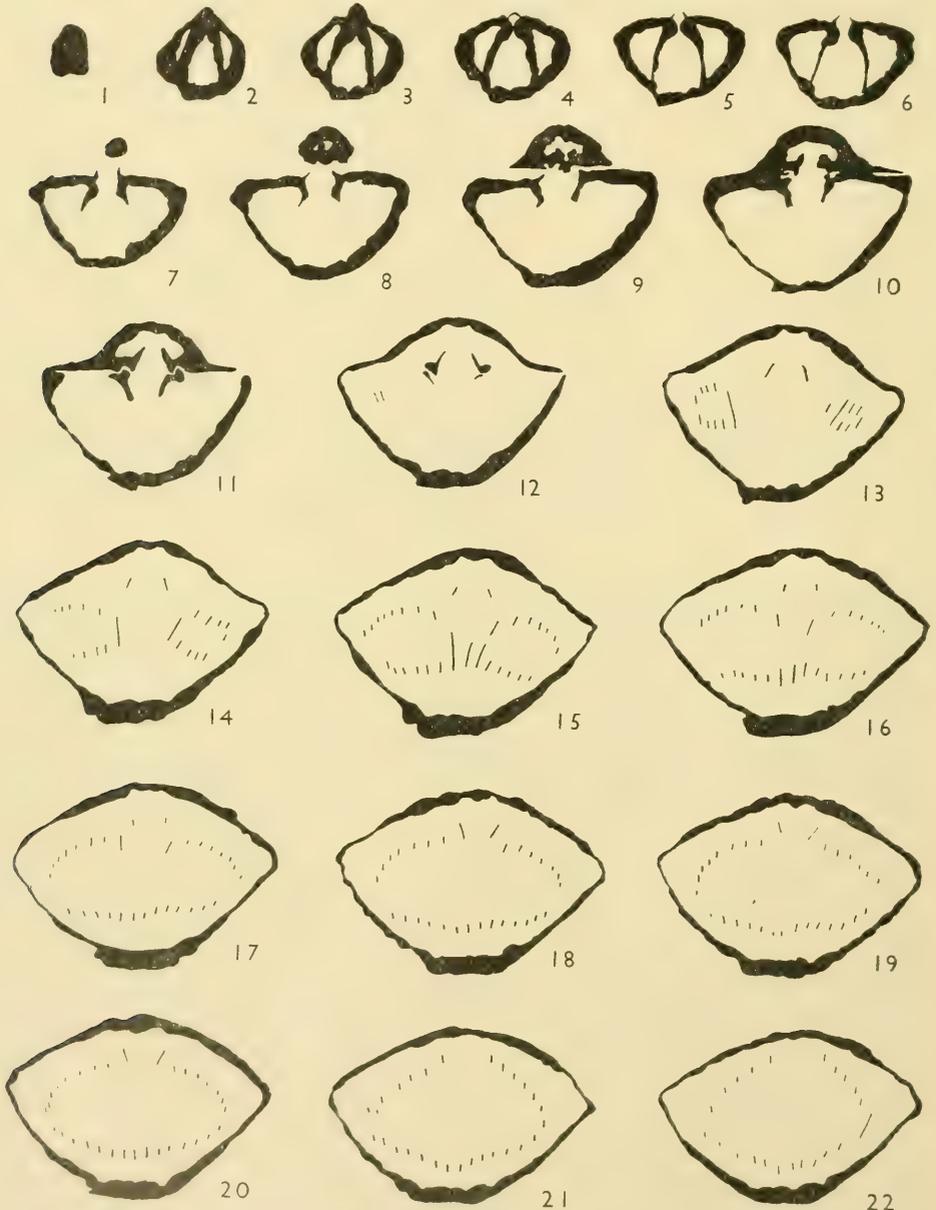
Ornamentation is only slightly impressed on the surface of the shell substance but is similar over both valves except for a concentration of growth lines toward the anterior margin. Radiating striae are very fine, not generally visible to the naked eye nor on any untreated specimens. In practically all cases it was necessary to remove the adhering shelly material from an external mould, and this was only made possible after the application of heat before gently chipping the shell with a sharp needle. The arrange-

ment of the striae was fairly uniform, from fourteen to eighteen occurring within the space of a millimetre.

A large proportion of the shells were sufficiently well preserved to exhibit concentrically developed growth lines which also were not deeply marked on the surface of the shell.

*Internal Characters.*

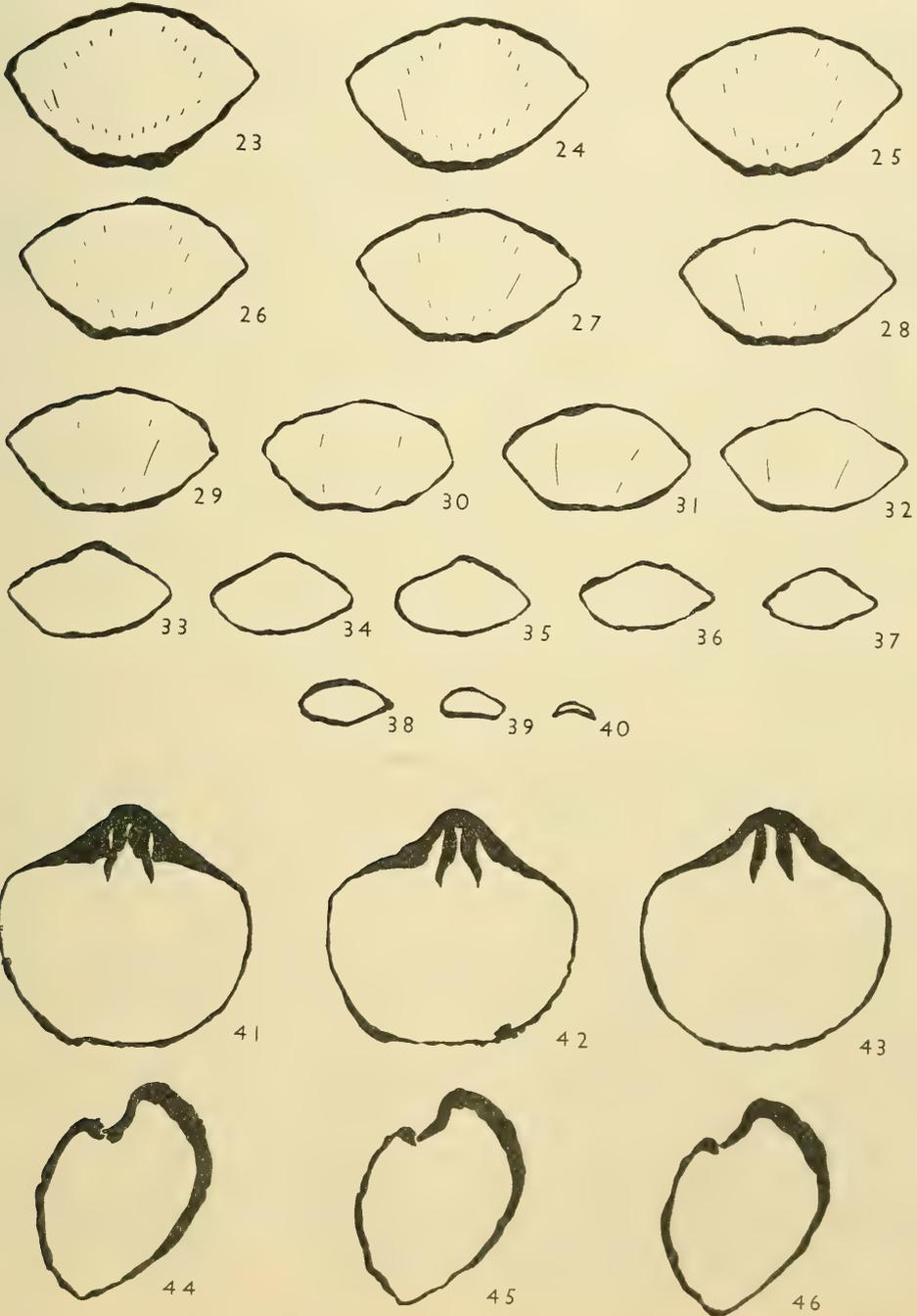
*Articulation.*—Articulation of the two valves is effected by the interlocking of a pair of blunt hammer-head shaped teeth in the ventral valve situated at the dorso-



Text-fig. 2.—Serial sections of *Spirinella caecistriata*, n. sp. Sections 1-40, Specimen A, perpendicular to length at 0.4 mm. intervals and drawn with the dorsal valve above, ventral valve below. Sections 41-43, Specimen B, perpendicular to thickness at 0.2 mm. intervals. Sections 44-46, Specimen C, perpendicular to breadth (hinge-line) at 0.4 mm. intervals. All  $\times 2$ .

lateral corners of the delthyrium with a corresponding pair of dental sockets lying outside the crural bases in the dorsal valve. The articulatory processes, although well developed, are not specialized; no cardinal process is present, while indications of secondary articulatory processes adjacent to the tooth and socket union are observed in transverse sections.

*Ventral Valve.*—The umbonal region of the ventral valve is divided into three cavities, a central or delthyrial cavity (Schuchert and Cooper, 1931, 1932; Miloradovitch, 1937) and two lateral umbonal cavities, by two well developed apical plates (George



1927, 1932; dental plates or dental lamellae of most authors; lamellae apicales Frederiks, 1927; delthyrial supporting plates North, 1920 and Thomas, 1910). There is little secondary thickening in the region of the apical plates, so that the cavities extend right to the umbo. On their dorsal (cardinal) side the apical plates extend from the umbo along the margins of the delthyrium to the teeth, and ventrally about one-fifth of the distance from umbo to anterior commissure along the floor of the valve. They are curved processes, inclined towards one another posteriorly, with a concave anterior margin and are continuous cardinally with the deltidial plates. Lines of growth, indicating addition of shelly material along their anterior margin and having a curved contour, can be seen when the specimens have been broken along one of these apical plates. No median septum is present. Thus the apical apparatus (apical plates and median septum) corresponds in development to the Cardinalis group (Frederiks, 1926 and 1927) characterizing the subfamily Munellinae.

*Dorsal Valve.*—In the umbonal region of the dorsal valve a medially divided hinge plate supports the dental sockets which lie outside the crural bases, and behind this is a small umbonal cavity. The spiralia are attached to the hinge plate through the crural bases, which separate from the latter and as descending lamellae continue more or less parallel to the inner surface of the dorsal valve but slightly divergent from one another. Seven to eight volutions of a ribbon-like coil are observed in transverse sections 12–32 (Text-fig. 2), showing that the spiralia are symmetrically arranged in the thickness and breadth directions and more or less parallel to the transverse outline of the shell. The spires are dorso-laterally directed and occupy about two-thirds of the interior from the hinge line to the anterior commissure. In none of the sections prepared, nor in any intermediate stage of their production, was there any indication of the union of the descending lamellae by a jugum or jugal processes.

*Musculature.*—The outline and nature of the muscle scars cannot be determined from the prepared internal moulds, only their position and extent could be distinguished in the two valves. In the *ventral valve* the area of muscular attachment is situated posteriorly just below the beak, and lying between the apical plates, with an approximately equivalent extent anteriorly to these latter. This area could not be differentiated into adductor and diductor scars except that there were indications of long narrow central adductors bounded by more extensive diductors.

In the *dorsal valve* the adductor scars are posteriorly situated, just anterior to the beak and are more or less rounded in outline. The point of attachment of the diductors in this valve was not indicated but probably was posterior in position between the crural bases.

*Pallial Markings.*—In describing *Martinia glabra* (Martin), George (1927, p. 113) observed radially arranged ridges anterior to the muscle scars on internal moulds of the ventral valve and “in the median plane of all forms there is a well-marked ridge which extends from the umbonal region to the anterior margin”. These he takes as vascular markings. Corresponding to these in *Spirinella caecistriata*, internal moulds of the ventral valve usually reveal seven radiating ridges, equivalent to depressions in the shell, with a fairly constant arrangement. A central ridge extends from the umbonal region but fades out before reaching the anterior commissure. On either side is another, adjacent to the central edge of the apical lamellae, while beyond each is a further pair a little closer to one another than the central three. These two lateral pairs do not extend quite as far towards the umbo, and also fade out before reaching the anterior commissure. None of the ridges bifurcate.

No corresponding structures were seen on any internal moulds of the dorsal valve, the surface of which is quite smooth so that pallial markings are apparently absent (cf. George, 1927, p. 113).

*Shell Structure.*—The shell wall is usually thin, especially in the anterior region, as it is only in the posterior portion of both valves that any thickening occurs. This is best developed at the muscle attachments, along the apical plates and other internal structures meeting the floor of the valves. In this region the shell often attains a thickness of 0.75 mm., while the outer layer bearing the ornamentation is usually absent. The nature of the shelly material of the internal structures is similar to that of the

outer shell wall (i.e., fibrous and impunctate). A longitudinal section through the plane of symmetry of the valves shows that the fibres are inclined at varying angles to the junction line between shelly material and matrix, and that they are arranged so that the greater angles occur in the posterior portion, becoming gradually smaller toward the anterior where the fibres are more or less tangential. Punctae were not observed even in heated specimens, which process (Thomson, 1927, p. 107) renders them more easily visible in the terebratuloids.

#### *Classification.*

Of the classifications and divisions of the family Spiriferidae, none proves at present very satisfactory. Frederiks (1926) proposes a rather arbitrary system in which *Spirinella* fits into the subfamily Munellinae. Schuchert and Le Vene (1929), on the other hand, do not define subfamily limits, so that the affinities of *Spirinella* are not determined (cf. George, 1933).

#### *Distribution and Stratigraphical Range.*

All of the specimens here described were collected from the Cliftonwood locality, but the form is listed by Shearsby (1912, p. 113), from the Yass Beds at Wargeila. It is also known from the southern end of Rossi Street (sewerage trenches) and near Racecourse Trig. Station, Yass. The stratigraphical position of this horizon at Cliftonwood is given in detail by Shearsby (1912, p. 112). In the upper portion of the Yass Beds, above the *Leperditia shearsbyi* Chapman and *Rhombopteria laminosa* de Koninck horizon, a thickness of sediments, shales, sandstones, mudstones and limestones of about 170 feet occurs before the outcrop is reached. Above this *Spirinella* limestone follows a further series of sandstones and calcareous shales about 150 feet thick with a few indeterminate fossils, before the beds are overlain by the Laidlaw Series. The associated fauna is given by Shearsby (1912, p. 112).

*Age.*—The Yass Beds are members of a conformable series of alternating tuffs and sediments, lying stratigraphically above the Bango Beds containing *Halysites pycnoblatoïdes* Etheridge fil. (Shearsby, 1912, p. 110) and below the Hume Beds. Graptolites were recorded from these latter beds by Sherrard (1936, p. 142) and Sherrard and Keble (1937, p. 307). These authors conclude that "the graptolites indicate Zones 26 to 35 of the Silurian as divided by Elles and Wood (1913), which makes the beds at Silverdale equivalent to the Wenlock-Ludlow junction beds of England and to the Melbournian Series of Victoria (Chapman and Thomas, 1935; Keble and Harris, 1934)".

Thus the *Spirinella* limestone has its age restricted to a position in the Silurian intermediate between the *Halysites pycnoblatoïdes* horizon and the graptolite zones as given above.

*Preservation and Matrix.*—The shells are preserved in calcite, set in a matrix of impure tuffaceous limestone of light greyish colour, breaking with a hackly fracture. This latter adheres firmly to the shell and consequently difficulty is experienced in obtaining specimens showing the external surface ornamentation.

#### *Previous References.*

The only previous reference to this brachiopod is given by Shearsby (1912, pp. 112, 113), who lists the name *Meristina australis* (?) Dun from Cliftonwood and *Meristina* (?) *australis* Dun from Wargeila, but no description, nor figure, nor diagram was presented. However, the specimens described here correspond (according to Shearsby—verbal communication) to those intended for that name.

As well as considerable dissimilarity in internal structure, *Atrypoides australis* (Dun) differs from *Spirinella caecistriata* in having a much shorter hinge-line, rounded outline, no areas, smoother shell, and is grouped (Schuchert and Le Vene 1929, p. 20) with the Atrypinae.

#### *Acknowledgments.*

The generous help of Dr. Ida A. Brown, under whose guidance this work was originally undertaken, as well as critical discussion on reading the manuscript, is gratefully acknowledged. To Mr. A. J. Shearsby, of Yass, I am indebted for considerable

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EXPLANATION OF PLATE VII.

*Spirinella caecistriata*, n. sp.

- 1.—Dorsal view of holotype. Australian Museum No. F39376, × 2.
- 2, 3, 4.—Lateral, ventral and anterior marginal views respectively of same specimen, × 2.
- 5.—Portion of external ornamentation. Paratype. Australian Museum No. F39378, × 4 approx.
- 6, 7, 8, 9.—Dorsal, lateral, ventral and anterior marginal views respectively of a topotype. Australian Museum No. F39377, × 2.
- 10, 11.—Dorsal and ventral internal moulds. Paratype. Australian Museum No. F39379, × 2.

NOTES ON THE MEASUREMENT OF SOME PHYSICAL AND OPTICAL  
PROPERTIES OF THE NEW SOUTH WALES TORBANITES.

By J. A. DULHUNTY, B.Sc., Linnean Macleay Fellow of the Society in Geology.

(Four Text-figures.)

[Read 30th July, 1941.]

*Introduction.*

In the investigation of the New South Wales torbanites, it has been found that certain physical and optical properties are of considerable importance, providing fundamental data and results which have a direct bearing on classification, micro-constitution and the nature of the materials which vary widely in type and quality.

The present paper is confined mainly to descriptions of methods and principles involved in the investigation of some of the more important physical and optical properties which promise to be of value in different branches of the study of torbanite.

*The Determination of Percentages of Essential Constituents.*

Certain essential constituents are present in all the torbanites occurring in the Kamilaroi Coal Measures of New South Wales (Dulhnty, 1938). The accurate determination of the quantities of these constituents or macerals, constitutes an important part of the microscopical study of the torbanites and the investigation of the inter-relationship between optical, physical and chemical properties.

*Alternative Methods.*

The essential constituents are extremely small, necessitating the use of thin transparent sections of torbanite and the employment of microscopic methods for determining the amounts present. Such methods depend directly or indirectly on the estimation of the total area occupied by each of the constituents in the thin section being examined.

By using a microscope fitted with an eyepiece containing a fine net, and an objective giving a magnification of at least one hundred diameters, the number of squares occupied by each of the constituents can be counted in the microscope field, and the percentages by volume determined. In using this method it is necessary to make a number of determinations at different points, in order to obtain average results for the whole section. This is slow and particularly trying to the operator, as numerous determinations are necessary and considerable difficulty is experienced in counting the squares by inspection through the eyepiece.

The foregoing method may be considerably improved by projecting the microscopical field onto a ground-glass plate on which a net has been marked. This may be achieved by using a strong light source and a microscope fitted with an eyepiece and an objective giving a magnification of about forty diameters. A ground-glass plate marked with one-tenth inch squares is placed at a distance of twenty-four inches from the eyepiece. The field is focussed onto the ground plate, giving a magnification of 100 to 150 diameters, and the number of squares occupied by each constituent may be counted with much less difficulty than in the case of the eyepiece net.

In either of the above methods the degree of magnification required means that a very small area of the thin section, no more than one millimetre in diameter, is examined in each determination. Consequently it is necessary to make as many as ten estimations on a thin section of one square inch, to obtain average results. It is possible in this way to reduce the limits of error to about two per cent.

An alternative and much more successful method of estimating the quantities of the constituents is by using a mechanical stage fitted with an integrating micrometer, on a

microscope giving a magnification of about one hundred diameters. With this instrument a line is taken across the full width of the thin section, and the sums of the small distances occupied by the different constituents along the line are determined. From these figures the percentage by volume for each constituent is readily calculated. Estimations are made along several lines across the section, and the results, with an error of no more than one per cent., may be obtained quickly and easily. The integrating micrometer has many advantages over the methods involving the use of a net. The estimations are more rapidly carried out, giving much more accurate results, and each estimation is made across the full width of the thin section, as compared with the small circular areas in which the net counts are made.

*Relation Between Apparent Percentages and Thickness of Section.*

The most important factor influencing the accuracy of percentage determinations by either of the methods already described, is the thickness of the transparent sections of torbanite. The bodies of gelosite and retinosite are roughly disc shaped, appearing round in sections cut parallel to the bedding and ellipsoidal in sections at right angles. The discs are separated from each other and completely surrounded by the opaque matrix of the torbanite. As a result of this arrangement, the area occupied by the transparent bodies increases as the thickness of the section is reduced during the grinding process. Estimates of percentages will therefore increase as the section becomes thinner. Theoretically the absolute percentage by volume would be obtained only at infinite thinness, and all other estimates would represent apparent volumes. Actually the rate of increase of apparent volume decreases as a function of the thickness. Thus the error in volume determinations due to thickness of section rapidly becomes very small as the thickness is reduced, and it is negligible at thickness less than 0.01 mm. This may be illustrated by plotting apparent volumes against thickness during the preparation of a thin section. Fig. 1 shows curves obtained in this manner for three different types of torbanite (A, B and C) containing varying quantities of the transparent constituents gelosite and retinosite. It will be noted that the same general relationship exists in each case, although the actual volume of constituents varies greatly, and the increase in volume becomes negligible after a thickness of about 0.01 mm. is reached. It is evident from the shape of the curves that the shape of the gelosite and retinosite bodies is not the only factor involved in the rate of increase of apparent volume. Such features as variations in the size of the bodies in any one section, and differences in the

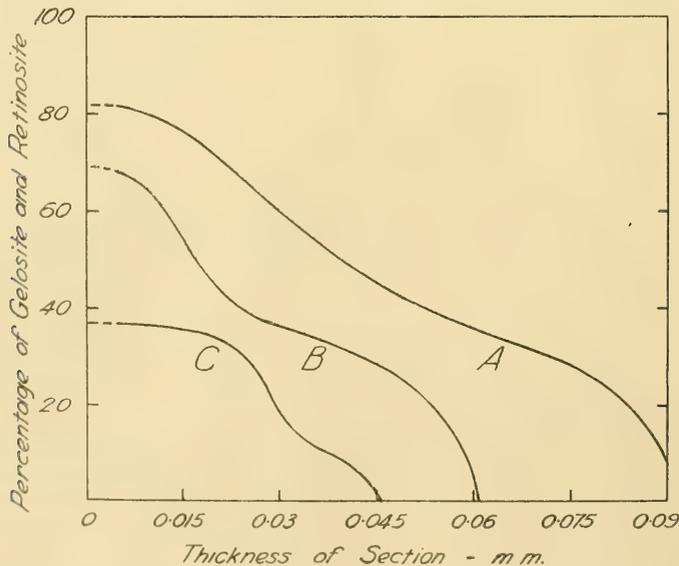


Fig. 1.—Diagram illustrating the relation between apparent volume of transparent constituents and thickness of section for three different torbanites, A, B, and C.

numbers of bodies of certain sizes, would also affect the relationship between apparent volume and thickness. Therefore such curves could not be used in correcting volume estimations for different thicknesses, and it is necessary to reduce all torbanite sections to less than 0.01 mm. before estimating the percentages of constituents.

*The Determination of Thickness of Section.*

The accurate determination of the actual thickness of section may be made by using a microscope fitted with a micrometer screw focussing adjustment graduated to at least 0.005 mm., and an objective giving a magnification of not less than 150 diameters. The difference between two readings made at the positions of focus on the top and bottom of the section gives its thickness. The focussing mechanism of the microscope should be in good order, and the accuracy of the micrometer adjustment should be checked against a micrometer screw gauge by determining the thickness of a thin glass plate such as a cover-glass. After some practice sections can be accurately measured to 0.005 mm. and estimated with reasonable accuracy to 0.0025 mm.

If it is desired to measure the thickness of a section at various stages during the grinding down process, for the purpose of obtaining relationships such as the increase in apparent volume of constituents with decreasing thickness of section, the following procedure may be adopted. A slice of torbanite is prepared by polishing one side and cementing to a glass slide with Canada balsam. It is ground down with fine carborundum powder till the first signs of transparency appear. The surface is then made as smooth as possible by rubbing on a fine grained and high quality honing stone in a stream of water. When smooth, a cover-glass is attached to the surface by means of a drop of oil or water, and the thickness of the section, the quantities of gelosite and retinosite and any other determinations may be made. The cover-glass is then removed and the section made a little thinner by rubbing on the honing stone. This may be repeated, determinations being made at intervals of about 0.005 mm. until the section is as thin as it can be made, usually between 0.005 and 0.0025 mm.

*The Transmission of Visible Light.*

In preparing thin sections of torbanite, the first evidence of transparency is obtained at a thickness varying between 0.05 and 0.025 mm., the colour being dark red. As the section is made thinner the colour becomes lighter, passing from dark red through light red to orange-yellow, and in some cases pale yellow, as greater amounts of visible light are transmitted. The study of the relationship between transmission of visible light and the nature and volumes of constituents, as well as other properties of torbanite, constitutes an important part in the investigation of the fundamental nature of the material of which it is composed.

*Apparatus and Results.*

For the purpose of obtaining values representing the degree of transparency or amount of light transmitted by thin sections of torbanite, the use of photo-electric determination appears to be the most satisfactory. A constant light source is arranged so that a beam of light, about half an inch in diameter, may be directed onto the photo-electric cell of an exposuremeter at constant distance. The thin sections of torbanite, mounted in the usual manner for microscopic examination, are placed in the beam of light close to the lens of the exposuremeter. A reading is made for the amount of light passing through the glass slide, film of Canada balsam and cover-glass, away from the section of torbanite. The slide is then moved so that the thin section comes into the beam of light and a second reading is made. The difference between the two readings represents the amount of light reduction due to absorption by the thin section of torbanite. This is inversely proportional to the amount of light transmitted, so that values suitable for general practical purposes in comparing the degrees of transparence of different torbanites may be obtained by means of the following simple formula, in which  $V$  is the required value, and  $a$  and  $b$  are the first and second readings respectively on the exposuremeter:

$$V = 100 - \frac{(a-b) 100}{a}$$

The amount of light transmitted depends primarily on the thickness of the section, so that it is necessary to determine its thickness before making the test. This may be accomplished by using a microscope fitted with a micrometer screw adjustment, as already described in this paper.

The amount of light transmitted depends also on the quantities and inherent nature of the constituents present in the particular torbanite being examined. The relationship between the light-transmitting power and the quantity of gelosite and retinosite in different torbanites can be studied by determining the amount of light transmitted and the percentages of essential constituents in sections of standard thickness, usually 0.01 mm. Such results are important in connexion with variations in the nature of gelosite and retinosite in different types of torbanite.

During the preparation of a thin section of torbanite, the apparent percentages of gelosite and retinosite, and the amount of light transmitted, both vary as the section becomes thinner. The relationship between the rates of increase of these two factors is important in connexion with the possibility of estimating the percentages of constituents by determining the amount of light transmitted by sections of known thickness, and also in studying the light-transmitting power of the constituents in any one type of torbanite. For the purpose of investigating these features, determinations should be made at different thicknesses during the preparation of sections, using the method already described for examining the relation between apparent volumes of constituents and thickness.

Curves showing the relationship between light transmission and thickness of section for different types of torbanite are illustrated in Fig. 2. The form and positions of the curves are influenced by the rate of increase in apparent volume of transparent

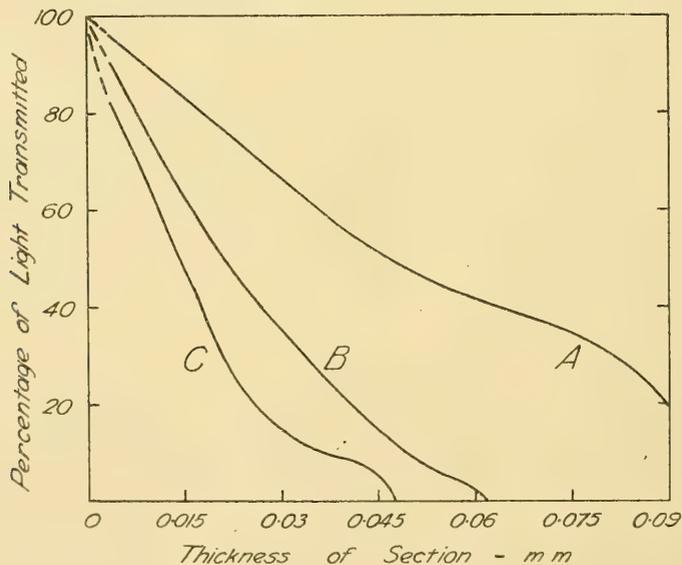


Fig. 2.—Diagram illustrating the relationship between transparency and thickness of section, for three different torbanites, A, B and C.

constituents, the absolute volumes of constituents and the intrinsic light-transmitting power of the transparent macerals. It will be noted, however, that all the curves, if projected beyond the thickness at which the last determination was made, would reach a point representing 100 per cent. of light transmission at infinite thinness. This constitutes an important check on the accuracy of the apparatus and methods used in making the determinations.

*The Transmission of Infra-red Radiation.**Apparatus and the Preparation of Standard Thick Sections of Torbanite.*

It has been found that sections of torbanite sufficiently thick to be opaque to all visible light, will transmit varying amounts of infra-red radiation. In the method devised for determining the relative powers of transmission possessed by different torbanites, sections of standard thickness and orientation with regard to direction of bedding-planes are subjected to a strong electric light source and the infra-red transmitted by the section is recorded photographically on an infra-red sensitive film. The amount of infra-red radiation transmitted by the torbanite determines the density of the exposure on the film, and this may be measured by means of a suitable densitometer or photo-electric cell exposuremeter.

The apparatus used is illustrated in Fig. 3. The infra-red radiation is produced by means of a 100 watt electric lamp, (*a*). An exhaust fan, (*b*), is necessary to keep the film and torbanite sections cool, and avoid any secondary radiation of infra-red

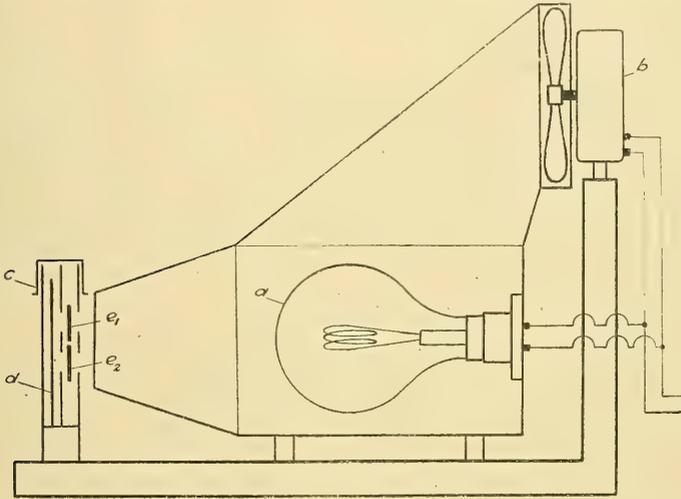


Fig. 3.—Diagrammatic illustration of apparatus used in recording infra-red radiation transmitted by torbanite.

from the metal or torbanite. The metal holder, (*c*), consists of two compartments which contain the film, (*d*), and two sections of torbanite (*e*<sub>1</sub> and *e*<sub>2</sub>). The compartments are separated by a metal plate with two holes three-eighths of an inch in diameter, placed opposite openings of the same size in the outer wall of the compartment containing the sections. These holes allow the passage of the infra-red through the torbanite onto the film.

The amount of infra-red transmitted varies with the direction in which the section is cut in relation to the bedding-planes of the specimen of torbanite. Transmission is maximum in sections cut at right angles to the bedding, and minimum in those cut parallel to the bedding. It has been found most convenient to use sections cut at right angles to the bedding in all cases.

Transmission also varies as a function of the thickness of the sections. In the case of certain torbanites, sections two millimetres in thickness will transmit appreciable amounts of infra-red. The standard thickness adopted as being the most suitable is 0.75 mm. Such sections are opaque to visible light, and require reasonable short exposures in the infra-red tests.

The actual length of exposure varies according to the nature of the torbanite, from one second to thirty minutes. Any section, 0.75 mm. in thickness, which gives no result at an exposure of thirty minutes may be considered opaque to infra-red radiation. Such sections have been exposed up to two hours without result.

The standard sections are prepared by grinding down slabs of torbanite three-quarters of an inch square to about 1.5 mm. in thickness using coarse carborundum. Then a fine carborundum powder, of grade 500, is used on a glass plate to reduce the sections to the standard thickness of 0.75 mm. A micrometer screw gauge is used in measuring the thickness of the section. It is necessary to use a carborundum powder of standard grade to complete the sections, so that the depth of the grain cuts on the surface of the torbanite will be the same in each case.

#### *Method of Recording Results.*

The following method is suggested by the writer for obtaining relative numerical values in comparing the power of different torbanites to transmit infra-red radiation.

In each determination two sections are used, one of unknown value being tested against one for which a value has already been determined. The densities of the two exposed spots on the film are then compared and a value allotted to the test piece. This method has been adopted as the results obtained are reasonably independent of length of exposure and variations in the processing of the film, provided that greatly over- and under-exposed spots are avoided.

Before making the actual test on an unknown torbanite, it is necessary to make a trial test to determine the approximate length of exposure which will produce a spot of medium density on the film. A torbanite section of known value is then selected which will give a spot of suitable density at the exposure required by the test piece, and the two are tested together. To obtain numerical results in comparing the densities of the two exposed spots on the film, a photo-electric exposuremeter is used in a manner similar to that already described for determining the transmission of visible light by thin sections of torbanite. The exposed spots are placed in the beam of light, and the amount of light reduction in the case of each spot is determined by making direct readings with the exposuremeter.

The torbanite from the Ulan deposit has been selected as an original standard and given a value of 100. In calculating results, the transparencies of other torbanites are compared with the original standard and allotted relative values depending on their powers of transmitting infra-red by the following method:

If  $Vt$  is the required value for the test piece,  $Vk$  the value already determined for the torbanite section against which it is being tested, and  $t$  and  $k$  the exposuremeter readings for the test piece and known sections respectively, then the difference between the two can be expressed as a percentage, which is

$$\% = \frac{k \cdot 100}{t}$$

Then the relative value of the test piece compared with the known section will be

$$\frac{k \cdot 100}{t} = \frac{Vt \cdot 100}{Vk}$$

which simplifies to

$$Vt = \frac{k \cdot Vk}{t}$$

This formula can be used in comparing a test piece with the Ulan material or any other torbanite for which a value has been determined.

It has been found that the power of infra-red transmission possessed by any particular torbanite depends more on the inherent nature of the constituents than the actual amounts present. The study of this property constitutes yet another means of investigating the fundamental differences which exist between the macerals of torbanites from different deposits; thus it is important in connexion with classification and the interrelationships between the various properties of different torbanites.

#### *The Power of Expansion and Contraction of Torbanite when Heated and Cooled.*

##### *The Determination of Expansion.*

The apparatus devised for measuring the linear expansion of torbanite when heated is illustrated in Fig. 4. The piece of torbanite ( $t$ ) to be tested is held between two invar rods ( $a$  and  $b$ ). One rod ( $a$ ) is clamped firmly to the framework and the other rod ( $b$ ), which moves through the supports ( $c$  and  $e$ ), is held against the torbanite

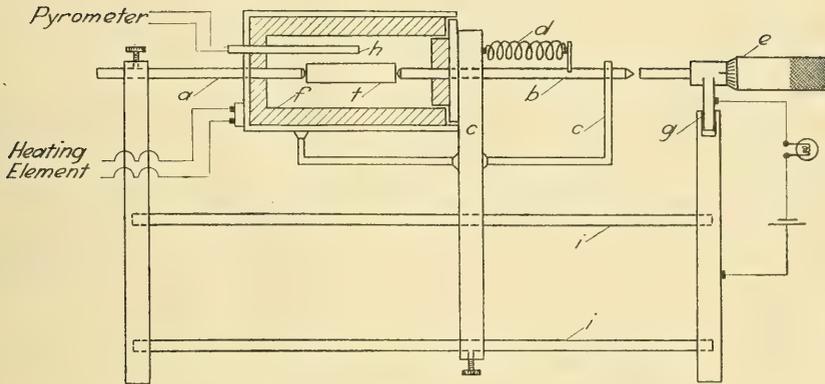


Fig. 4.—Diagrammatic illustration of apparatus used for the determination of linear expansion of torbanite when heated.

by means of a light spring (*d*). A micrometer gauge (*e*) is clamped to the framework so that the movement of the rod (*b*) can be measured. The electrically heated chamber (*f*) is so constructed that it may be moved back along the rod (*a*) for the purpose of introducing and removing the piece of torbanite. The micrometer gauge support is insulated from the framework at the point (*g*). A small electric light globe and single cell battery are connected in series to the micrometer and framework. When the actual point of contact is obtained between the rod of the micrometer and the movable rod (*b*), the circuit is closed and the globe lights up. This enables the amount of movement of the rod (*b*), due to expansion of the torbanite, to be measured very accurately. The temperature of the electrically heated chamber is controlled by means of a suitable variable resistance. A thermocouple (*h*) is situated within the chamber, and the temperature recorded by means of a pyrometer. The horizontal supporting rods (*i* and *i*) are constructed from a nickel-iron alloy possessing a constant coefficient of expansion between the limits of temperature resulting from external radiation by the heating chamber.

Rods of torbanite 40 mm. in length and about 7 mm. square are used for the expansion tests. The length of the rods must be exact and may be measured by means of a micrometer gauge. The cutting of torbanite in preparing such rods presents considerable difficulty as the finely divided silica in the torbanite prevents the use of a metal saw, and the soft elastic nature of the material makes the use of a diamond armed metal disc impossible. It has been found, however, that a rotating aluminium disc armed with a paste of carborundum and water will rapidly cut the torbanite without excessive abrasion of the disc. The carborundum becomes embedded in the aluminium and successfully cuts the torbanite. The aluminium disc used for this purpose is one-sixteenth of an inch in thickness, nine inches in diameter and rotated at 1,400 revolutions per minute by means of a one-quarter horse power electric motor.

The accuracy of the instrument may be tested by carrying out determinations on a metal rod of definite length and known coefficient of expansion. Readings are taken at intervals over the temperature range required in testing torbanite, and the calculated expansion of the metal rod deducted from the amount of expansion recorded by the instrument. A curve showing the amount of error involved at any temperature may be obtained in this way, and used in correcting subsequent torbanite expansion determinations. Using the apparatus described, it is possible to obtain results varying by less than 0.5 per cent. when duplicate determinations are carried out on torbanite rods cut from the same specimen.

In any one specimen of torbanite the coefficient of expansion varies considerably in different directions in relation to the bedding-plane. Expansion is always greatest at right angles to the bedding, and minimum in parallel directions. Thus it is necessary to cut the rods of torbanite in known directions in relation to the bedding. The amount

of expansion also varies greatly with different specimens from the same deposit, as well as specimens from different deposits.

*The Development of Permanent Expansion and Contraction.*

A rod of torbanite cut in a direction normal to the bedding when heated will undergo a certain amount of expansion, but on cooling it will not contract to its original length. A certain amount of permanent expansion is developed. This may represent as much as 25 per cent. of the total expansion when heated, but usually lies in the vicinity of 5 to 15 per cent., amounting to about 1.2 per cent. of the original length of the torbanite rod. The amount of permanent expansion developed is approximately proportional to the rise in temperature up to 350°C. This suggests that the development of permanent expansion is due to some physical effect rather than the result of chemical changes which would be expected to be more pronounced at the higher temperatures.

A rod of torbanite cut parallel to the bedding, when heated and then cooled, will contract to less than its original length, thus developing permanent contraction. The amount of permanent contraction developed is not always proportional to the rise in temperature, but a certain amount is always developed for all temperature rises. It has been noted that in the cases where it is not proportional a greater amount of permanent contraction is developed between 30° and 200°C. than between 200° and 350°C. This indicates a physical rather than a chemical change, as in the case of rods cut normal to the bedding. The amount of permanent contraction developed at any given temperature, may be equivalent to as much as 50 per cent. of the total expansion when heated, but usually amounts to about 15 to 20 per cent., representing about 0.6 per cent. of the original length of the rod.

Considering the permanent contraction and expansion to be the amounts of permanent linear distortion caused when rods parallel and normal to the bedding respectively are heated, then the permanent distortion in relation to the total expansion is greatest in the case of rods parallel to the bedding, although the actual amount of distortion is always less than in the case of rods normal to the bedding.

*Permanent Volume Changes and Specific Gravity.*

The fact that torbanite when heated develops permanent contraction parallel to the bedding and permanent expansion in a direction at right angles means that permanent volume changes occur when a piece of torbanite is heated. The amount of volume change depends on the relative amounts of permanent contraction and expansion developed, and also the shape of the piece concerned. Considering rectangular blocks with sides parallel and at right angles to the plane of the bedding, the fact that permanent expansion is greater than permanent contraction, will mean that there will be an increase in volume after heating, unless the dimensions of the block parallel to the bedding-plane are sufficiently great to give a decrease in volume.

The foregoing results may be of considerable importance in connexion with different branches of scientific research on torbanite, as well as mechanical and industrial processes. An important application is to be found in the determination of the specific gravity of torbanite. In the usual method, the specimen is weighed in air, then boiled in water to remove air bubbles and finally weighed in water when cold. During this procedure the specimen is heated to 100°C., which means that a permanent volume change is almost certain to occur, resulting in an apparent value being obtained for the specific gravity. If an irregular piece of torbanite is used it is impossible to apply corrections, but this may be accomplished if a rectangular block cut at right angles to the bedding is employed, and the amounts of permanent contraction and expansion developed on heating to 100°C. are known. The correction would be as follows:

If  $S$  and  $S_a$  are the true and apparent specific gravities respectively,  $E$  and  $C$  the permanent expansion and contraction developed at 100°C. in inches per inch,  $a$  the dimension of the block normal to the bedding and  $b$  and  $c$  the dimensions parallel to the bedding-plane in inches, then:

$$S = S_a \times (1 + E.a.b.c. - 2 C.a.b.c.).$$

For example, a specific gravity determination was made on a specimen of torbanite from the Newnes deposit. The material developed a permanent expansion of 0.017 in.

per in. in a direction normal to the bedding and a permanent contraction of 0.004 in. per in. in a parallel direction, when heated to 100°C. The specific gravity was determined on a block which measured two inches at right angles to the bedding, and one inch in each direction parallel to the bedding. The result was a value of 1.230. The necessary correction factor for volume change due to boiling in water was calculated to be 1.018, giving a true specific gravity of 1.252. These results illustrate the possibility of an appreciable error occurring in specific gravity determinations where methods have been used involving the boiling of the specimen in water. This may be of important consequence in connexion with scientific research or the estimation of reserves in a torbanite deposit for industrial purposes.

In addition to the bearing which the study of expansion and contraction has on specific gravity determinations, there is evidence that certain relationships exist between these properties and the fundamental differences between various types of torbanite. It has also been noted that the powers of expansion of different specimens of torbanite from any one deposit are related to their contents of volatile hydrocarbons.

*Reference.*

DULHUNTY, J. A., 1938.—The Torbanites of New South Wales. Part i. The Essential Constituents and their Relations to Physical Properties. *J. Roy. Soc. N.S.W.*, lxxii, 179-198.

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*TRICHILOGASTER MAIDENI* (FROGGATT) (HYMENOPT., CHALCIDOIDEA),  
A WASP CAUSING GALLS ON *ACACIA IMPLEXA* BENTH., AND  
*A. MAIDENI* F.V.M.

WITH OBSERVATIONS ON AUSTRALIAN CHALCIDOID GALLS.

By N. S. NOBLE,\* D.Sc.Agr., M.Sc., D.I.C.

(Plate viii; five Text-figures.)

[Read 30th July, 1941.]

*Introduction.*

From 1935 to the close of 1938 the writer had under observation galls formed on the petioles and stems of Hickory (*Acacia implexa*)† growing in the Sydney district. These were mainly at the junction of the petiole of the phyllode, and incorporated some of the latter, and occasionally portion of the stem as well. The galls, which reached maturity in the late spring, were then rather irregular in shape, dark brown, rough-surfaced and woody (Pl. viii, C).

*A. implexa*, which suckers freely, grows very abundantly in the northern suburbs of Sydney, and the majority of the trees examined were galled. The height of the galled trees ranged from only eighteen inches up to ten feet. On the smaller trees the galls were scattered along the main stem, but in larger trees they were mainly on the laterals.

Emergence of wasps from these galls extended over a period of many months during the late spring, and then on through the summer and autumn, and even into the following winter. In the spring of 1936 just prior to the emergence of any adults, large numbers of galls were placed in containers, and the insects emerging were found to include twelve species of Hymenoptera, of which nine were Chalcidoids. These latter included *Trichilogaster maideni* (Froggatt), and when subsequently females of this species were enclosed with young new growth of *A. implexa* which was abundant on the trees at the time, they readily oviposited therein. The trees which were two years old were isolated, and growing at the home of the writer. In the following spring a limited number of the typical galls developed. All the other species of Chalcidoids were at various times enclosed with such young growth on *A. implexa*, but displayed no interest.

In the present paper the life-history of this species of gall-forming *Trichilogaster* is set out, together with notes on some of the other species of gall inhabitants. The writer (1940) discussed the life-history of *Trichilogaster acaciae-longifoliae* (Froggatt), a perilampid wasp causing galling of the flower buds of *Acacia* spp., in the Sydney district, and pointed out that there is difficulty in distinguishing, on a morphological basis, various described species in the genus *Trichilogaster*.

From 1935 to 1937 the writer also made observations on elongate fleshy galls on the stems of *Acacia Maideni* (Pl. viii, D). These were seen only on two trees, one at Roseville and the other at Artarmon, suburbs of Sydney, and were far less common than the galls on *A. implexa*. A species of *Trichilogaster* was bred from these galls, and

\* This is the last of a series of papers on Australian Chalcidoidea, submitted in August, 1937, to the University of Sydney, in fulfilment of the requirements for the degree of Doctor of Science in Agriculture. Some observations made after that date are also included.

† The writer wishes to acknowledge his indebtedness to Mr. R. H. Anderson, National Herbarium, Sydney, for his identifications of the various species of *Acacia* mentioned.

though slightly different in size and colour, was identical morphologically with *Trichilogaster maideni* bred from the galls on *A. implexa*. As will be pointed out later when discussing this species in relation to the galls on *A. Maideni*, there are a number of points in its biology and in its host associations in which it differs constantly from *Trichilogaster maideni* on *A. implexa*. While no attempt will be made to designate subspecific or varietal names for the two forms under discussion, the ways in which they differ from one another and also from Froggatt's specimens of *Trichilogaster maideni*, will be set out, and it is felt that when more detailed taxonomic studies of the genus as a whole are undertaken, it will be desirable to give subspecific or varietal names to the various forms at present considered as *Trichilogaster maideni*.

In their morphology and biology the forms of *Trichilogaster maideni* causing galls on *A. implexa* and on *A. Maideni*, resemble very closely *Trichilogaster acaciae-longifoliae* (Froggatt) (see Noble, 1940).

#### TRICHILOGASTER MAIDENI CAUSING GALLS ON ACACIA IMPLEXA.

##### MORPHOLOGY.

##### *The Adult.*

Froggatt (1892) described this species as *Cynips maideni*, stating that the specimens were bred from thick fleshy galls on the twigs of *Acacia longifolia* at Elizabeth Bay and Rose Bay, Sydney. Referring to Froggatt's description, Girault (1916) stated: "Froggatt does not describe the species *maideni*. This is such a case of carelessness as to cause astonishment. His pseudo-description represents nothing like the actual specimens." Mayr (1905) established the genus *Trichilogaster* and redescribed *Trichilogaster (Cynips) maideni*, this being the type species of the genus. The writer examined specimens of *T. maideni* bred by Froggatt from one of the type localities, and apart from some colour variation, these differed little from specimens bred by the writer from *A. implexa*.

The female of *Trichilogaster maideni* (Fig. 1) from *Acacia implexa* averages 2.95 mm. in length, and has the head, thorax and abdomen mainly black, apart from

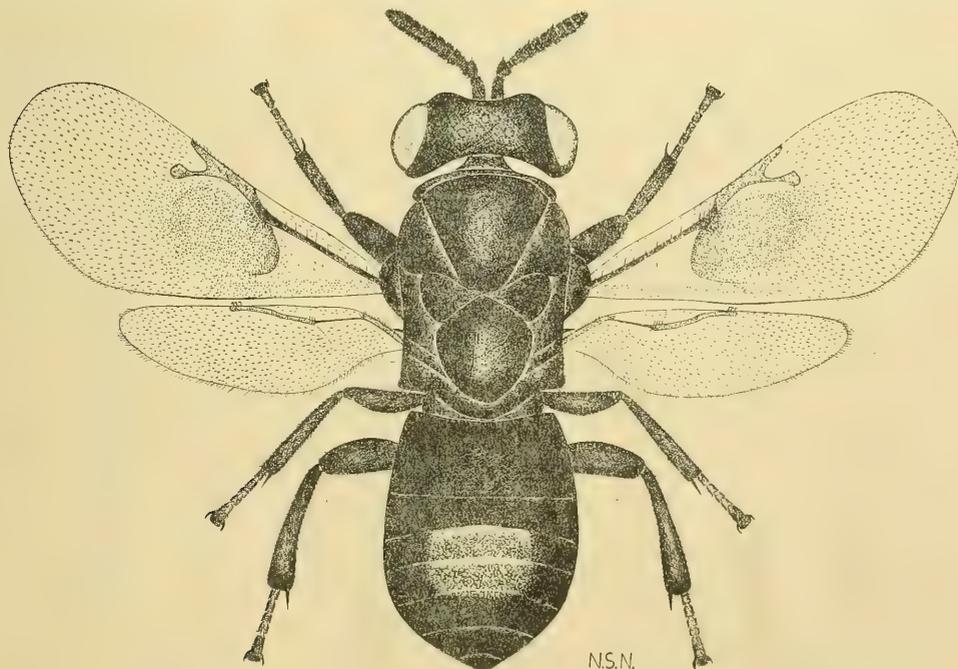


Fig. 1.—*Trichilogaster maideni* (Froggatt). Adult female from galls on *Acacia implexa* ( $\times 22$ ).

a variable ochreous patch on the dorsal surface of the third and fourth abdominal segments. This light patch stands out quite clearly in specimens preserved in alcohol, but in dry mounts the abdomen contracts and this light patch is mainly hidden, the abdomen then appearing entirely black. The eyes are red, the antennae are brown to dark brown; the venation is brown, the submarginal vein being a darker shade than the remainder. The coxae, trochanters and all but the distal portions of the femora are dark brown to black. The remainder of the legs are brown to ochreous, there being some variation in different individuals. The surface of the thorax is shining and rugose, the corrugations running in wavy transverse lines. There is a fuscous patch on each forewing, a notable feature being the scant development of the setae on the wings. The setae are particularly short and are sparsely scattered, and are wanting from their upper margins.

In different individuals there is some variation in the depth of pigmentation of the various parts. In some the dorsal surface of the first and second abdominal segments is only dark brown, and in others there is a narrow ochreous patch on the front margin of the fifth abdominal segment, while in others the third segment is dark brown and only very little lighter than either the first or second. In general appearance the female is rather robust, being broad in proportion to its width, and the abdomen is slightly depressed.

The antenna (Fig. 2E), the mandible (Fig. 2F), the stigmal knob (Fig. 2G), the tip of the stylet (Fig. 2H) and the tip of the sheath of the ovipositor (Fig. 2I) are illustrated. It will be seen that neither the stylet nor the sheath is barbed, but the stylet is particularly sharp and curved.

Specimens of females of *Trichilogaster maideni* collected by Froggatt are much the same size as those bred by the writer from *A. implexa*. However, in Froggatt's mounted specimens examined by the writer the entire dorsal surface, except the first two segments and the tip, is ochreous. Moreover, there is an ochreous patch between the eyes and the lateral ocelli on the vertex and extending a variable distance down the face. The pronotum is ochreous, as also are the lateral margins of the scutum.

#### The Egg.

As with other primary gall wasps studied, the newly emerged female has the abdomen filled with fully developed eggs. Newly deposited eggs for study were obtained by placing females in tubes with uninfested Hickory twigs, the eggs being dissected out from the latter soon after deposition.

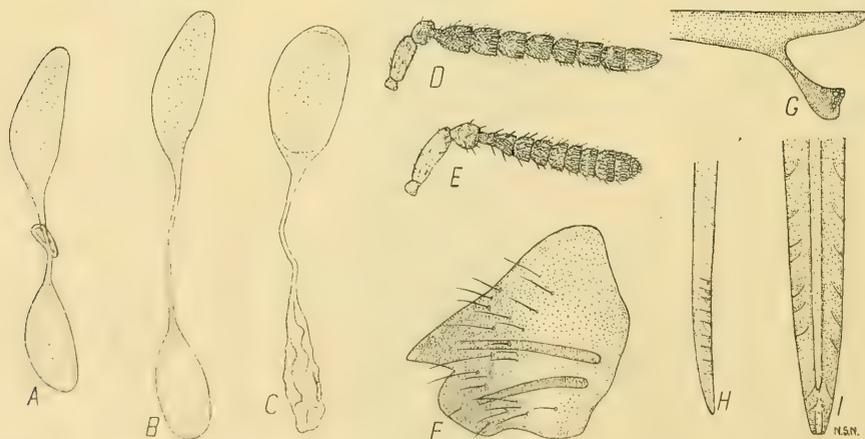


Fig. 2.—*Trichilogaster maideni*. A, B, Ovarian eggs ( $\times 115$ ); C, Egg twenty-four hours after deposition ( $\times 115$ ); D, Antenna of male ( $\times 40$ ); E, Antenna of female ( $\times 40$ ); F, Mandible of female ( $\times 115$ ); G, Stigmal knob of female ( $\times 61$ ); H, Lateral view of tip of ovipositor stylet ( $\times 200$ ); I, Ventral view of tip of ovipositor sheath ( $\times 200$ ).

The eggs are white, and in the ovary, consist of two large bodies joined by a narrow connecting tube which is at first folded (Fig. 2A), but just prior to deposition becomes extended (Fig. 2B) and after deposition all the protoplasm passes into one end of the egg, producing one white oval body, with a long twisted and flaccid pedicel (Fig. 2C). The dimensions of the egg are set out in Table 1. It will be seen that there is considerable variation in the dimensions of its two bodies, as well as in the total lengths of ovarian eggs with the connecting tubes extended. The average dimensions of the egg are remarkably similar to those of *Tepperella trilineata* (Noble, 1938b).

TABLE 1.  
*Dimensions of Egg of Trichilogaster maideni (in Millimetres).*

	Mature eggs dissected from ovaries.							Eggs immediately after deposition.	
	Length with connecting tube folded.	Length with connecting tube extended.	Larger body.		Smaller body.		Width of connecting tube.	Body length.	Body width.
			Length.	Width.	Length.	Width.			
Average ..	0.396	0.497	0.183	0.062	0.129	0.058	0.004	0.172	0.083
Maximum ..	0.409	0.538	0.198	0.066	0.139	0.069	0.005	—	—
Minimum ..	0.373	0.436	0.172	0.056	0.119	0.053	0.003	—	—

#### *The Larva.*

Based on the distribution and size of the integumentary setae, the shape and size of the mandibles, and the number and size of the spiracles, five larval stages can be recognized. The various larval stages of *T. maideni* in general appearance, in the distribution of setae and sensillae, and in the development of the respiratory system, are similar to the various larval stages of *T. a.-longifoliae*, details of which have already been published by the writer (Noble, 1940).

*Stage I.*—The mandible of the first stage larva (Fig. 3C) is very pale amber, and measures 0.007 mm. in length. The average width between the two anterior tentorial rami is 0.043 mm. The first stage larva is only just visible to the unaided eye, and the smallest larva measured was 0.18 mm. in length and 0.082 mm. in width.

*Stage II.*—The smallest second stage larva measured was 0.24 mm. in length and 0.16 mm. in width. The mandible which is amber, averages 0.015 mm. in length. The width between the two anterior tentorial rami is 0.096 mm., which is more than twice as wide as in the first stage.

*Stage III.*—The mandible of the third stage (Fig. 3D) is amber and averages 0.025 mm. in length. The smallest third stage larva measured was 0.46 mm. in length and 0.28 mm. in width.

*Stage IV.*—The fourth stage larva (Fig. 3A) resembles the fifth in many respects. The smallest larva measured was 0.74 mm. in length and 0.35 mm. in width. The mandible (Fig. 3E), which is light brown, is more heavily chitinized than in the preceding stages, but is still unevenly bidentate with one rather long curved tooth. It averages 0.036 mm. in length and is more or less triangular in outline. Occasionally, there is evidence of a division of the minute second tooth.

The larva, which is cylindrical and arched and tapering to both ends, consists of a head and thirteen segments, and is greenish-white. The distribution of setae and sensillae on the head is similar to that of the fifth stage. On the underside of the head, and dorsally and laterally on the first segment, and in very limited numbers on the dorsal surface of the second and third segment, are minute papillae, visible only at high magnifications. The abdominal segments carry setae of variable length and number, in different individuals. These are quite prominent on the first segment and form a complete median circlet. The length of these setae on the first segment varies on the same larva, the average length of the largest on a number of larvae measured,

being 0.023 mm. On the second segment, the setae are much smaller, more limited in number and confined to the dorsal and lateral surface. On the succeeding segments, the distribution of these setae is variable. There is at least a pair of lateral setae on each segment and in some of the posterior segments the number varies from two to four. On the median segments these setae are only just visible at very high magnifications, but are slightly larger on the posterior segments.

The respiratory system is very well developed, there being nine pairs of spiracles, one pair on each segment from the second to the tenth inclusive. The first pair of spiracles is much the largest, and the third pair much the smallest. Internally, profusely branching tracheae pass to the various organs.

*Stage V.*—The fifth or last stage larva (Fig. 3B) which is white, is cylindrical and arched, and tapers conspicuously to both ends. It consists of a head and thirteen segments, segmentation being very distinct. The average length at maturity is 3.59 mm., the maximum being 3.75 mm. and the minimum 3.23 mm. The average width at the widest point is 1.23 mm., the maximum being 1.41 mm. and the minimum 0.83 mm. The mandible (Fig. 3F) is brown and bidentate, there being one large curved and sharp tooth, so that the general triangular outline is still maintained; its length averages 0.066 mm.

All over the first and second segments, and dorsally and laterally on succeeding segments, there are numbers of short pointed papillae, which become less numerous, smaller in size, and more confined to the dorsal surface on the posterior segments. In some larvae a very limited number of minute papillae are present on the ventral surface of the head. To the sides and also just above the mandibles, there is a pair of setae, and immediately beneath the mandibles there are two minute setae, three sensillae, and outside these two truncate cone-shaped structures of unknown function, and outside these and slightly below, there is a further pair of large setae.

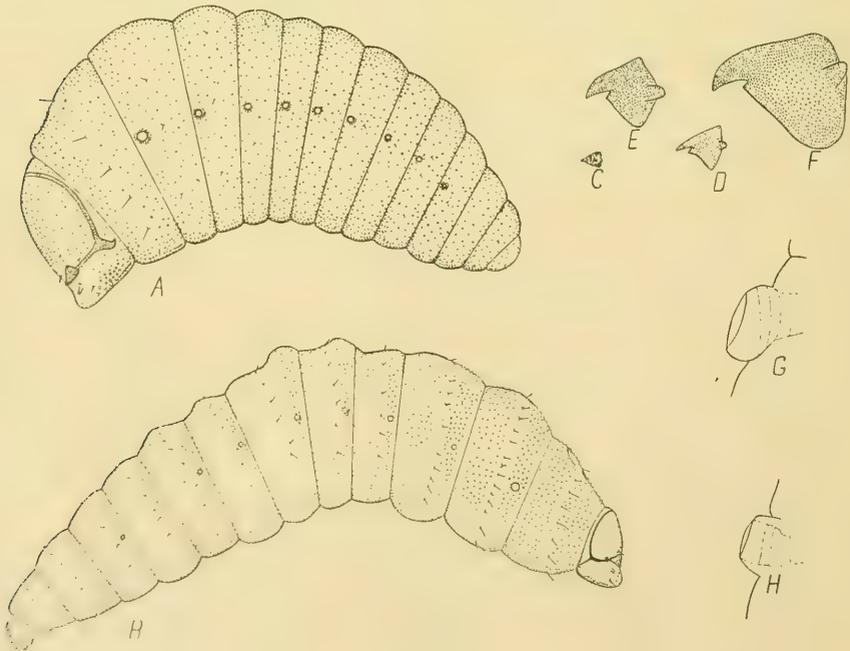


Fig. 3.—*Trichilogaster maideni*. A, Lateral view of fourth stage larva ( $\times 78$ ); B, Lateral view of mature larva ( $\times 23$ ); C, Mandible of first stage larva ( $\times 256$ ); D, Mandible of third stage larva ( $\times 256$ ); E, Mandible of fourth stage larva ( $\times 256$ ); F, Mandible of fifth stage larva ( $\times 256$ ); G, Lateral view of spiracle from second segment of mature larva ( $\times 256$ ); H, Lateral view of spiracle from third segment of mature larva ( $\times 256$ ).

Every segment of the body carries a large number of amber setae, which are quite long and stand out conspicuously. These setae vary greatly in size, even on the same segment, and in different larvae, some setae on the first segment being over three times the length of the smallest seta on the same segment. On all but the last segment these setae are in a fairly regular median circlet, and they completely surround the first three segments, being dorsal and lateral in all but the last segment, where prominent setae of variable size are scattered over the whole surface.

The respiratory system is very much the same as that of the preceding stage, nine pairs of open spiracles being present, and these project slightly from the general surface of the integument (Figs. 3G, H). The first pair of spiracles are the largest, and the third pair are slightly smaller than the remainder.

#### BIOLOGY.

##### *The Adult.*

As only limited numbers of adults of *T. maideni* emerged even though many hundreds of galls were collected, detailed longevity tests were not carried out. When kept in tubes with green twigs taken from Hickory trees and fed on honey and water, females lived only a few days.

Females are rather sluggish and can be handled with ease in the laboratory, and seldom take to flight. In the field on bright sunny days, however, they have been observed in flight, and they fly readily from tree to tree, but sustained flight was never observed.

##### *Oviposition.*

Just prior to the emergence of adults in the late spring, the host trees produce considerable quantities of new and delicate spring growth, there being on the ends of each branch, numbers of minute developing stems and miniature phyllodes.

Wasps are ready to lay immediately after emerging from the galls. A female, when about to oviposit, alights on a twig, and then crawls quickly up towards its tip until it encounters the new growth, and utilizing the tips of the antennae it finally selects a suitable oviposition site, which is usually at the point of union of the young phyllode and the stem. Occasionally, the egg is deposited within the base of the phyllode and less commonly directly in the stem, usually somewhere near its junction with the phyllode. In the process of oviposition, there is nothing unusual. The ovipositor is brought down independently, so that its tip rests on the plant surface, and it is then slowly worked down into the tissues. After depositing an egg, the ovipositor is withdrawn, the female moves slightly forward, and repeats the process a number of times in the vicinity of each phyllode.

##### *Total Eggs Within Females.*

In 1936 ten newly emerged females were found to contain the following eggs: 269, 369, 288, 346, 334, 343, 310, 388, 174 and 305, the average being 312.6. In October, 1937, the eggs in each of ten newly emerged females were found to range from 246 to 496, the average being 347.1, a figure which is somewhat higher than that obtained in the preceding spring.

##### *Larval Development.*

Five larval stages occur and have been described.

In 1936 adults of *T. maideni* were observed to emerge from 3rd November to 28th November, and as they oviposit immediately on emerging and the length of adult life is short, the greatest oviposition that year occurred during November.

In Table 2 are set out the results of the dissection of galls from 14th January to 20th September, 1937, the date on which the first adults were cut from the galls. In the spring of 1937, adults commenced emerging on 5th October, almost a month earlier than in the preceding year. It is evident that there is considerable variation in the time spent in the various larval stages, and that as early as 26th January, 1937, all larval stages were present, though it was not until 6th May, 1937, that fifth stage larvae were again dissected. It will be seen that the larval stage extended over a period of at least nine

months, being far the longest period of the life-cycle, and that pupation occurred mainly in the early spring in September and October, there being some variation from year to year.

TABLE 2.  
*Results of Dissection of Galls on Acacia implexa showing Stages of Trichilogaster maideni Present.*

Date of dissection.	No. of Cells examined.	Larvae.					Pupae.	Adults.
		Stage I.	Stage II.	Stage III.	Stage IV.	Stage V.		
14.i.1937	2	—	—	1	1	—	—	—
26.i.1937	8	1	1	2	3	1	—	—
20.ii.1937	4	3	1	—	—	—	—	—
12.iii.1937	6	1	5	—	—	—	—	—
22.iv.1937	19	—	13	5	1	—	—	—
6.v.1937	10	—	—	—	8	2	—	—
25.vi.1937	32	—	—	1	9	22	—	—
22.vii.1937	24	—	—	—	—	24	—	—
12.viii.1937	33	—	—	—	2	31	—	—
31.viii.1937	24	—	—	—	—	24	—	—
20.ix.1937	59	—	—	—	—	8	50	1

First adult of *T. maideni* emerged 5.x.1937.

Last " " " " " " 4.xi.1937.

#### *The Pupa.*

The pupa is at first white, but changes within a few days to dark brown to shining black. The average length of the female pupa is 2.67 mm., the maximum being 3.07 mm. and the minimum 2.19 mm. Odd pupae were cut from the galls during the latter half of September, 1936, and larvae were pupating freely during October.

#### *Emergence of Adults.*

In 1936, pupae of *T. maideni* were cut from galls and placed in petri dishes in the laboratory, and the first adult emerged on 21st October, thirteen days before the first adult ate its way out of the galls. Adults were found in the galls for the first time on 24th October, ten days before any emerged naturally. Emergence commenced on 3rd November, and continued until 28th November, 1936, a period of 26 days. In the spring of 1937, a much larger series of galls was collected from various localities in the northern suburbs of Sydney, and from these 343 adults of *T. maideni* emerged, the first emergence occurring on 5th October, and the last on 4th November. The emergence period varies somewhat from year to year, but emergence of adults takes place in the spring in October or November.

#### *Time Spent in the Various Stages of the Life-Cycle.*

The life-cycle is annual. Oviposition occurs mainly during October or November, and dissections early in January, 1937, showed that in all the cells examined larvae were present. As the pupal period is at most six weeks, it is evident that, as with the other gall species studied, the larval period is very extensive and occupies from nine to ten months.

#### OBSERVATIONS ON THE DEVELOPMENT OF THE GALLS.

The eggs are deposited at the junction of young phyllodes and stems, and oviposition occurs mainly during November.

Examination of the trees on 5th January, 1937, failed to reveal any unevenness in the petioles or stems, and first stage larvae were present at that time.

On 14th January, examination revealed very slight unevenness and swelling at the bases of some phyllodes, and on cutting these open both first and second stage larvae of *T. maideni* were found. It is therefore evident that as with other gall species, there is no external evidence of gall formation until some time after the larvae have hatched.

By 22nd January, 1937, minute but very definite swellings were visible. Some of these were entirely on the petioles of the phyllodes, others appeared to have formed partly on the young stem and partly on the phyllode, so that if the phyllode were torn

off the fracture occurred through the middle of the gall. Less commonly the galls were to be seen developing in the stems themselves, between adjoining phyllodes.

A further examination on 18th February showed that the more advanced galls were now well developed, and up to a quarter of an inch in diameter, but on the petioles of many phyllodes swellings were only just commencing. These galls were almost all bright green both internally and externally.

Frequent observations were then made on subsequent gall development until the emergence of the adult wasps.

By the end of May, 1937, the galls (Pl. viii, A) were about half grown, and while all the galls were still quite easy to cut, and contained masses of cells containing a high percentage of fluid, the outer surface of many galls was cracked and rough, this imparting a dark grey colour to the galls. Other galls were still bright green and smooth-surfaced.

There was a steady increase in the size of the galls during July and August, and some appeared to have reached their full size at the close of the latter month, and the remainder of the galls reached their full size during September, when the gall-forming larvae within them had also reached maturity.

As the galls increase in size more and more of the green coloration is lost, and the gall surfaces become roughened, cracked and irregular with a layer of scaly bark through which a little green sometimes shows, though many galls still present an entirely brown appearance (Pl. viii, C).

The phyllode above the gall may persist at the time the galls mature, but as early as 21st July, 1937, a number of the phyllodes had died and dropped, leaving only the gall attached to the stem, while in other cases the phyllode, though dead, still persisted.

Throughout larval development the galls can be cut readily with a razor, and internally consist of green cells of high fluid content. With the continued growth of the galls and their contained larvae there is a steady decrease in the amount of moisture present. By the time the galls mature in September, though still cutting readily, they are very much drier and harder internally, and are becoming woody. At the time the adults are commencing to emerge, the galls are rough and irregular in shape, the surface being covered with dark brown to black scaly bark, and they are so hard and woody that they can only with difficulty be cut. On some of the smoother galls a reddish or maroon coloration is visible.

During the early larval stages, the plant tissues are in contact with the larvae, there being a well developed and extensive nutritive layer. Gradually the latter is consumed by the larvae and the galls become more and more woody; a considerable space develops round the larvae, and by the time they reach maturity the larvae are to be found in a cell which is many times their own volume. Compared with many other galls on acacias, these galls are comparatively small considering the number of occupants. The number in each of 127 galls ranged from 1 to 16, the average being 3.99 cells per gall, and galls containing ten or more cells were quite common. The partitions of plant tissue separating the larvae become smaller and smaller as the larvae feed, and at maturity they are only separated from one another by very narrow partitions.

Where there is no crowding the individual cells are oval or spherical, but where oviposition has been heavy, they may assume a great variety of shapes. Unilocular galls, which are not common, are at maturity more or less spherical, fairly smooth, and tinted with red or maroon on one side.

While in some areas the individual galls remain more or less distinct, in others, due to heavy oviposition in stems as well as petioles, rather long irregular galls develop, which incorporate a number of adjoining petioles and the intervening stem.

Though at maturity, the phyllodes above many galls have died and fallen, sometimes they may still be present and alive at the time the galls mature. Heavily galled lateral twigs frequently die soon after the adults have emerged, but less heavily infested twigs are less affected and have been seen carrying numbers of vacated galls, and apparently functioning normally, at least two years after the occupants have left. In other instances, the remains of vacated galls, many years old, have been seen scattered along limbs which are now quite large, alive and apparently normal.

INSECTS ASSOCIATED WITH *T. MAIDENI* IN GALLS ON *ACACIA IMPLEXA*.

Two species of Lepidoptera, one species of Coleoptera and twelve species of Hymenoptera were bred from the galls, but many of these occurred in limited numbers only.

It was found that a high percentage of the galls was mined by two species of moth larvae, and in many instances only the outer gall-covering remained. These larvae in mining thus destroyed the normal hymenopterous occupants of the galls, it being quite common to find in such mined galls, dead and mouldy larvae and pupae of *T. maideni* and other species. In galls collected and held in jars in the laboratory in the spring, the larvae on maturing left the galls and spun cocoons and pupated at the sides of the containers and between adjacent galls. Large numbers of adult moths emerged in October and November, 1936, and again in 1937.

A number of adults of the dried apple beetle, *Doticus pestilens*, emerged from the galls in November, 1936. The larvae of this Anthribid are known to develop in apples which have dried up on the trees, and it has been bred from woody excrescences on *Acacia decurrens* (Allen *et al.*, 1898).

The Hymenoptera included two species of Ichneumonid, one Braconid and nine Chalcidoids. One species of Ichneumonid belonged to the genus *Mesostenoides*, while the other, which was more abundant, was *Poecilocryptus nigromaculatus* Cameron. This species has frequently been bred from galls in New South Wales. Pupae were found in the galleries mined by the lepidopterous larvae, this Ichneumon apparently being a parasite of these gall-miners. Adults of *P. nigromaculatus* emerged from 22nd October to 12th November, 1936.

The Chalcidoids bred included the primary gall former, *T. maideni*, *Coelocyba nigrocincta* Ash., three species of *Eurytoma*, including *Eurytoma gahani* Noble, *Eurytoma* sp. B., and two species of *Megastigmus* including *Epimegastigmus* (*Megastigmus*) *trisulcus*.

*Epimegastigmus* (*Megastigmus*) *trisulcus*.

This species has already been discussed by the writer (Noble, 1938a), having been bred from citrus stem galls, where it was found in cells together with the remains of the larvae of the primary gall former *Eurytoma fellis*.

Adults of this species emerged both before, during and after all of the adults of *T. maideni* had emerged from the galls on *Acacia implexa*. Moreover, adults of *E. trisulcus* continued to emerge periodically until 31st August, 1937, from galls which were mature, and were collected and placed in jars in October, 1936, and which during all this time (approximately ten months) were hard, dry and woody.

On 5th October, 1938, when examining some mature galls caused by *T. maideni* on *Acacia implexa*, an adult of *E. trisulcus*, which has a relatively long ovipositor, was observed with this organ completely embedded in the hard gall. A few minutes later this female removed the ovipositor, and after moving further along the surface of the gall and after playing the tips of the antennae over its surface, again oviposited. The gall was then removed and cut open, and in two cells within the gall, newly deposited eggs of *E. trisulcus* were found. In the first gall cell examined, the egg was adhering to a fourth stage larva of *Eurytoma* sp., the only living occupant of the gall cell, the host larva (*T. maideni*) on reaching the last larval stage having been killed. In the second cell the egg of *E. trisulcus* was adhering to the body of a mature larva of *Eurytoma* sp. which had completely devoured the host.

The newly laid egg of *E. trisulcus* is comparatively large (Fig. 4D) and is visible to the unaided eye as a white, glistening, smooth, oval body. Under the microscope it is seen to consist, in addition to the main body, of an anterior short pointed pedicel and a long posterior pedicel. The latter was twisted and flaccid, but measured approximately one and a half times the length of the body of the egg. The body of the egg was 0.416 mm. in length and 0.136 mm. in width. As these eggs were laid in mature galls, which would shortly be hard and dry, it would appear that the main source of food of the larva of *E. trisulcus* must be the other insect occupant of the gall. *E. trisulcus* occurring in galls on citrus, has been found in cells with only the remains of the host larva, and it is not

known whether in the ovipositions observed, the larva of *Eurytoma* sp. eventually would have destroyed the larva of *E. trisulcus* or *vice versa*.

Though the detailed life-history of *E. trisulcus* has not been studied, the presence of a long ovipositor on this and closely allied species found in galls, indicates that oviposition frequently takes place in galls in which the occupants of the cells are well protected beneath a deep layer of plant tissue. Moreover, the protracted and irregular emergence of the adults of *E. trisulcus* indicates an absence of any close correlation with the primary gall formers in the various instances, such as the writer has shown to exist in *Epimegastigmus brevivalvus* and *Megastigmus acaciae* (Noble, 1938a, 1939b). *E. trisulcus* does, however, destroy the larvae of the primary gall-forming species, and when laying in mature galls it is very doubtful if its larva feeds at all phytophagically.

#### *Eurytoma* spp.

As was found to be the case in flower bud galls on various species of *Acacia* caused by *T. acaciae-longifoliae*, three species of *Eurytoma* were present in the galls on *Acacia implexa* and all resulted in the destruction of the primary gall former. There was considerable competition amongst the various species and also amongst individuals of the same species of *Eurytoma*. This is indicated in Table 3, where, although only one individual could survive, up to nine eggs of various species might be laid in a single gall cell. Of the three species of *Eurytoma* present, *E. gahani* Noble and *Eurytoma* sp. B. occurred most commonly, emerging from the galls in much larger numbers than did the primary gall former *T. maideni*. The egg of a third species of *Eurytoma* was also occasionally observed in the gall cells. This egg, which was dark brown, consisted of an oval body and a short and a long pedicel (Fig. 4E) and had the surface of the body covered with short, sharp-pointed black spines, and was similar to one described by the writer (Noble, 1940) found occasionally in galls on acacias caused by *T. acaciae-longifoliae*.

TABLE 3.

Results of Examinations of Single Cells from Galls on *Acacia implexa* caused by *Trichilogaster maideni*.

Date of dissection.	Stages and condition of <i>T. maideni</i> larvae present.	<i>Eurytoma</i> sp. B.		<i>Eurytoma</i> sp. eggs.	Total eggs and larvae present in cell.
		Eggs.	Larvae.		
14.i.1937	.. Third stage—alive .. ..	2	—	1	6*
23.i.1937	.. Third stage—dead .. ..	—	1 first.	1	3
	.. Third stage—dead .. ..	—	1 first.	5	7
	.. Fourth stage—dead .. ..	1	1 third.	—	3
	.. Fifth stage—dead .. ..	5	1 second.	—	7
25.i.1937	.. Third stage—dead .. ..	5	1 first.	—	7
	.. Second stage—dead .. ..	7	1 first.	—	9
26.i.1937	.. Fourth stage—dead .. ..	4	2 first (dead).	—	8
	.. ..	—	1 third (alive).	—	—
	.. Third stage—dead .. ..	4	1 first.	—	6
6.v.1937	.. Fourth stage—dead .. ..	4	1 first.	—	6
	.. Fifth stage—alive .. ..	—	1 first.	—	2

\* Two unidentified larvae.

#### *Eurytoma gahani* Noble.

This species was also found by the writer in association with *Tepperella trilineata* Cameron (see Noble, 1938b), and with *Trichilogaster a-longifoliae* (see Noble, 1940), and the detailed life-history in association with *Tepperella trilineata* has already been published by the writer (see Noble, 1939a). Its life-cycle is annual. Its egg is laid alongside the egg or larva of *T. maideni*, the two species of larva living phytophagically in a normal association for many months until the larva of *T. maideni* reaches the last stage and is maturing. The larva of *E. gahani* on reaching the fifth stage devours the larva of *T. maideni*, pupates in the gall cell, and eventually emerges as an adult from the gall.

Of 507 gall cells examined in October, 1936, 165 contained normal larvae of both species, while in a further 231 cells the larvae of *T. maideni* had already been devoured; *T. maideni* was present alone in only 94 cells, figures which indicate the dominance of *E. gahani*. The great majority of the larvae of *T. maideni* are devoured during October, though a few are devoured some time before this, and a period of many months may then elapse before *E. gahani* eventually emerges as an adult, and most of this time is spent in the mature larval stage.

Emergence of adults of *E. gahani* commenced on 3rd November, 1936, the same day as the first adult of *T. maideni* emerged, but emergence continued until 6th April, 1937, an emergence period of over five months. By far the greatest numbers emerged during the month of January, and at this time on sunny days large numbers were to be seen either on the wing or ovipositing within the minute new season galls. Adults of *E. gahani* which emerged as late as April, 1937, were quite normal, but in most instances would have to deposit their eggs alongside larvae of *T. maideni* which had reached the third or fourth stage.

#### *Eurytoma* sp. B.

This species occurred very abundantly in the galls on *Acacia implexa* and has already been mentioned by the writer, it having been observed in association with *T. a-longifoliae* (Noble, 1940, p. 33). Specimens were forwarded to the late Mr. A. A. Girault, who informed the writer that he was describing the species as new, but a description has not yet been seen.

*The Adult.*—The adult female is a typical member of the genus *Eurytoma*, being dominantly black, with the abdomen laterally compressed and varying from reddish-brown to black. The abdomen is strongly curved and keeled, being drawn out to a fine, slightly upturned tip. Its length averages 3.33 mm., the maximum being 3.54 mm. and the minimum 3.07 mm.

*The Egg.*—The ovarian egg (Fig. 4B) consists of a white oval body, a short pointed anterior pedicel and a long posterior pedicel. After deposition (Fig. 4C) the egg becomes dark brown and the shell can be found in the gall cell months after the larva has hatched. The total length of the egg averages 0.998 mm., the anterior pedicel being 0.082 mm. and the posterior pedicel 0.523 mm.; the body of the egg averages 0.394 mm. in length and 0.140 mm. in width. Sometimes the long pedicel becomes somewhat twisted after deposition, but it may more or less retain its original shape, and the size of the body of the newly deposited egg is much the same as that of the egg just prior to deposition.

*First Stage Larva.*—The first stage larva (Fig. 4A) is more or less translucent and consists of a head and thirteen clearly defined segments. It is more or less straight in outline, and is somewhat dorso-ventrally flattened. The third, fourth and fifth segments are widest, the larva tapering conspicuously to both ends. The head and the first abdominal segment are much more heavily chitinized than the remainder of the larva and are amber. The smallest larva measured was 0.512 mm. in length and 0.17 mm. in width, the width of the head being 0.12 mm.

The head is somewhat triangular in outline, the mouth being situated on a downwardly directed prominence. Dorsally, the head carries a pair of cylindrical short antennae and on the dorsal surface of the head there is one pair of long setae and behind these a shorter pair. On the ventral surface of the head there is also a pair of long setae, and there are two lateral and shorter pairs with a minute pair above the mandibles, making a total of six pairs of setae on the head. The mandibles are amber, sharp pointed, curved and unidentate, the tips overlapping, their length averaging 0.016 mm.

All the body segments bear large numbers of minute short pointed spines. On each segment there is a dorsal pair of long setae. On the first three segments there are two ventral pairs of long setae, and on each of the succeeding segments there is a pair of ventral setae which becomes shorter on the posterior segments. On the first abdominal segment there are two minute semi-circular chitinized structures of unknown function. In newly hatched larvae no tracheal system could be distinguished, but during the first larval stage an open respiratory system develops. Four pairs of spiracles are present,

one pair on segments 2, 4, 5 and 6. There are two delicate longitudinal tracheal trunks and a limited number of fine branches.

In general structure, shape and setae distribution, the first stage larva of *Eurytoma* sp. B. is remarkably similar to that of *Eurytoma rosae*, a parasite of *Cynips coraria* (see Parker, 1924).

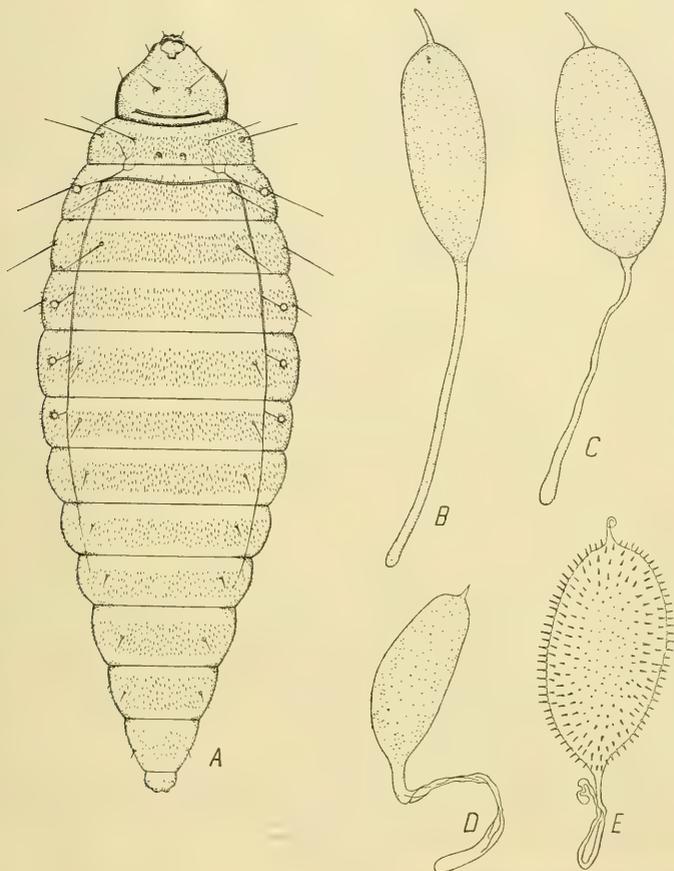


Fig. 4A.—*Eurytoma* sp. B. Ventral view of first stage larva from gall cell on *Acacia implexa* ( $\times 130$ ); Fig. 4B.—*Eurytoma* sp. B. Ovarian egg ( $\times 70$ ); Fig. 4C.—*Eurytoma* sp. B. Egg shortly after deposition ( $\times 70$ ); Fig. 4D.—*Epimegastigmus* (*Megastigmus*) *trisulcus*. Egg dissected from gall cell on *A. implexa* a few hours after deposition ( $\times 70$ ); Fig. 4E.—*Eurytoma* sp. Egg found in cell of gall on *A. implexa* caused by *Trichilogaster maideni* ( $\times 70$ ).

**Oviposition.**—*Eurytoma* sp. B. mated readily under laboratory conditions and was observed on a number of occasions ovipositing in the field. The female of *Eurytoma* sp. B. is apparently able to detect the presence of *T. maideni*, and with the ovipositor, penetrates the plant tissues and deposits an egg alongside whatever stage of *T. maideni* happens to be present. In 1936, the first adult of *Eurytoma* sp. B. emerged on 7th November, only four days after the first adult of *T. maideni* emerged, so that at this time the egg of *Eurytoma* sp. B. is deposited alongside the egg of *T. maideni*. Emergence continued until August, 1937, a period of almost ten months, and by the time the last adults emerged *T. maideni* had reached the last larval stage in the new season galls, and the eggs of *Eurytoma* sp. B. are then laid alongside these larvae. The eggs, being dark, stand out conspicuously and often adhere to the integument of the larvae of *T. maideni* when the latter are removed from the galls.

During late 1936, and early 1937, the eggs of *Eurytoma* sp. B. were found in cells with first, second, third and fifth stage larvae of *T. maideni*; the exact stage of development of the host at the time *Eurytoma* sp. B. oviposits appears to be of little significance.

*Larval Development.*—It is evident that *Eurytoma* sp. B. is a parasitic species, and soon after its characteristic larva hatches it attacks and destroys any other eggs or larvae which are in the cell, including those of the same species, in cases of super-parasitism.

These active first stage larvae have frequently been found in cells with the dead remains of host larvae of various stages, and the crushed eggs and first stage larvae of its own species and the eggs of *Eurytoma gahani*. In Table 3 are set out the results of the examination of a number of cells in galls on *Acacia implexa*. It will be seen that the number of original occupants, including eggs and larvae, ranged from two to nine in single cells, six and seven being quite common. It is evident that there is a considerable struggle for existence, as only one occupant of each cell can hope to reach the adult stage.

In dissections in March, 1937, it was not uncommon to find no living occupant in the gall cells, but masses of debris which, examined microscopically, proved to be egg shells and dead larval remains of various species of wasps, the intensity of the competition having resulted in the death of all the occupants. In this struggle, the larvae of *T. maideni* suffer severely, and the great majority which hatch are destroyed by the various species of *Eurytoma* before they mature. This accounts for the very limited emergence of *T. maideni* adults as compared with those of other species, its survival, no doubt, being assisted by its ability to lay eggs in such large numbers.

As the life-cycle is annual and the larva of *Eurytoma* sp. B. is only quite small when its host has been destroyed, the remainder of its larval life must be spent phytophagically. (For an account of somewhat similar behaviour in *Eurytoma studiosa* and *E. auriceps* see Triggerson, 1914.)

*Emergence of Adults.*—Adults commenced to emerge on 7th November, 1936, and emergence continued until August, 1937, a period of almost nine months after the last adult of *T. maideni* emerged. Galls from which these adults emerged were picked from the trees on 30th October, 1936, and for many months were hard and dry, and could have supplied no food to the insects. Dissections in the intervening period always showed some mature larvae lying in hard dry cells, so it is evident that this species, like *Eurytoma gahani*, can spend very long periods in the mature larval stage in hard dry galls and yet emerge normally.

Females of *Eurytoma* sp. B. in the laboratory, lived longer than any of the other gall-infesting species studied, many being alive and active a month after emergence.

#### TRICHILOGASTER MAIDENI CAUSING GALLING OF THE STEMS OF ACACIA MAIDENI.

##### *Introduction.*

*T. maideni* has been found by the writer to cause fleshy elongate, irregular stem galls on *Acacia Maidenii* (Pl. viii, D). Two infested trees, only, have been observed by the writer in the Sydney district, but on both trees there were few stems which were ungalled, the entire trees presenting a gnarled and unhealthy appearance. Observations on the development of these galls were made over a period of two years, commencing in 1936.

The morphology of the egg and larval stages was indistinguishable from similar stages of *T. maideni*, causing galls on *Acacia implexa*, but there were minor differences in the adults, and distinct differences in biological behaviour. At various times adults of *T. maideni* bred from galls on *Acacia Maidenii* were enclosed with young twigs from *Acacia implexa*. They displayed no interest, though *T. maideni* bred from galls on *A. implexa*, readily oviposited under similar conditions. As suggested earlier, there are apparently two subspecies or varieties of *Trichilogaster maidenii* involved.

The emergence period of adults of the two forms is more than a month apart; different hosts are selected; oviposition occurs in somewhat different positions and produces galls of entirely different appearance, and while no males of *T. maideni* were ever observed in galls on *A. implexa*, males of this species emerged quite freely from galls on *Acacia Maidenii*.

*The Adult.*

*The Female.*—While resembling adults bred from galls on *A. implexa* very closely, they are slightly smaller. Their average length is 2.81 mm., the maximum being 3.13 mm. and the minimum 2.66 mm. The general appearance, and the general pigmentation of the head, thorax, abdomen and legs of the two are much the same, but the ochreous markings on the dorsal surface of the third and fourth segments usually extend further down the sides of the abdomen, and in most specimens there is also a variable ochreous patch on the posterior portion of the dorsal surface of the fifth segment; thus the ochreous patch on the abdomen frequently appears divided into two unequal areas by the dark brown anterior portion of the fifth segment.

*The Male.*—The average length of the male is 2.15 mm., the maximum being 2.29 mm. and the minimum 1.93 mm. It is much shorter and less robust than the female. The head is black, apart from the eyes, which are dark reddish-brown, and the antennae are brown. The thorax is black and the abdomen varies from dark brown to black, the legs being similar in colour to those of the female.

*The Egg and Oviposition.*

The egg, which is similar in every way to that laid by *T. maideni* in *Acacia implexa*, is inserted by the females in the young twigs which have developed at the tips of the branches a few weeks earlier. The female after laying an egg moves on a little, and repeats the process, and it is quite common to see a number of females laying in various parts of the same twig, the extensive galls which develop subsequently representing the result of the deposition of many hundreds of eggs by a number of females. As the adults are short lived and emerge mainly in November and December, oviposition mainly occurs during those two months.

The eggs in ten newly emerged females were counted, the average being 397.3, the maximum being 589, and the minimum 262.

*Larval Development.*

In 1937 periodic dissections of galls were made from 10th May until 26th October, and the various stages of larvae present are set out in Table 4. In May definite, but very small, galls were present, and it will be seen that only second and third stage larvae were dissected. It will be noted that there is a steady development of the larvae during the winter and following spring, coinciding with the gradual increase in size of the galls themselves. Fifth or last stage larvae were first dissected on 9th September, and prepupae were first found on 26th October. On 29th October, several hundred gall cells from this same tree were examined, and while most were occupied by either immature or mature larvae, a few cells contained pupae and several contained adults of *T. maideni*, so that there is considerable overlapping of the various stages.

TABLE 4.  
*Results of Dissection of Galls on Acacia Maideni showing Stages of Trichilogaster maideni Present.*

Date of dissection.	No. of cells examined.	Larvae.					Prepupae.
		Stage I.	Stage II.	Stage III.	Stage IV.	Stage V.	
10.v.1937 .. ..	27	—	8	19	—	—	—
28.vi.1937 .. ..	28	—	3	13	12	—	—
9.viii.1937 .. ..	30	—	5	23	2	—	—
9.ix.1937 .. ..	23	—	—	—	2	21	—
5.x.1937 .. ..	44	—	—	—	7	37	—
26.x.1937 .. ..	40	—	—	—	—	35	5

First adult of *T. maideni* emerged 6.xi.1937.  
Last " " " " " " 28.xii.1937.

*The Pupa.*

The female pupa is at first white, but becomes pigmented fairly rapidly. The head and the thorax become black, but only the anterior borders of each abdominal segment become black, the remainder being brown, so that the abdomen presents a striped

appearance. The average length of the female pupa is 2.46 mm., the maximum being 2.71 mm. and the minimum 2.19 mm. The male pupa remains lighter in colour during the greater part of the pupal period, but it exhibits the banded appearance of the abdomen as does the female. Its length averages 1.90 mm., the maximum being 2.08 mm. and the minimum 1.77 mm.

#### *Emergence of Adults.*

In 1936, emergence began in the latter half of November, and adults emerged in large numbers during the first half of December, and limited numbers emerged until towards the close of that month. In 1937, the first adult of *T. maideni* emerged on 6th November, and emergence continued until 28th December, an emergence period of almost two months.

#### *Total Life-Cycle.*

The life-cycle is annual, and, as with other acacia gall wasps, the incubation period and the pupal period are relatively short, the larval period being by far the most extensive stage of the life-cycle.

#### OBSERVATIONS ON THE DEVELOPMENT OF THE GALLS.

Egg-laying in the young acacia twigs takes place mainly in November and December, but it is not until some months later that there is any definite external evidence of galling.

Examination of the tree on 11th April, 1937, showed some of the twigs were swollen and uneven on the surface, this being the first indication of gall formation (Pl. viii, B). Moreover, some twigs in which galls subsequently developed appeared to be quite normal at this time.

The progress of gall development is a steady one extending through the late autumn, the winter and the spring. By 10th May, 1937, while a few of the galls were just about half grown, others were just showing a slight roughening of the surface. Second and third stage larvae of *T. maideni* were present at this time. The surface of all of the galls at this time was fairly regular. By 28th July, 1937, the smallest galls were about half their full size. At this time the galls were soft and fleshy, and could be cut with ease.

Growth appears to accelerate in the early spring and inspection on 9th September showed that the more advanced galls were almost their full size. Such galls were found to contain larvae of the last stage, though they were not mature. By the 5th October, 1937, most of the galls had reached their full size, and of 44 larvae dissected on that date 37 were in the last stage. On 26th October, 1937, all galls were full size, and none could be found which did not contain last stage larvae of *T. maideni*.

As development progresses, the galls become more irregular in outline, and at maturity consist of a number of rounded swellings which stand out above the general surface of the gall (Pl. viii, D.). The outer surfaces of the galls are bright olive green, and for the most part this general colour is maintained throughout gall development. In some instances there is a cracking or scaling of portion of the gall surface, which gives it a brownish coloration. The individual lengths of galled twig vary from less than an inch up to one foot, and while usually the galls incorporate the whole of the circumference of the twig, occasionally small galls containing a limited number of occupants develop on one side of the stem only. Though the percentage of moisture in the galled tissue does decrease as the galls mature, they never become hard and woody as do those on *Acacia implexa*.

Soon after adults emerge from the galls, the latter commence to turn black, and in most instances the twig dies, though the previous season's galls may persist in a dead condition on the trees for at least twelve months. Sometimes the twig and foliage beyond the galled stem have remained alive for twelve months after the emergence of the adults, and quantities of gum may exude from the emergence holes.

Several hundred adults may emerge from a single elongate gall, the individual cells in the gall being very close to one another, and not regularly arranged. In crowded galls some of the occupants are sometimes deep down and completely overlain

by others, and though as many as twelve males have been found in adjoining gall cells, the two sexes appear to be scattered irregularly through the galls.

The plant tissues at first fit closely around the larvae, and while with larval development a small space does develop between the larva and the wall of the cell, a large cell is never formed, the gall cell or chamber being only slightly larger than the larva at maturity.

#### INSECTS ASSOCIATED WITH TRICHILOGASTER MAIDENI IN GALLS ON ACACIA MAIDENI.

No lepidopterous larvae were found in these galls, but, as well as the Anthribid *Doticus pestilens*, seven species of Chalcidoids emerged from the galls, in addition to the primary gall former, *T. maideni*. These included *Eurytoma gahani*, *Eurytoma* sp. B., *Megastigmus trisulcus* and *Coelocyba nigrocincta*; the two first mentioned species have been discussed earlier.

#### *Coelocyba nigrocincta* Ashmead.

Numbers of adults of this species emerged from the galls on *A. Maideni*. The species was first described from agromyzid galls on *Eucalyptus corymbosa*, and was bred by the writer from galls on *Acacia decurrens* caused by *Tepperella trilineata*, from galls on *Acacia implexa* caused by *Trichilogaster maideni*, and occasionally from galls on *Acacia floribunda* caused by *Trichilogaster acaciae-longifoliae*.

Examination showed that adults and pupae of *C. nigrocincta* were to be found in separate cells in the galls, scattered through the other gall cells occupied by various stages of the primary gall formers. In a number of instances the pupae of *C. nigrocincta* were removed from cells and all the debris was mounted on slides and examined, and on several occasions the mandibles of mature larvae of *Trichilogaster maideni* were also found in the cells.

The detailed life-history of this species has not been studied, but an egg (Fig. 5E) was dissected from a globular flower head on *Acacia decurrens*, in which the eggs of *Tepperella trilineata* had already been deposited. It is evident that *C. nigrocincta* causes the death of the primary gall former, but that the latter is at least able to reach the last larval stage before destruction.

On the various species of *Acacia* under discussion, where unilocular galls were found to contain only pupae or adults of *C. nigrocincta*, these were similar in appearance to unilocular galls in which the primary gall former only was present.

*The Adult*.—This species was described by Ashmead (1900), the genus *Coelocyba* being also then established. He placed it in the family Pteromalidae. Girault (1916, p. 222) considered it incorrectly placed and removed the species to the family Perilampidae.

The writer found that there was considerable variation in the size of the adult, the average length of the female being 2.74 mm., the maximum being 3.18 mm., and the minimum 2.45 mm. The male is very much smaller than the female, the average length being 1.83 mm., the maximum being 2.03 mm., and the minimum 1.46 mm. Occasionally very minute adults emerged from galls on *Acacia Maideni*, one such female measuring 1.46 mm., and one male 0.99 mm. The antenna (Fig. 5B), mandible (Fig. 5D) and stigmal knob (Fig. 5C) of the female, and the antenna (Fig. 5A) of the male are figured.

Both sexes are remarkably active, and when confined in tubes or jars in the laboratory run around rapidly.

*The Egg*.—The ovarian egg (Fig. 5F) differs little in shape from the egg after deposition (Fig. 5E). Both are smooth-surfaced, elongate and oval, slightly arched with rounded ends. The average length is 0.31 mm., and the average width 0.065 mm.

*Emergence of Adults*.—Emergence of adults is rather irregular. Galls were collected from *A. Maideni* on 1st November, 1937, and a number of *C. nigrocincta* emerged on that day. The first adults of *T. maideni* did not emerge until 6th November, and adults of *C. nigrocincta* continued to emerge periodically throughout, and after the emergence period of the primary gall former.

*Parasitic Nematodes associated with C. nigrocincta.*—In 1936 and also in 1937 in dissecting adults of *C. nigrocincta* from galls on *Acacia decurrens*, *A. Maideni* and *A. implexa*, parasitic nematodes were to be found free in the abdomens of both sexes (Fig. 5J). The parent nematodes at this time were capable of only very slight movement, but, within, young nematodes could be seen twisting and turning and at times temporarily thus changing the outline of the parent. When the integument of the parent nematode was torn open, numbers of crescent-shaped living young floated out (Fig. 5G).

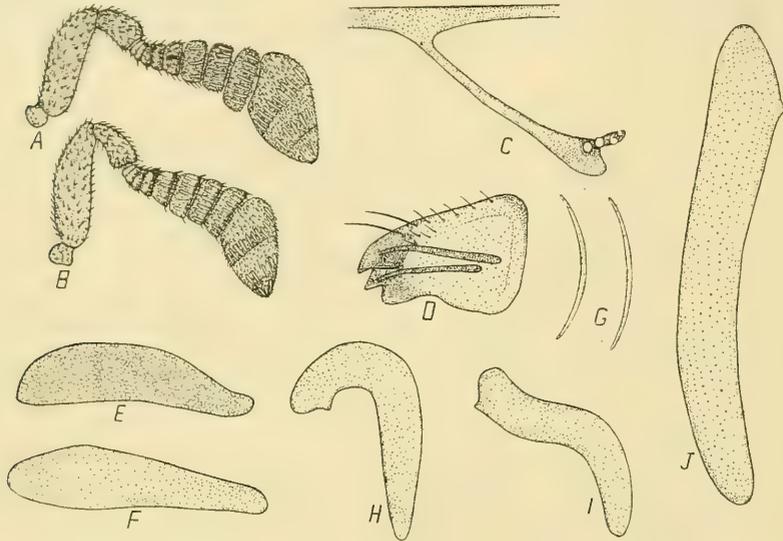


Fig. 5.—*Coelocyba nigrocincta*. A, Antenna of male ( $\times 65$ ); B, Antenna of female ( $\times 65$ ); C, Stigmal knob of female ( $\times 122$ ); D, Mandible of female ( $\times 122$ ); E, Egg after deposition ( $\times 122$ ); F, Ovarian egg ( $\times 122$ ); G, Young nematodes dissected from abdomen of adult of *C. nigrocincta* ( $\times 42$ ); H, I, Immature nematodes dissected from pupa of *C. nigrocincta* ( $\times 42$ ); J, Mature nematode containing living young dissected from adult of *C. nigrocincta* ( $\times 42$ ).

The mature nematode varies from translucent to light green, and was always found in the abdomen of the wasp.

Nematodes in each wasp ranged from one to twenty, the average number being 4.9. The average length of the gravid nematodes was 1.29 mm., the average width being 0.20 mm. The largest gravid nematode measured 1.6 mm. in length and 0.24 mm. in width, while the smallest nematode measured 0.90 mm. in length and 0.19 mm. in width.

One gravid nematode was found to contain 75 young. The size of the young nematodes found floating freely in the host haemocoel varied somewhat, the average length being 0.39 mm. and the width at the widest point 0.013 mm.

In 1936, of 72 females of *C. nigrocincta* examined, 28 contained nematodes, while only 3 of the 14 males examined were nematode infested. In 1937, only 6 out of a total of 50 females contained nematodes and 9 out of 38 males were nematode infested.

In both 1936 and 1937, pupae of *C. nigrocincta* were dissected from galls and were found to contain nematodes which were not quite fully developed. The average length of three was 0.74 mm. and the average width 0.12 mm. (Fig. 5H, I); none of these contained living young, but usually in adult wasps young nematodes were present within their parents.

Both males and females of *C. nigrocincta* infested with nematodes were quite active and just as large as those which were uninfested, so that the presence of the nematodes could only be detected by dissection. Internally, infested individuals were found to be in an unthrifty condition. The alimentary tract was intact, but there was a notable absence of fat-body, and in the case of female wasps the ovaries were

distinctly reduced, and in some instances almost wanting. The general condition of all the internal organs was definitely unhealthy.

#### AUSTRALIAN CHALCIDOID GALLS.

Detailed life-history studies of a number of species of Australian gall-forming Chalcidoidea have now been published (Noble, 1936, 1938*b*, 1940). General observations on a number of other species of gall formers have also been made, and all have certain features in common.

In the citrus gall wasp, *Eurytoma fellis* (Noble, 1936), the ovarian egg consists of an oval body and a short anterior, and a very long posterior pedicel. The ovarian egg of *Tepperella trilineata* (Noble, 1938*b*), of all species of *Trichilogaster* studied, and of several other species of gall-forming wasps under observation, consists of an oval body and an elongate pedicel, which has become so enlarged posteriorly, that the egg now appears as a bilobed structure joined by a narrow connecting tube. This greatly enlarged pedicel is apparently a device to facilitate the passage of the egg down the narrow ovipositor. The plant tissues within which the eggs are deposited are always delicate, and it is important that the wasp in inserting the egg should cause a minimum amount of injury to the host plant. Following oviposition in all cases, the protoplasmic contents pass into the body of the egg, the vitelline membrane soon surrounding the developing embryo, cutting it off from the now flaccid pedicels.

In their oviposition behaviour the various wasps studied also behave somewhat similarly. The eggs are invariably laid in some recently formed plant tissues, either leaves, stems or flower buds, which are still very soft and young, and which under ordinary circumstances in the ensuing months, even in the absence of insect attack, would have undergone great development and increased considerably in size. *Eurytoma fellis* and *Trichilogaster maideni* select for oviposition recently developed stems, but *Trichilogaster acaciae-longifoliae* (Noble, 1940) and *Tepperella trilineata* select for oviposition, minute flower buds at a very early stage of development.

The life-cycle of all primary gall-forming wasps so far studied in Australia is annual, the adult wasps emerging from the galls each year during the late winter, spring or early summer. In all cases the incubation periods and pupal periods are rather limited, the larval period representing by far the longest period of the life-cycle and lasting nine months or more. The length of adult life in all species is comparatively short, the female wasps always being ready to lay immediately after they emerge from the galls; by far the greatest oviposition occurs during the first twenty-four hours after emergence.

Slight abnormalities in the plant tissues usually manifest themselves within a few months of oviposition, but while gall development in each case only occurs once in each twelve months, there is considerable variation in the length of the period which elapses after oviposition, before the first signs of galling become evident. In citrus stem galls caused by *Eurytoma fellis* first signs of twig unevenness appear soon after the larvae have hatched, and external gall development is complete when the larvae are still in the first stage. In *Trichilogaster maideni*, which also produces twig swellings, the galled stems increase in a regular manner throughout the entire larval period, and reach their full size in the following spring at the time the larvae reach maturity. With *Tepperella trilineata* and *Trichilogaster a-longifoliae*, which oviposit in the minute flower buds, no definite evidence of galling is present until some months after the larvae have hatched. This is especially true of *T. a-longifoliae* where, following oviposition in *Acacia floribunda* and *A. longifolia*, only extremely minute galls are to be seen six months later, the typical large green fleshy galls being present on the trees for only a few months of the year.

In the earlier stages of gall development the plant tissues are in contact with the various species of larvae and at this time these have either a closed or very limited open respiratory system. With the progress of larval growth, a limited space develops between the inner wall of the nutritive layer and the integument of the larva, this being accompanied by a further development of the respiratory system.

At maturity the larva is to be found in a cell, which is always somewhat larger than the larva itself and, although enclosed in the gall, the larva then possesses nine pairs of open spiracles and a well developed respiratory system, which appears to be just as complete as that possessed by an external feeding larva of this group.

#### *Types of Gall.*

It is evident that the galls caused by Australian Chalcidoids may be divided into two general groups. In the first, oviposition and subsequent larval development results in generalized twig swellings, in which, even at maturity, the original botanical units can still be distinguished, though they are somewhat abnormal. Galls of this type are the twig swellings on various species of citrus caused by *Eurytoma fellis*, and twig swellings on *Acacia Maideni* caused by *Trichilogaster maideni*. Similar twig swellings caused by another species of *Eurytoma* have also been observed by the writer on various species of *Eucalyptus* in the Sydney district. The effect of such twig galling varies somewhat with the different species of trees and the insects, as well as the age and the portions of the trees attacked, but under all conditions the general effect on the growth and further development of the entire tree, or infested limbs, is rather severe. Twig swellings of this type, though large, may persist in a living condition with the various conducting tissues functioning for some years. In an experiment in November, 1931, the main stem of a seedling lemon tree was infested with the gall former, *E. fellis*. The seedling was then only six months old. Typical galls developed in the following autumn and winter, and each year since that time, up to 1939, the tree has put out new growth above the galls of the previous year, this new growth each spring being infested by the newly emerged wasps. Plant food to reach the upper leaves must be carried through several feet of galled tissues. This tree, though still alive, is extremely stunted and abnormal. Where galls have been caused by *Trichilogaster maideni* on *Acacia Maideni*, it is not uncommon for the entire tissues above the galled stem to die within a few months of emergence of the adults, though occasionally such galled stems have been observed to function for at least twelve months after the emergence of the wasps. The galling of a limited number of lateral stems has only a comparatively slight effect on the general health of the tree, as abundant new growth develops from the ungalled twigs, but after years of infestation, almost every new twig on the tree is galled each spring, and the entire tree eventually assumes an extremely unhealthy and unsightly appearance. In young trees, if heavy oviposition and galling occur in the main stem, the tree never develops satisfactorily if the galls are left, and if the galled tissue is cut away, the shape of the tree is ruined.

The second general group of galls is that in which oviposition and subsequent larval development result in the production of outgrowths or proliferations of various parts of the host. Such galls stand out conspicuously, and, though at times very large, they are often only connected to the tree by very narrow attachments. Examples of such galls are those formed in the flower buds of *Acacia decurrens* by *Tepperella trilineata*, the galled flower buds of various species of *Acacia* caused by *Trichilogaster a-longifoliae* and small globular galls caused by Chalcids on the leaves of various species of native shrubs. In such galls it is often extremely difficult, once gall formation has progressed very far, to trace the changes in the original botanical units. After the wasps emerge from such galls the latter shrivel within a few weeks and die, and eventually drop from the trees, though it may be a year or more before all of the previous year's galls ultimately disappear. In these galls it appears that the host plant succeeds in cutting off and isolating the invading insects, so that in their final effect upon the tree, they are far less injurious than the wasps which cause twig swellings.

Recently the writer has studied a Chalcidoid which oviposits in the young leaf buds of Turpentine (*Syncarpia laurifolia*); subsequent larval activity eventually results in the development of large numbers of minute unilocular galls on the foliage, as many as 142 galls having been counted on a single leaf. As the leaves eventually fall and are replaced by others, such insects have little ultimate effect on the vitality of the tree,

unless almost all the leaves are so heavily infested that they cannot function normally. However, this seldom appears to occur.

It is known also that in Australia some species of Chalcidoids infest the seed capsules of various native plants causing some abortion of the tissues and a loss of seed, but no detailed observations on these have yet been made.

#### *The Experimental Production of Galls.*

For the detailed study of the life-history of a gall wasp, undoubtedly the ideal method is to produce numbers of galls experimentally so that these, with a known history, can be dissected from time to time and the stages of the insect present noted. This, however, may prove either extremely difficult or even impossible. This has been confirmed by Kinsey (1920, p. 323), who has worked extensively with American cynipid gall wasps. He considered, moreover, that trees on which galls are to be produced must be in a very vigorous condition.

When working with the citrus gall wasp, *Eurytoma fellis*, the writer found little difficulty in producing galls experimentally in the insectary, and for several years large numbers of potted citrus seedlings were experimentally galled and were infested both with *E. fellis* and its parasite, *Epimegastigmus brevivalvus*, and the potted trees used for this work were certainly growing vigorously at the time of infestation. Similarly, little difficulty was experienced in inducing the experimental production of galls on *Acacia longifolia* growing in pots, by merely enclosing newly emerged females of *T. a-longifoliae* with these trees in large cellophane sleeves.

However, with *Tepperella trilineata*, which causes galls on the flower buds of *Acacia decurrens* var. *pauciglandulosa*, the writer met with no success. For four consecutive years, in the spring, many hundreds of adults were enclosed in cellophane sleeves of various sizes with twigs and large branches on particularly vigorous young host trees. In addition, branches bearing mature galls were hung in these trees during the early emergence period of *T. trilineata*, but though extensive oviposition was observed on many occasions, and some galls commenced to develop, not a single mature gall was secured. An inspection of a number of host trees of the same variety in various localities failed to show any vigorous young trees carrying galls caused by *T. trilineata*. Such galls were only found on trees which had been growing for many years, and the only tree observed by the writer which was very heavily galled was one which was in a very unthrifty condition, borer infested, and on which a number of the limbs were already dead.

It would appear that while, in many instances, a certain vigour in the host plant is an essential pre-requisite to successful gall formation, in others, a vigorously growing host is apparently not essential.

#### *The Causes of Gall Development.*

While it is clear that the hypertrophy which results in the development of galls is in some way attributable to the insect, the exact nature of the stimulus which results in gall development has never been discovered. The findings of workers with Cynipids can in certain respects be substantiated by observations of the writer with the Australian chalcidoid gall wasps. The insertion of the ovipositor or any fluid which might be injected together with the egg, or the presence of the egg itself, in all species studied by the writer, is in no way directly connected with gall formation.

It has been suggested that the secretion of some product or products by the larva may cause the plant tissues to hypertrophy. Triggerson (1914) considered that in the case of the Cynipid, *Dryophanta erinacei*, the development of the gall is due to the excretion of a fluid from the malpighian vessels in the larva.

The writer (1936) sectioned, at various stages of development, galls on citrus caused by *E. fellis*. These showed that the egg is deposited between the xylem and phloem in contact with the cambium layers, and the young larva commences development in this position. In this species, as well as in all the others studied, there was no evidence of gall formation until some time, at least, after the larva had hatched, and in every instance gall formation was complete either during larval development or at latest by the time the larvae reached maturity. Thus it is evident that the formation of galls

has in some way been due to the presence of the gall wasp larva, and the effect of the latter on the meristematic tissues. In experimental trees in which *E. fellis* had oviposited, occasionally, galls were observed to partly develop, and then hypertrophy ceased, and dissection showed that all the gall wasp larvae were dead. This suggests that the continued activity of the wasp larva is essential for the completion of gall development.

It would appear that whatever the stimulus, it must be continued throughout larval life, or at least to a stage in larval development at which the galls reach their full size.

Sometimes the larvae of *T. a-longifoliae* are killed by the larvae of a species of *Eurytoma* at an early stage in gall development and in plurilocular galls, that portion of the gall nearest the cell in which the host larva has been destroyed, and in unilocular galls, the entire gall, ceases to increase in size, though the larva of *Eurytoma* may continue to occupy the gall cell for many months. This suggests that whatever the stimulus, it must be specific to the larva of the particular gall wasp concerned and the suggestion that some larval glandular secretion is responsible for gall formation appears to be a definite probability.

#### *The Effect of Parasitism on Gall Formation.*

It has been stated by Froggatt (1892) that the activities of parasites in the galls result in the formation of masses of tissue which have not the shape of normal galls produced by the host gall wasp alone. From the writer's observations, this is only true when parasitism results in the death of the gall wasp larva at an early stage in development and when the galls are only partly grown. If the parasite does not cause the death of the host larva before the latter is maturing, the development of galls is in every way quite normal.

Mature galls on citrus in which a very high percentage of the cells contained larvae of the gall former *E. fellis*, within which there were larvae of *Epimegastigmus brevisulvus*, could not be distinguished from galls in which the host larvae were present alone, but this parasite only destroys maturing host larvae.

Associated with the larvae of *Tepperella trilineata* which cause galls on *Acacia decurrens* was an internal parasite, *Megastigmus acaciae* (Noble, 1939b), and also *Eurytoma gahani* (Noble, 1939a). The larvae of both of these wasps destroyed the host larvae only when the latter were approaching maturity, and mature unilocular galls containing either species of these parasites were similar in every respect to such galls occupied by the host alone.

The larvae of a species of *Eurytoma* destroyed the larvae of *Trichilogaster a-longifoliae* and *T. maideni* at an early stage in gall development, and where numbers of these parasitic larvae were present in plurilocular galls, completely misshapen and abnormal galls resulted, while mature unilocular galls, though spherical, were hard and woody and only a small fraction of the size of normal unilocular galls occupied by host larvae alone.

#### *Phytophagy and Parasitism in a single species of gall inhabitant.*

Gahan (1922) published a list of world species of Chalcidoidea recorded as being phytophagous, and pointed out that such habits in this group were at one time strenuously disputed. Of the phytophagous Chalcidoids listed by Gahan a comparatively limited number produce galls. The Cynipoidea are the dominant gall formers in other countries, but in Australia their place appears to have been taken by an extensive chalcidoid gall-forming fauna, and it is clear that in time there will be large numbers of Australian Chalcidoids to be added to Gahan's world list.

Gahan (1922) in discussing the development of phytophagy in the Chalcidoidea instances, as a point of confirmation of its recent development, the fact that several authors had asserted that certain species of Eurytomidae are parasitic in their early stages and finish their development as plant-feeders (cf. Nielsen, 1906; Rimsky-Korsakov, 1914; Triggerson, 1914; Phillips, 1917, 1927). Published records of such behaviour are still limited and appear to have been confined to the genus *Eurytoma*.

Investigations of the writer have shown that individual species which feed both phytophagically and parasitically occur in Australia, and the life-histories of two such

species have been studied in some detail; both of these species belong to the genus *Eurytoma*, viz., *Eurytoma gahani* Noble and *Eurytoma* sp. B. The latter species deposits its eggs alongside the larvae of various species of *Trichilogaster* in galls on *Acacia* spp., and the larva of *Eurytoma* sp. B., on hatching, destroys the host larva and then completes its development phytophagically. *Eurytoma gahani* lays its eggs alongside the eggs or larvae of *Tepperella trilineata* and various species of *Trichilogaster* in galls on *Acacia* spp.; the two species live together in the one cell normally and phytophagically, until the host larva is maturing. At this time the larva of *E. gahani* destroys the host larva and, feeding on its contents, reaches maturity. This appears to be the first record of such behaviour in the Chalcidoidea (see Noble, 1939a).

Apart from these two species, the writer has observed five others in which the evidence suggests that these, too, are phytophagous during their early larval period, but later become parasitic or predatory and destroy the host larva. Pupae of two of these, an unidentified species of *Eurytoma* and *Megastigmus* sp. B., have been found in galls on *Acacia longifolia* with the pupal remains of the gall former, *Trichilogaster a-longifoliae*. The writer (Noble, 1940, p. 35) has already pointed out that these host pupae though dead are sometimes almost entire, but are also sometimes entirely devoured. While this indicates some variation in the behaviour of these larvae, it is quite evident that, in some instances, they could not possibly have obtained sufficient nutriment from the host pupa, as *Megastigmus* sp. B. is actually a larger species than its temporary host. As immature *Megastigmus* larvae were several times found in cells with normal host pupae, it is evident that in the earlier part of their life they must have fed phytophagically.

Gahan (1922) concluded that partial phytophagy was probably first forced upon the parasite by the premature exhaustion of the natural food supply, due to attacking a host which was insufficient in itself to furnish food to complete development. It will be noted that in several of the species mentioned above this position is actually reversed, these feeding in the earlier part of their larval life phytophagically and later behaving as parasites. The point arises as to whether, in such species, the parasitic behaviour is one which will eventually give way to complete phytophagy, while it may even be possible that such species may, according to Gahan's theory, have become phytophagous, and that this brief period as a parasite may be recently acquired. It has already been suggested by the writer in regard to *Eurytoma gahani* (1939a) that this parasitic habit may arise, not owing to a shortage of parasitic food, but, on the contrary, due to an insufficient supply of plant food, owing to the fact that at the time the host larva in these galls is maturing, a hard woody protective layer surrounds it, and even host larvae alone consume the whole of the nutritive layer prior to pupation.

It is evident that in the genus *Eurytoma* and also the genus *Megastigmus* there exist many species which exhibit a high degree of plasticity, and in view of this the study of species occurring in these groups, particularly in Australian galls, will yield valuable data regarding the evolutionary trends in the Chalcidoidea.

#### SUMMARY.

The life-history of *Trichilogaster maideni*, a wasp causing galling of the petioles of the phyllodes of *Acacia implexa* and the stems of *Acacia Maidenii*, is described. In their biology and host relationships the forms of *Trichilogaster maideni* on *A. Maidenii* and *A. implexa* exhibit marked differences. The life-cycle in both cases is annual. The incubation and pupal periods are comparatively limited, the larval period occupying nine to ten months. Adult wasps emerge from galls on *Acacia implexa* during October and November, and from *A. Maidenii* from the middle of November throughout December, there being some variation from year to year. No males of *T. maideni* were found in galls on *Acacia implexa*, but they were quite common in galls on *A. Maidenii*. The egg and the five larval stages are described. Oviposition commences on the day of emergence, eggs being inserted in the petioles of recently formed phyllodes and young stems.

On *A. implexa*, minute galls are present by the end of January and these increase in size during the following winter and early spring, being their full size at the time the larvae reach maturity. On *A. Maidenii*, definite galls are not present until late in the summer, and there is steady growth through the following winter and spring, galls being their full size at the end of October.

Lepidopterous larvae were commonly found mining the galls on *A. implexa*, and the Anthribid, *Doticus pestilens*, emerged from galls on both species of *Acacia*. Eleven other species of Hymenoptera were bred from galls on *A. implexa*, of which eight were Chalcidoids, while in addition to *T. maideni*, seven species of Chalcidoids were bred from galls on *A. Maideni*. Biological notes on some of these species are included.

A number of pupae and adults of both sexes of a Perilampid, *Coelocyba nigrocincta*, which emerged from galls on *A. Maideni*, were found to contain parasitic viviparous nematodes.

The various types of gall caused by Australian Chalcidoids, and experimental gall production, are discussed. Evidence in regard to gall formation indicates that the stimulus is associated only with the larva, and is possibly a secretion. The effect of parasitism on gall development is discussed.

Previous records of the larva of a species being both phytophagous and parasitic are limited, but the writer has observed in Australian galls a number of species of *Megastigmus* and *Eurytoma* which exhibit this behaviour.

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#### EXPLANATION OF PLATE VIII.

Stages in the development of galls on *Acacia implexa* and *A. Maideni* caused by *Trichilogaster maideni*.

A.—Partly developed galls at the junctions of phyllodes and stems on *Acacia implexa*. Photographed 5.v.1937.

B.—Partly developed galls on the stems of *Acacia Maideni*. Photographed 11.iv.1937.

C.—Mature galls on *Acacia implexa*. Photographed 1.x.1936.

D.—Mature galls on *Acacia Maideni*. Photographed 11.xii.1936. Note occasional emergence holes.

N.B.—The tips of the phyllodes have been cut off.

AN ILLUSTRATED KEY TO SOME COMMON AUSTRALIAN CULICINE MOSQUITO LARVAE, WITH NOTES ON THE MORPHOLOGY AND BREEDING PLACES.

By A. R. WOODHILL and G. PASFIELD, Department of Zoology, University of Sydney.\*

(Eleven Text-figures.)

[Read 27th August, 1941.]

*Introduction.*

In any scheme of mosquito control it is essential to determine the species present in the area under consideration. This may be done by identifying either the larvae or adults, but breeding out the adults requires time and special equipment which is not always available, and the work is greatly facilitated if an immediate determination of the larvae can be made. The aim of the present paper is to enable such a determination to be made by an examination of the 4th stage larvae under a binocular microscope, without the necessity of making a special preparation or obtaining a cast skin. The only previous work of this type in Australia is that by Cooling (1924), but no key is given and the illustrations are not accurate. The value of the key is necessarily lessened by the fact that it includes only a small proportion of the described Australian species, but it includes most of the commoner species with the exception of *A. (O.) vittiger* Skuse and *A. (O.) theobaldi* Taylor. Any species not included in the key should be easily recognized as such by comparison with the drawings and descriptions.

Keys to the adult mosquitoes of the Australasian region have been published by Edwards (1924). A key to the Australian species of Anopheline larvae and adults has been published by Mackerras (1927), while Taylor (1927) has described the species of Anophelinae and given an account of their bionomics. With regard to the relation of mosquitoes of the Australian region to human disease, Taylor (1933) should be consulted.

The notes given here on the breeding places include much material already published by Taylor (1928, 1938), Mackerras (1926), Hamlyn-Harris (1927, 1929) and Woodhill (1936, 1938), together with observations made by the senior author. The nomenclature used throughout is that given by Taylor (1934).

*Species of Larvae Figured and Described.*

*Aedes (Stegomyia) aegypti* Linnaeus, *A. (Finlaya) notoscriptus* Skuse, *A. (F.) alboannulatus* Macquart, *A. (Ochlerotatus) vigilax* Skuse, *A. (Pseudoskusea) concolor* Taylor, *A. (Mucidus) alternans* Westwood, *Megarhinus speciosus* Skuse, *Culex (Culex) annulirostris* Skuse and *C. (C.) fatigans* Wiedemann are figured and described.

*Morphological Features of 8th and 9th Segments in Culicine Larvae.* (Fig. 1.)

The following terminology is that used by Marshall (1938) with some slight modifications and additions. The 8th segment bears on each side a series of irregularly placed scales, known as the *lateral comb*, and posterior to this, five hair tufts, the *pentad hairs*, which are designated  $\alpha$ ,  $\beta$ ,  $\gamma$ ,  $\delta$ ,  $\epsilon$ , as in Fig. 1. The pentad hairs may be single hairs or multiple tufts, and may be either simple or plumose.

Articulating with the 8th segment, in a posterior dorsal position, is a chitinized tubular structure known as the *siphon*. The length of this structure (exclusive of the

\* The services of the junior author were made available by the University of Sydney as the result of a grant from the Commonwealth Government Research Fund.

valves) divided by the width at the base is known as the *siphonal index*, but this figure may vary somewhat within a single species. A projection occurs on each side of the base of the siphon, and the term *baso-siphonal projection* is proposed for this structure.

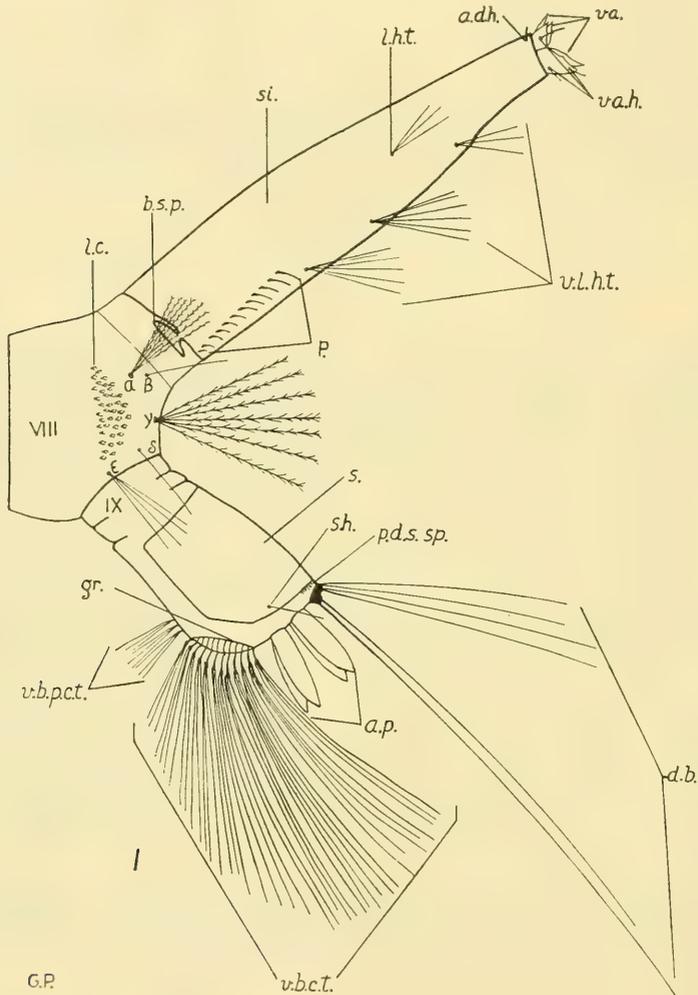


Fig. 1.—Morphological features of terminal segments of Culicine mosquito larvae. VIII, eighth segment; IX, ninth segment; *a.d.h.*, apico-dorsal hair; *a.p.*, anal papillae;  $\alpha$ ,  $\beta$ ,  $\gamma$ ,  $\delta$ ,  $\epsilon$ , pentad hairs; *b.s.p.*, baso-siphonal projection; *d.b.*, dorsal brush; *gr.*, grid; *l.c.*, lateral comb; *l.h.t.*, lateral siphonal hair tuft; *p.*, pecten; *p.d.s.sp.*, posterior dorsal saddle spines; *s.*, saddle; *s.h.*, saddle hair; *si.*, siphon; *va.*, valves; *va.h.*, valve hairs; *v.b.c.t.*, cratal hairs of ventral brush; *v.b.p.c.t.*, pre-cratal hairs of ventral brush; *v.l.h.t.*, ventro-lateral siphonal hair tufts.

On each side of the basal half of the siphon, in a ventro-lateral position, is a row of spines known as the *pecten*. A varying number of *siphonal hair tufts* also occur on each side of the siphon, and these are known as the *ventro-lateral hair tufts*, and *lateral hair tufts* according to their position. In some species a single row of dorsal or ventral median hair tufts occurs.

Articulating apically with the siphon are five *valves*, consisting of a ventral pair, a latero-dorsal pair, and one medio-dorsal valve. These carry minute hairs or hair tufts known as the *valve hairs*. On each side of the siphon, anterior to the latero-dorsal valves, is a small hair, known as the *apico-dorsal hair*.

The 9th segment carries a chitinous plate known as the *saddle*. This may occupy only a small area on the dorsal aspect of the segment, or may extend almost to the mid-ventral line, or may completely surround the segment as a continuous ring. Frequently the saddle bears minute spines on its posterior dorsal margin. The *saddle hair* is borne near the posterior margin of the saddle, and may sometimes take the form of a hair tuft consisting of two or more hairs. A series of long paired hairs or hair tufts arising from small chitinous bosses on the posterior dorsal aspect of the 9th segment, is known as the *dorsal brush*. A row of hair tufts projecting posteriorly and ventrally in a median position is known as the *ventral brush*. The ventral brush includes what are termed the *cratal* and *pre-cratal hair tufts*. The cratal tufts arise from a structure known as the *grid*, which consists of a series of chitinous transverse bars enclosed by a chitinous border, the whole having a grid-like appearance. The pre-cratal tufts arise anteriorly to the grid and are usually much shorter than the cratal tufts.

The 9th segment bears at its apex two pairs of elongated thin-walled structures known as the *anal papillae*. Between the bases of the papillae is the anal opening. What is known as the *gill saddle index* is the figure given by dividing the length of the anal papillae by the length of the saddle at its longest part. This figure is not very reliable, as the length of the papillae may vary according to the chemical composition of the water.

#### *Explanation of Figures.*

In all the figures in the present paper the paired structures on the 8th segment and on the siphon are shown for one side only, in order to avoid confusion. Where a hair tuft is not on the median ventral or dorsal line, this is clearly indicated by the fact that its base is situated within the outline of the drawing. Any structures shown as arising from the margin can be taken as being on, or very close to, the median line.

*N.B.*—The hairs of the dorsal brush actually arise on each side of the median line, but very close to it, and in the drawings *all* the hairs of the dorsal brush are shown.

The transverse line shown below the siphon, indicates a fold in the cuticle produced by the movement of the siphon, but in some specimens this is not very clearly defined and it is never as distinct as the division between the 8th and 9th segments.

The number of pecten spines, lateral scales, and hairs in the various tufts, represents an average of a large number of specimens, the maximum and minimum number observed being given in the description.

With regard to the hair tufts, these are noted as being plumose when the plumosity is plainly visible under a magnification of 60. In some cases a very fine plumosity is visible under a much higher magnification, but this is not described as such.

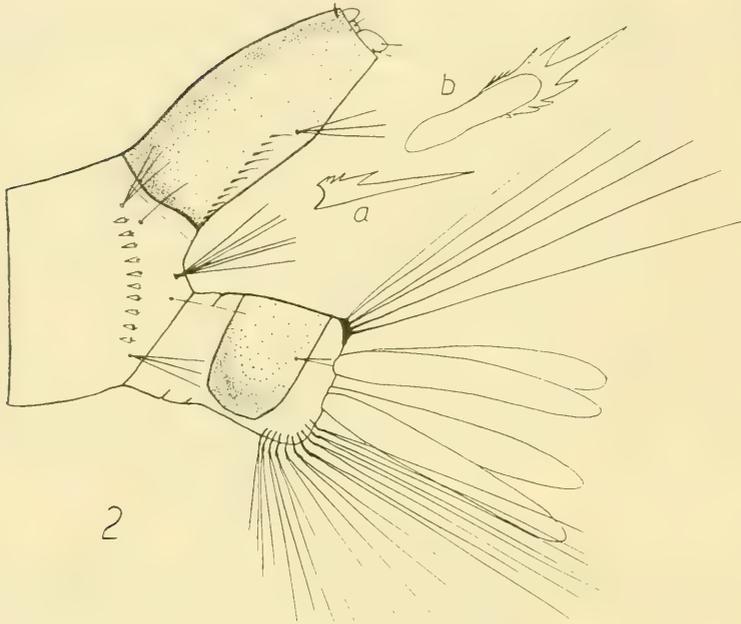
It will be noted that in the drawings the teeth of the pecten spines are sometimes shown on the left and sometimes on the right hand side of the spine. This has no significance, since it is due entirely to the position of the siphon varying in the different preparations. In all the species examined the teeth occur on the side of the spine which faces towards the base of the siphon.

It would appear that some at least of the variations shown by authors in the pecten spines and comb scales are due to the angle from which these are viewed. While it is possible to distinguish the genera *Aedes* and *Culex* by an examination of the pecten spines and lateral comb scales, some of the species of *Aedes* dealt with in this paper definitely cannot be distinguished by these structures alone.

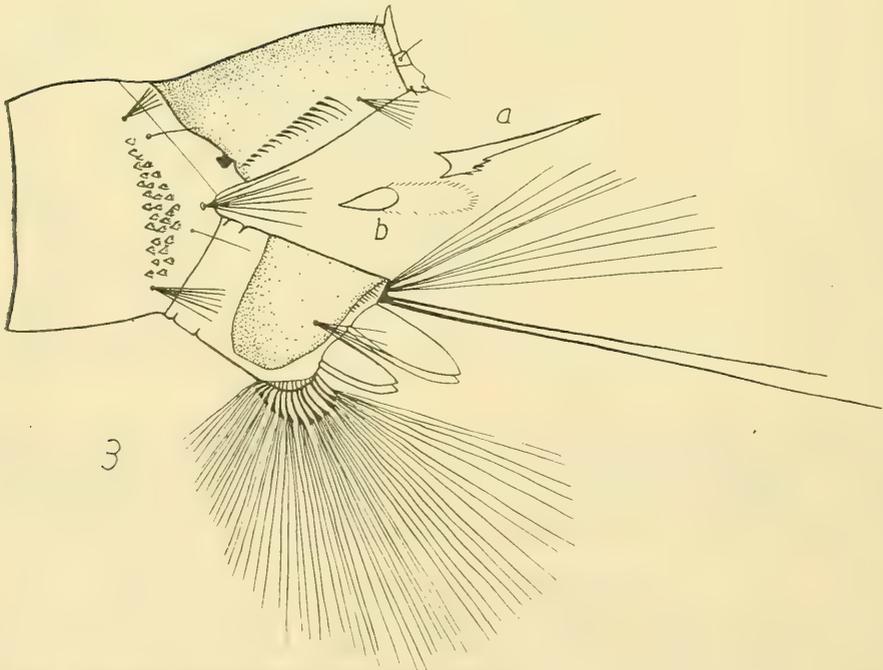
#### DESCRIPTION OF TERMINAL SEGMENTS.

##### AÈDES (STEGOMYIA) AEGYPTI Linnaeus. Fig. 2.

*Lateral Comb.* 7 to 12 elongated scales in a single row. *Pentad hairs.*  $\alpha$ , 3 to 5;  $\beta$ , 1;  $\gamma$ , 4 to 8;  $\delta$ , 1;  $\epsilon$ , 2 to 4;  $\gamma$  sometimes weakly plumose, remainder always non-plumose. *Siphon.* Siphonal index approx. 2.4. *Baso-siphonal projection.* Absent. *Pecten.* 13 to 18 spines. *Apico-dorsal hairs.* A pair of small single hairs. *Valve hairs.* Each ventral valve with a single hair at apex and base, and latero-dorsal valves each with a single hair. *Siphonal hair tufts.* One pair of ventro-lateral non-plumose hair tufts, each of 2 to 4 hairs. *Saddle.* Short, as in Fig. 2, extending almost to mid-ventral line.



2



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FIG. 2.—*Aedes (Stegomyia) aegypti* Linnaeus  $\times 42$ . *a*, pecten spine  $\times 335$ ; *b*, lateral comb scale  $\times 335$ .

FIG. 3.—*Aedes (Finlaya) notoscriptus* Skuse  $\times 42$ . *a*, pecten spine  $\times 335$ ; *b*, lateral comb scale  $\times 335$ .

*Saddle hairs.* 1, or a tuft of 2, on each side. *Dorsal brush.* One pair of single hairs, and a pair of tufts each composed of 2 to 4 hairs. Total variation in dorsal brush 6 to 10. *Ventral brush.* 9 to 10 tufts of 2 hairs each. The grid is imperfectly developed, having transverse bars but no chitinous border. *Anal papillae.* Usually about three times as long as saddle, blunt at apex. *Pecten spines and comb scales.* As in Fig. 2, with slight variations.

*Breeding Places.*—This is one of the common domestic species, always breeding in or near human dwellings in artificial containers or tree holes. It does not usually occur in ground water, and should therefore be one of the easiest species to control. It rarely occurs in very foul water.

AÈDES (FINLAYA) NOTOSCRIPUS Skuse. Fig. 3.

*Lateral comb.* Approx. 22 to 36 rather elongated scales, in 3 to 4 irregular rows. *Pentad hairs.*  $\alpha$ , 3 to 6;  $\beta$ , 1;  $\gamma$ , 4 to 7;  $\delta$ , 1;  $\epsilon$ , 4 to 8; normally these hairs are non-plumose, but an occasional specimen shows plumosity on  $\gamma$ . *Siphon.* Siphonal index approx. 1.8. *Baso-siphonal projection.* Distinct and roughly rectangular as in Fig. 3. *Pecten.* 12 to 18 spines. *Apico-dorsal hairs.* A pair of single hairs. *Valve hairs.* Two single hairs present on each of the ventral valves and one on each of the latero-dorsal valves. *Siphonal hair tufts.* One pair of ventro-lateral tufts consisting of 2 to 6 non-plumose hairs. Occasionally a very fine plumosity occurs on these hairs. *Saddle.* Extends almost to the mid-ventral line and carries distinct spines on its posterior dorsal margin. *Saddle hairs.* A tuft of 3 to 5 non-plumose hairs on each side. *Dorsal brush.* One pair of long single hairs, and a pair of shorter hair tufts each composed of 4 to 6 hairs. *Ventral brush.* 12 to 14 cratal tufts, arising from a well-marked grid, each tuft consisting of from 4 to 7 hairs. *Anal papillae.* One pair about as long as the saddle, the other pair frequently shorter. *Pecten spines and comb scales.* As in Fig. 3, with slight variations.

*Breeding Places.*—This species occurs in freshwater rock holes, tree holes, and in artificial containers. It is a very common domestic species, as well as occurring in the field.

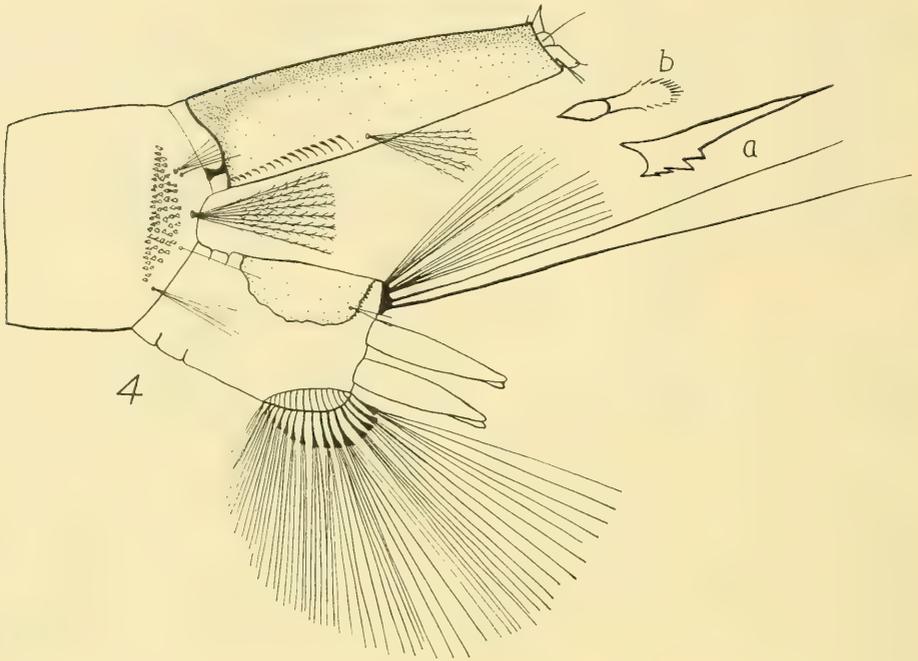
AÈDES (FINLAYA) ALBOANNULATUS Macquart. Fig. 4.

*Lateral comb.* Approx. 60 to 105 elongated scales, in 4 to 5 irregular rows. *Pentad hairs.*  $\alpha$ , 2 to 6;  $\beta$ , 1;  $\gamma$ , 9 to 15;  $\delta$ , 1;  $\epsilon$ , 5 to 9;  $\gamma$  distinctly plumose and remainder non-plumose. *Siphon.* Siphonal index approx. 3.6. *Baso-siphonal projection.* Longer than wide and narrower in centre than at apex, as in Fig. 4. *Pecten.* 15 to 32 spines. *Apico-dorsal hairs.* Present as a pair of small single hairs. *Valve hairs.* Each ventral valve bears a small hair at its apex, and at its base, either a single hair or a tuft of 2 or 3 larger hairs. Each latero-dorsal valve bears either a single or double hair. *Siphonal hair tufts.* One pair of ventro-lateral hair tufts of 7 to 12 hairs, distinctly plumose. In 2 specimens out of 50 examined, three pairs of very minute hair tufts, each consisting of 2 hairs, were observed in a dorso-lateral position on the siphon. *Saddle.* Extends slightly less than half the distance from the mid-dorsal to the mid-ventral line, and shows very minute projections on its posterior margin. *Saddle hairs.* May be single, or a tuft of 2 or 3 non-plumose hairs on each side. *Dorsal brush.* One pair of long single hairs, and a pair of shorter hair tufts each composed of 6 to 11 hairs. *Ventral brush.* 14 to 18 cratal tufts of 6 to 12 hairs, arising from a well-marked grid. *Anal papillae.* Slightly longer than the saddle. *Pecten spines and comb scales.* As in Fig. 4, with slight variations.

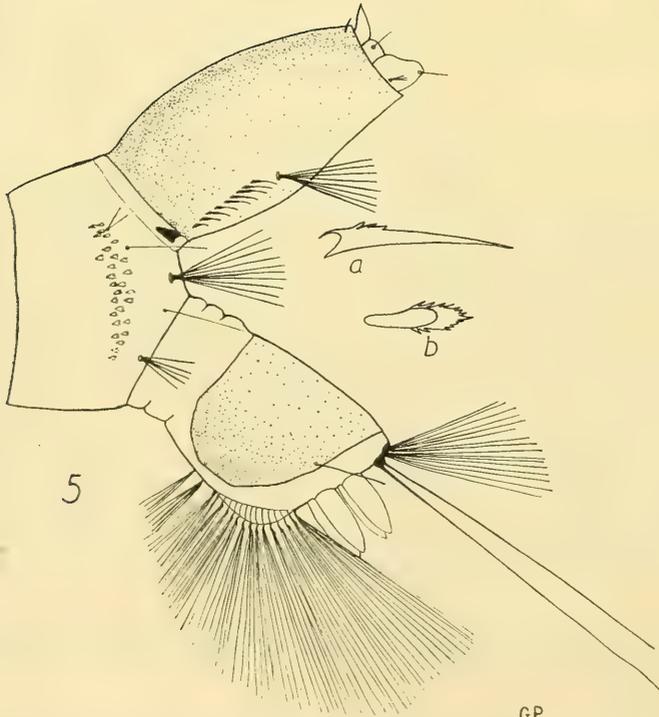
*Breeding Places.*—This is one of the commonest species found in freshwater rock pools, and also occurs in freshwater swamps and soakings, but has not been recorded as breeding in artificial containers in or near dwellings.

AÈDES (OCHLEROTATUS) VIGILAX Skuse. Fig. 5.

*Lateral comb.* Approx. 19 to 28 scales in 2 to 3 irregular rows. *Pentad hairs.*  $\alpha$ , 2 to 4;  $\beta$ , 1;  $\gamma$ , 6 to 10;  $\delta$ , 1;  $\epsilon$ , 3 to 5; in the majority of specimens all these hair tufts are non-plumose, but a small percentage shows plumosity on  $\gamma$ . *Siphon.* Siphonal index approx. 2.3. *Baso-siphonal projection.* Wider at apex than base, as in Fig. 5. *Pecten.*



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G.P.

Fig. 4.—*Aedes (Finlaya) alboannulatus* Macquart  $\times 42$ . *a*, pecten spine  $\times 335$ ; *b*, lateral comb scale  $\times 335$ .

Fig. 5.—*Aedes (Ochlerotatus) vigilax* Skuse  $\times 42$ . *a*, pecten spine  $\times 335$ ; *b*, lateral comb scale  $\times 335$ .

5 to 11 spines. *Apico-dorsal hairs*. A pair of small single hairs. *Valve hairs*. Each ventral valve bears a single hair at its apex, and at its base a tuft of 3 hairs. Each latero-dorsal valve bears a single hair. *Siphonal hair tufts*. One pair of ventro-lateral hair tufts of 8 to 12 hairs, usually non-plumose but occasionally showing some plumosity varying from very fine to quite obvious. *Saddle*. Extends nearly to mid-ventral line, with no spines visible under the binocular microscope. *Saddle hairs*. Either a single hair on each side, or absent. *Dorsal brush*. One pair of long single hairs, and a pair of shorter hair tufts each composed of 6 to 9 hairs. *Ventral brush*. 14 to 16 cratal tufts each of 4 to 9 hairs, arising from a well-marked grid, and either 1 or 2 pre-cratal tufts of 4 to 5 hairs each. *Anal papillae*. Slightly less than half the length of the saddle. *Pecten spines and comb scales*. As in Fig. 5, with slight variations.

*Breeding Places*.—This species breeds in enormous numbers in salt or brackish muddy pools at the margin of tidal swamps, but not in the portion of the swamp where tidal water runs in and out daily. An outbreak of this species is often associated with exceptionally high tides. It has also been recorded breeding in swampy freshwater pools, but has not been found breeding in large numbers in inland districts.

*AÈDES (PSEUDOSKUSEA) CONCOLOR* Taylor. Fig. 6.

*Lateral comb*. Approx. 90 to 110 small scales, in 8 to 9 irregular rows. *Pentad hairs*.  $\alpha$ , usually absent, occasionally present as a tuft of 2 very small hairs;  $\beta$ , 2 to 3;  $\gamma$ , 6 to 12;  $\delta$ , 1 to 4;  $\epsilon$ , 2 to 5;  $\gamma$  well developed and plumose, remainder simple and weakly developed. *Siphon*. Siphonal index approx. 2.1. *Baso-siphonal projection*. Absent. *Pecten*. 8 to 18 spines. Frequently the row of spines is not continuous, a small series of 2 to 4 spines at the base of the siphon appearing as a separate clump. *Apico-dorsal hairs*.

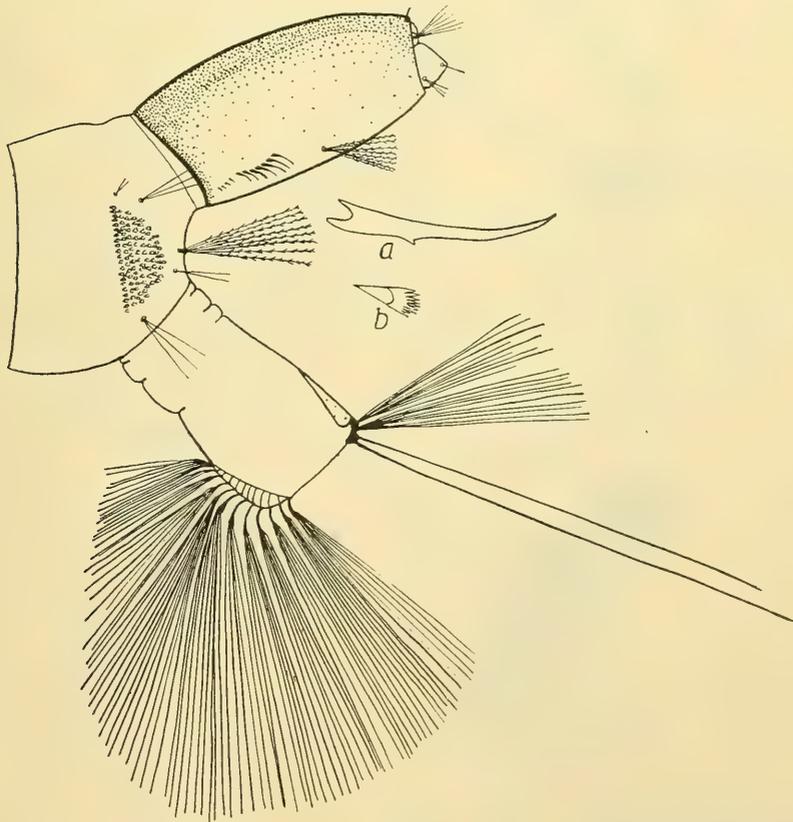


Fig. 6.—*Aedes (Pseudoskusea) concolor* Taylor  $\times 42$ . *a*, pecten spine  $\times 335$ ; *b*, lateral comb scale  $\times 335$ .

A well-developed single hair on each side. *Valve hairs*. Each ventral valve bears at its apex 1 to 2 hairs, and at its base a tuft of 2 to 6 hairs. The latero-dorsal valves bear a tuft of 3 to 6 hairs. *Siphonal hair tufts*. One pair of ventro-lateral plumose tufts of 4 to 12 hairs. *Saddle*. Extremely small, extending less than half-way to the base of the segment, and less than one-quarter of the distance from the mid-dorsal to the mid-ventral line. *Saddle hairs*. Absent. *Dorsal brush*. One pair of long single hairs, and a pair of shorter tufts each of 8 to 10 hairs. *Ventral brush*. 12 to 16 cratal tufts of 8 to 9 hairs, arising from a well-marked grid. *Anal papillae*. Absent. When the rectum is protruded four small rounded internal papillae are just visible, as previously described (Woodhill, 1938). *Pecten spines and comb scales*. As in Fig. 6, with slight variations.

*Breeding Places*.—This species breeds only in salt or brackish rock pools at or slightly above high-tide mark (Woodhill, 1936).

*AÈDES (MUCIDUS) ALTERNANS* Westwood. Fig. 7.

Unfortunately sufficient material of this species was not available, so that it was not possible to determine the range of variation in the various structures, and the following description is based on a few specimens only.

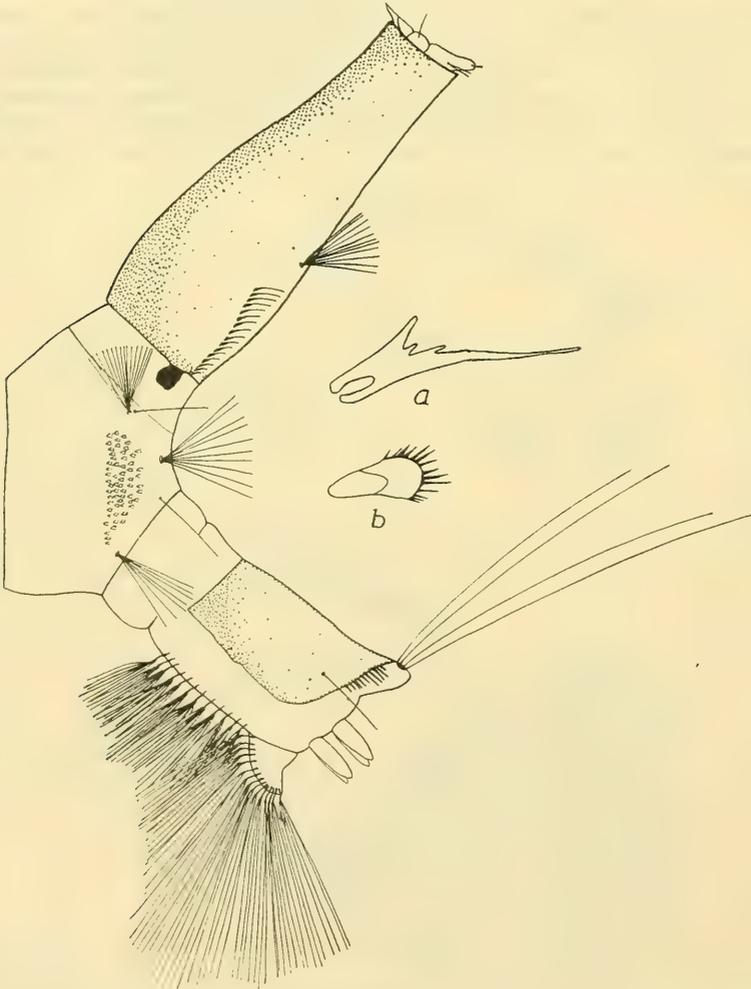


Fig. 7.—*Aedes (Mucidus) alternans* Westwood  $\times 27$ . a, pecten spine  $\times 335$ ; b, lateral comb scale  $\times 335$ .

*Lateral comb.* Approx. 60 scales in 4 to 5 irregular rows. *Pentad hairs.* Approx. numbers,  $\alpha$ , 16;  $\beta$ , 1;  $\gamma$ , 10;  $\delta$ , 1;  $\epsilon$ , 7; all tufts non-plumose. *Siphon.* Siphonal index approx. 3.1. *Baso-siphonal projection.* Roughly rectangular, and not markedly constricted at base, as in Fig. 7. *Pecten.* Approx. 16 spines. *Apico-dorsal hairs.* A small single hair on each side, often situated on the apical margin. *Valve hairs.* Each ventral valve bears a single hair at its apex and a double hair at its base, and each latero-dorsal valve bears a single hair. *Siphonal hair tufts.* One pair of ventro-lateral hair tufts, each tuft having approx. 11 non-plumose hairs. *Saddle.* Extends approx. two-thirds of the distance from the apex to the base of the segment, and approx. two-thirds of the distance from the mid-dorsal to the mid-ventral line, and bears pronounced spines on its posterior dorsal margin. *Saddle hairs.* A single well-developed hair on each side. *Dorsal brush.* Two pairs of single hairs. *Ventral brush.* In the position in which the grid is usually found a projection occurs, on which are borne approx. 15 tufts, each of 5 or 6 hairs. In shrunken specimens this projection is withdrawn. In

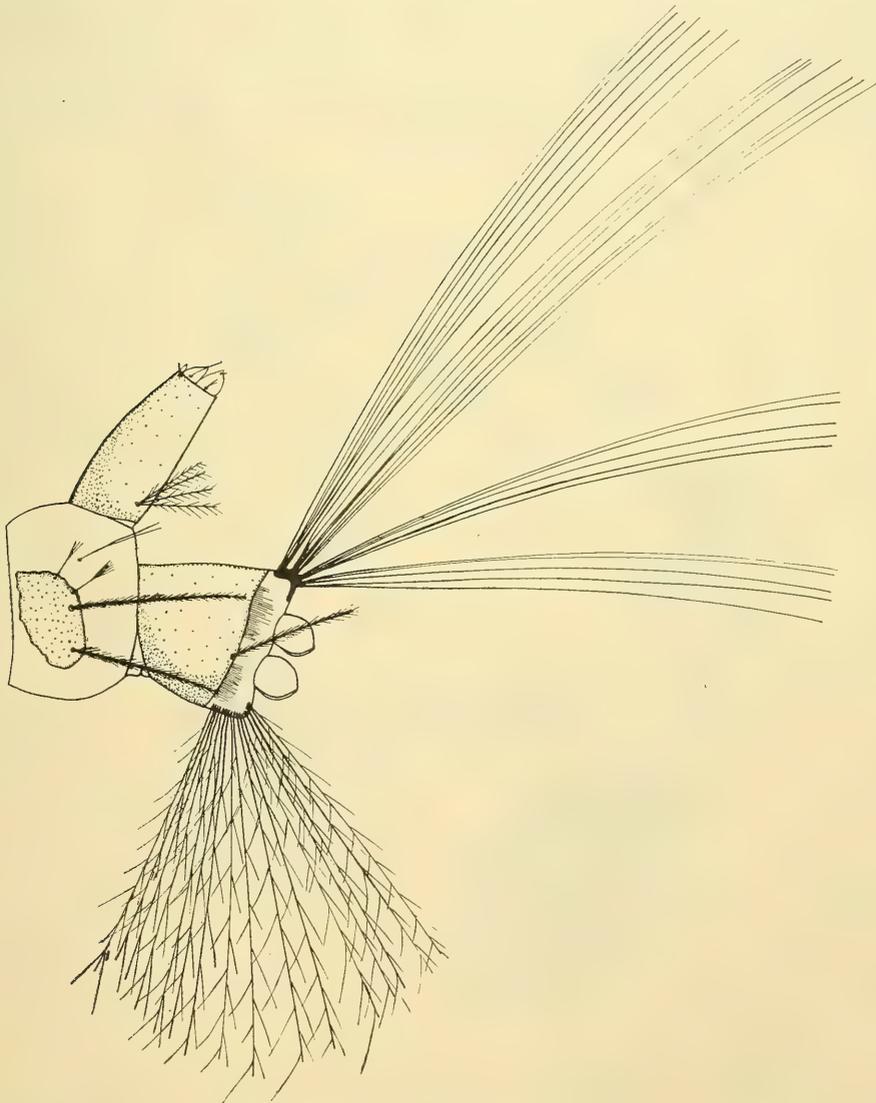


Fig. 8.—*Megarhinus speciosus* Skuse  $\times 17$ .

addition a series of 12 hair tufts, each of 5 to 7 hairs, extends along the ventral margin to a point in line with the anterior margin of the saddle. All of these 27 hair tufts arise from transverse chitinous bars, but there is no chitinous border, hence the structure cannot accurately be described as a grid. *Anal papillae*. Very small, narrow and pointed, approx. 0.3 times as long as the saddle. *Pecten spines and comb scales*. As in Fig. 7, with slight variations.

*Breeding Places*.—This species breeds in swamps or swampy pools, which may be either salt (Mackerras, 1926, Cooling, 1924), or fresh, and it occurs in both coastal and inland areas. The larvae are predacious, feeding on other mosquito larvae.

MEGARHINUS SPECIOSUS Skuse. Fig. 8.

*Lateral comb*. Absent. Situated somewhat anteriorly to the normal position of the lateral comb is a chitinized pigmented plate, bearing 2 small hairs, which may either be simple or may have up to 6 small branches at their apices, and 2 very large single plumose hairs, as in Fig. 8. *Pentad hairs*. These are represented by 1 hair tuft only, of 1 to 3 hairs. This may be the equivalent of either  $\alpha$  or  $\beta$ . *Siphon*. Siphonal index approx. 2.3. *Baso-siphonal projection*. Absent. *Pecten*. Absent. *Apico-dorsal hairs*. A small single hair on each side. *Valve hairs*. Each ventral valve bears a single hair at the apex and a tuft of 2 to 3 hairs at the base, and each latero-dorsal valve bears a single hair. *Siphonal hair tufts*. One pair of ventro-lateral tufts, each tuft bearing 2 to 6

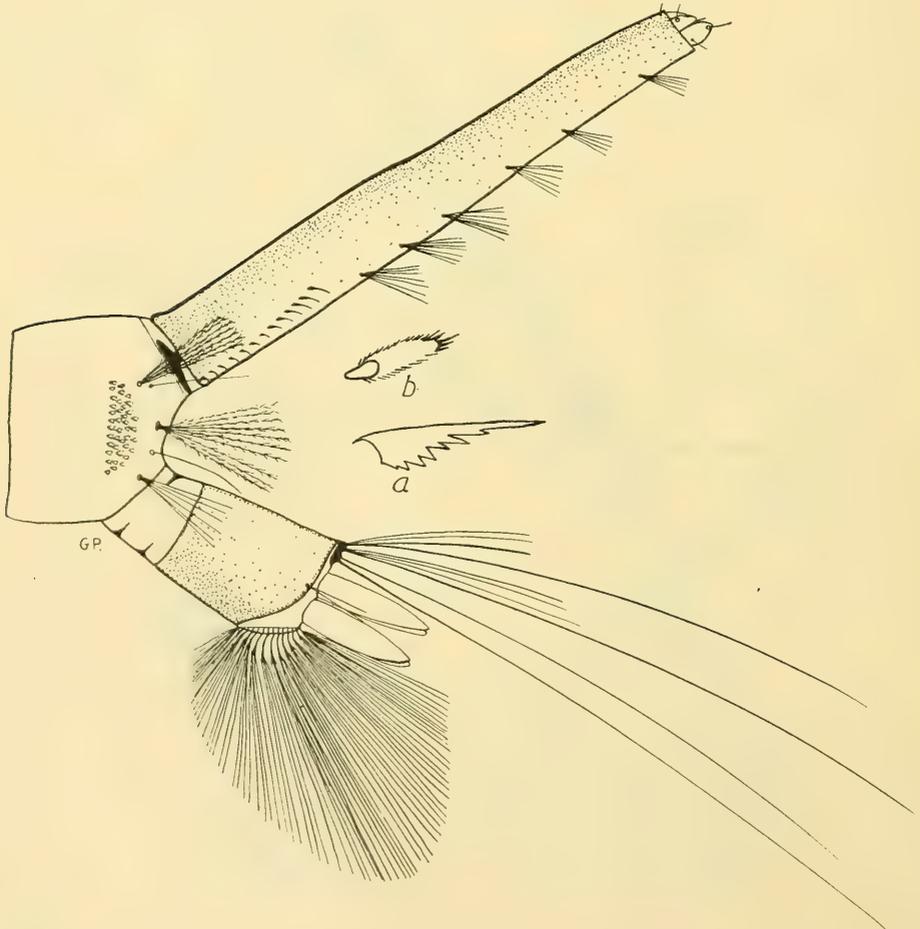


Fig. 9.—*Culex (Culex) annulirostris* Skuse  $\times 42$ . a, pecten spine  $\times 335$ ; b, lateral comb scale  $\times 335$ .

plumose hairs. *Saddle*. Forms a complete ring round the terminal segment and dorsally extends to the base of the segment. The posterior lateral margin of the saddle bears a row of conspicuous spines. *Saddle hair*. A single large plumose hair on each side. *Dorsal brush*. Two pairs of hair tufts, the ventral tufts bearing 3 to 5 hairs each and the dorsal tufts 5 to 8 hairs. *Ventral brush*. 10 to 18 long single plumose hairs. These hairs arise from the normal position of the cratal hairs but can hardly be described under that term, since they arise from chitinous bands without the chitinous margin, so that a true grid is not formed. *Anal papillae*. Short and rounded, approx. 0.3 times as long as the saddle.

*Breeding Places*.—These larvae occur in artificial containers, rain-water tanks, etc., and in tree holes, and are predacious on other species of mosquito larvae.

CULEX (CULEX) ANNULIROSTRIS Skuse. Fig. 9.

*Lateral comb*. Approx. 35 to 55 scales in 4 to 5 irregular rows. *Pentad hairs*.  $\alpha$ , 4 to 7;  $\beta$ , 1;  $\gamma$ , 7 to 10;  $\delta$ , 1;  $\epsilon$ , 5 to 7;  $\alpha$  and  $\gamma$  plumose, remainder simple. *Siphon*. Siphonal index approx. 7.2. *Baso-siphonal projection*. Very wide, and strongly constricted

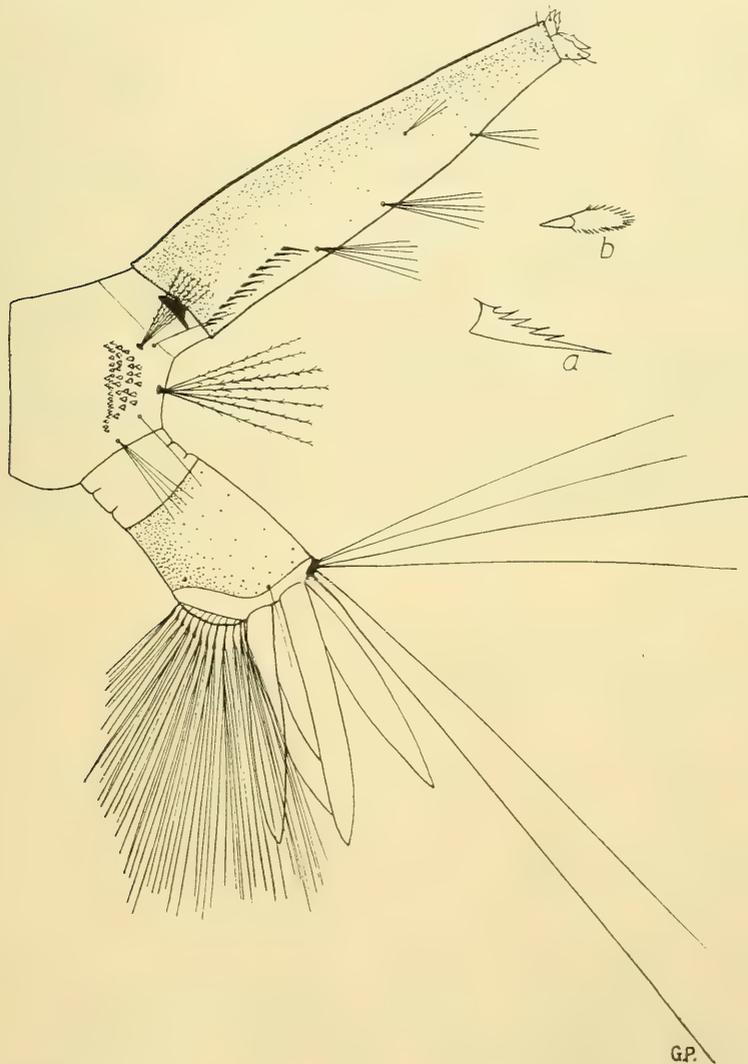


Fig. 10.—*Culex (Culex) fatigans* Wiedemann  $\times 42$ . *a*, pecten spine  $\times 335$ ; *b*, lateral comb scale  $\times 335$ .

at base as in Fig. 9. *Pecten*. 11 to 15 spines. *Apico-dorsal hairs*. A small single hair on each side. *Valve hairs*. Each ventral valve bears a single hair at the apex and the base, and each latero-dorsal valve bears a single hair. A single hair arises from the inner margin of the base of the medio-dorsal valve. *Siphonal hair tufts*. Six pairs of non-plumose ventro-lateral hair tufts, the number of hairs in each tuft varying from 3 to 9. *Saddle*. Forms a complete ring round the terminal segment. *Saddle hairs*. A tuft of 2 to 4 non-plumose hairs on each side. *Dorsal brush*. Two pairs of long single hairs, and 1 pair of shorter tufts, each tuft consisting of 3 to 4 hairs. *Ventral brush*. 12 to 14 cratal tufts, each of 7 to 8 hairs, arising from a well-marked grid. *Anal papillae*. From 0.6 to 0.8 times as long as the saddle. *Pecten spines and comb scales*. As in Fig. 9, with slight variations.

*Breeding Places*.—These larvae occur in fresh and brackish pools, or swamps, and are found in both inland and coastal districts. The larval stage of this mosquito has never been clearly differentiated from that of *Culex (Culex) sitiens* Wiedemann, which is stated to breed only in salt-water.

CULEX (CULEX) FATIGANS Wiedemann. Figs. 10, 11.

*Lateral comb*. Approx. 30 to 50 scales arranged in 4 to 5 irregular rows. *Pentad hairs*.  $\alpha$ , 4 to 7;  $\beta$ , 1;  $\gamma$ , 5 to 9;  $\delta$ , 1;  $\epsilon$ , 3 to 6;  $\alpha$  and  $\gamma$  plumose, remainder simple. *Siphon*. Siphonal index extremely variable, from 3.4 to 6.5 (Fig. 11). *Baso-siphonal projection*. Very wide and constricted at base, as in Fig. 10. *Pecten*. 8 to 14 spines. *Apico-dorsal hairs*. A small single hair on each side. *Valve hairs*. Each ventral valve bears a single hair at the apex and the base, and each latero-dorsal valve bears a single hair. A single hair arises from the inner margin of the base of the medio-dorsal valve. *Siphonal hair tufts*. Usually 3 pairs of ventro-lateral tufts and 1 pair of lateral tufts, all non-plumose. The two basal pairs of ventro-lateral tufts vary from 3 to 9 hairs each, the apical pair varies from 2 to 4 hairs in each tuft, while the lateral pair varies from 2 to 3 hairs in each tuft. These tufts, however, are variable and there may be 4 pairs of ventro-lateral tufts, or 3 tufts on one side and 4 on the other. The pairs may also be asymmetrically placed. These variations are shown from the ventral aspect in Fig. 11, the position of the tufts being indicated by dots. All variations shown have been found to occur in larvae from a single egg-raft. It is probable also that some larvae showing 2 pairs of lateral tufts are also *C. fatigans*, but this has not yet been definitely confirmed. *Saddle*. Forms a complete ring round the terminal segment. *Saddle hairs*. Either 1 hair or a tuft of 2 hairs, on each side, never plumose. *Dorsal brush*. One pair of long single hairs, and 1 pair of shorter tufts each varying from

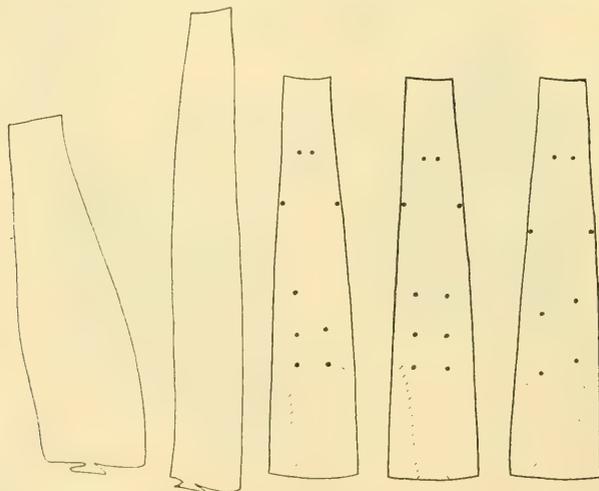


Fig. 11.—*Culex (Culex) fatigans* Wiedemann. Variations in siphonal index and siphonal hair tufts  $\times 36$ .

2 to 3 hairs. Occasionally one of these shorter tufts may only be represented by a single hair. *Ventral brush*. 10 to 12 cratal tufts, each of 4 to 7 hairs arising from a well-marked grid. *Anal papillae*. Usually about 1.7 times as long as the saddle. *Pecten spines and comb scales*. As in Fig. 10, with slight variations.

*Breeding Places*.—This is one of the common domestic mosquitoes, always breeding in or near human dwellings. It prefers foul water, but also breeds in clean water, and occurs in ground water as well as in artificial containers, thus differing in its habits from *Aedes (Stegomyia) aegypti* Linnaeus. This species will not develop in water with a salinity greater than 14 gm. of salts per litre (Woodhill, 1938).

*Key to Species of Larvae.*

1. Siphon with only one pair of hair tufts ..... 2
2. Siphon with four or more pairs of hair tufts ..... 8
3. No pecten, no lateral comb, a chitinized plate bearing two large and two small hairs on each side of 8th segment ..... *Megarhinus speciosus* Skuse (Fig. 8)
- Pecten and lateral comb present, no such chitinized plate in 8th segment ..... 3
4. Saddle extending less than half-way from apex to base of 9th segment, and less than one-quarter of the distance from the mid-dorsal to the mid-ventral line ..... *Aedes (Pseudoskusea) concolor* Taylor (Fig. 6)
- Saddle extending at least three-quarters of the way from apex to base of segment, and at least two-fifths of the distance from the mid-dorsal to the mid-ventral line ..... 4
5. Lateral comb, consisting of a single row of seven to twelve scales, baso-siphonal projection absent ..... *Aedes (Stegomyia) aegypti* Linnaeus (Fig. 2)
- Lateral comb of twenty or more scales, arranged in several irregular rows, baso-siphonal projection present ..... 5
6. Tufts of ventral brush extending at least three-quarters of distance from apex to base of 9th segment, posterior tufts of ventral brush rising from a distinct projection, no chitinous margin surrounding transverse bars from which tufts arise ..... *Aedes (Mucidus) alternans* Westwood (Fig. 7)
- Tufts of ventral brush not extending more than half-way from apex to base of 9th segment, posterior tufts not arising from a projection, and a distinct chitinous margin surrounding the transverse bars to form a true grid ..... 6
7. Saddle not extending below the mid-lateral line ..... *Aedes (Finlaya) alboannulatus* Macquart (Fig. 4)
- Saddle extending at least three-quarters of the distance from the mid-dorsal to the mid-ventral line ..... 7
8. One or two pre-cratal tufts present, saddle not bearing posterior dorsal spines ..... *Aedes (Ochlerotatus) vigilax* Skuse (Fig. 5)
- No pre-cratal tufts present, saddle bearing conspicuous posterior dorsal spines ..... *Aedes (Finlaya) notoscriptus* Skuse (Fig. 3)
9. Three or four pairs of ventro-lateral, and one pair of lateral siphonal tufts ..... *Culex (Culex) fatigans* Wiedemann (Figs. 10, 11)
- Six pairs of ventro-lateral, and no lateral siphonal tufts ..... *Culex (Culex) annulirostris* Skuse (Fig. 9)

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## AUSTRALIAN HESPERIIDAE. X.

ON HESPERILLA DONNYSA HEWITSON, 1868.

By G. A. WATERHOUSE, D.Sc., B.E., F.R.E.S.

[Read 27th August, 1941.]

This species was named by Hewitson in 1868, when in *Descriptions Hesperidae*, pt. ii, p. 39, he described a male and female giving as locality Australia (Moreton Bay). In his *Exotic Butterflies*, v, 1874, he described and figured the upperside of the male from the same locality, but omitted any mention of the female. In Kirby's *Catalogue of the Hewitson Collection*, 1879, p. 235, one specimen only is given with the locality Australia. I have seen the holotype male in the British Museum, which has a label "Austl." in Hewitson's handwriting, and have before me an excellent coloured drawing of it, which was carefully checked by Brigadier H. W. Evans and myself. It should be noted that the size given for *donnysa* is the same as Hewitson gave for *petalia* and *doctea*, described in 1868 at the same time. Therefore, as the holotype shows, it is not a very large specimen. Also these two species, as well as others, were from Moreton Bay and still have that locality label in Hewitson's handwriting.

I have reviewed this species and its races in *These PROCEEDINGS*, 1927, p. 278; 1932, p. 226; 1937, p. 118. I was never satisfied that Brisbane (Moreton Bay) was the correct locality for the holotype, but until last year I had seen only one poor male from the Brisbane district. Dr. C. P. Ledward has now bred several specimens at Burleigh Heads, about fifty-five miles south of Brisbane and from a similar type of country as no doubt existed near Brisbane in the earlier days. These specimens are distinctly larger than the holotype and somewhat different.

Both descriptions and figure given by Hewitson agree fairly well with the holotype male. His description of the female in 1868 as "without the small yellow spot of the anterior wing and the central orange of the posterior wings" shows it is not the female of *donnysa*. Females in all the races always have these characters. Hewitson must have realized this later, as he omits mention of the female in 1874 and there was only one specimen of *donnysa* in his collection over this name when he died. My suggestion is that his so-called female of 1868 had the label Moreton Bay and this locality was unwittingly transferred to his description of 1874. There is nothing to show that the holotype male had any locality beyond Australia as far as Hewitson was concerned. In 1936, I carefully searched for Hewitson's Australian specimens and found nearly all those mentioned by Kirby. I was not able to find any specimen that I could consider the so-called female of *donnysa*, 1868.

Since there is no direct evidence that the holotype came from Moreton Bay—indeed the evidence points the other way—it is necessary to select a suitable locality for it. Six entomologists have selected specimens from Sydney as agreeing best with the coloured drawing in my possession, four of them having picked the same specimen. I, therefore, select Sydney as the locality of the holotype. This conforms best with what is known, and the food-plant of the larvae was growing within five miles of the centre of Sydney a few years ago and is still found a little further away.

## HESPERILLA DONNYSA Hewitson, 1868.

This is the most widespread of that peculiarly Australian subfamily, the Trapezitinae. I have found some stage of its life-history in all the Australian States. On the east coast it extends as far north as Brisbane and on the west coast as far north as Geraldton. As well as being found within a few yards of the sea, it also occurs in the mountains up to 3,500 feet in New South Wales, Victoria, South Australia and Tasmania. The food-plants of the larvae are several species of *Gahnia*, differing in different localities and at different altitudes. The larva and pupa have been figured by me in "What Butterfly is That?", 1932, Pl. xxxi. The pupal head piece is very distinctive and does not vary to any appreciable extent in the various races.

Owing to its wide range, it is not surprising that it has developed into races. As a general rule the southern races have the markings on the upperside darker in colour and these usually have in the female one or two spots below the orange patch of the hindwing. Specimens from the sea coast are generally a paler brown above than those from the mountains. The individuals of the various races vary amongst themselves. This is not surprising as I have selected for the collection in the Australian Museum over 400 specimens from at least 1,000 specimens that have passed through my hands. It is difficult to give a general description that will cover all the races, but the following will be sufficient to denote the species and fuller details of the subspecific differences are given later.

*Male.* Forewing, apex acute, termen nearly straight. Above brown, with a large spot near end of cell, usually three small subapicals not always in a straight line, sometimes small spots in 4 and 5, larger spots in 2 and 3, these spots hyaline, usually with an opaque spot in 1a, sex mark from vein 4 nearly to termen. Hindwing brown with a central opaque patch. Forewing beneath, apex grey, hyaline spots as above, remainder of cell yellowish, a whitish patch on dorsum near tornus. Hindwing grey to brown with a spot in centre of cell, beyond which is a series of five spots *in a straight line* and another near base of 6.

*Female.* Forewing with termen not so straight as in male, all hyaline spots usually larger, usually hyaline spots in 4 and 5, always an opaque spot in 1a, sometimes another above it. Hindwing with central patch more conspicuous than in male. Beneath as in male.

Besides the shape of the wings, the most important character is the row of five spots *in a straight line* on hindwing beneath. These are variable in size and very rarely one or more may be absent. They may be small brown dots, but when large they often appear as dark rings with pale centres. This is more often found in the cell spot and the spots at either end of the straight line of spots; sometimes there is an additional spot in 7.

The holotype male *donnysa* is in the British Museum, those of the races in the Australian Museum, Sydney.

H. DONNYSA DONNYSA Hew., 1868. Male. Forewing above typically with moderate cell spot, three subapicals not in a straight line, moderate spots in 2 and 3, all yellow hyaline, a small opaque spot in 1a, yellow, sex mark thin, black from vein 4 nearly to termen. Hindwing with central darker yellow patch divided by veins 3 and 4. Beneath, apex of forewing and hindwing grey to reddish-grey, forewing with cell almost wholly yellow and pale patch on dorsum; hindwing with dots brown and small. Female. Larger than male, above spots larger and darker; beneath much as in male. It is double brooded.

I have before me seven males, bred by me from within a few miles of Sydney. Four of these have, as in the holotype, one opaque spot in 1a of forewing, two with none and one with two. Also six females, one of which has rings with paler centres on the underside of the hindwing. These were all bred by me from pupae found on a coarse species of *Gahnia* growing near the coast. Some further distance away they have been found on at least two other species of *Gahnia*. Specimens of this race in the Australian Museum Collection are from National Park to Lake Macquarie. The underside is figured in These PROCEEDINGS, 1927, Pl. xxvi, fig. 6.

H. DONNYSA ICARIA, n. subsp. I have before me one male, two females from Burleigh Heads, S. Qd., and an old male from Stradbroke I. The male is larger and darker brown than the typical race and the spots are smaller and paler, especially that of the hindwing. The holotype male (Burleigh, 19.x.1940) has the three subapicals in a straight line with a minute dot below and there is no opaque spot in 1a. Beneath, the apex of forewing and the hindwing are pinkish-grey and there are brown spots in 6 and 7. Dr. C. P. Ledward has two males, neither having the dot below the subapicals, one has no opaque spot in 1a, the other a minute dot. Both have the pinkish-grey underside. The females differ in the same way from females of the typical race. None have spots in 4 and 5 of the forewing. In one specimen the underside has the pink much deeper in colour. Dr. Ledward has bred this race in small numbers in spring and autumn. The larvae feed on *Gahnia erythrocarpa*. No specimens of *donnysa* have been recorded

from between Burleigh and Lake Macquarie, but some years ago I saw two females taken on the Richmond River, N.S.W.

**H. DONNYSA SAMOS, n. subsp.** This is a small dark mountain race. Male. Above with spots smaller and paler, especially the three subapicals, of which the middle is the smallest. The holotype male has an opaque spot in 1a, but in others this may be absent. The general colour on the underside is grey; the cell of the forewing has the yellow restricted so that the cell spot is very prominent; there is an additional brown spot in 7 on the hindwing. The female is similar to the male, but of different shape and larger. The holotype male is from a series of five males and three females from Blackheath, N.S.W., bred in November and December, 1934; a male of the series has only the lowest subapical spot present, and sometimes the spots of the underside of the hindwing are brown rings.

This race is very common on the Blue Mts., above 2,000 ft. I have collected extensively there and found it only in November and December with one specimen on 1st January, so it seems to have only one brood. The larvae feed on *Gahnia microstachya*. It is figured as *donnysa* in Butt. Aust., 1914, fig. 634, and 1927, Pl. xxvi, figs. 1, 2.

**H. DONNYSA PATMOS, n. subsp.** This is the Victorian race. It is about the size of the previous race, but the general colour above is paler brown and the spots are larger. In the holotype male and others there are two opaque spots in 1a of the forewing. The patch on the hindwing is larger. On the underside the cell of forewing generally has a greater extent of yellow. The general colour is variable and some of the spots of the hindwing may be brown rings. The female is similar to the male, larger and of different shape. The holotype male is from a series of eight males and five females from Mt. Evelyn (A. L. Brown) taken in November and December, 1933. One of the males has a spot in 5 of the forewing and a female a spot in cell, above the patch of hindwing on the upperside.

It is a common species in the Dandenong Ranges where it has been taken from November to 8th January in many localities. It has also been taken near Moe and near Gisborne. Specimens from the eastern side of Port Phillip on the flat country also seem to belong to this race which apparently has only one brood. It is figured as *donnysa* in Butt. Aust., 1914, fig. 633.

**H. DONNYSA FLAVESCENS** Waterh., 1927. This is the very yellow race from the volcanic soil of Altona Bay on the western shore of Port Phillip. Since I described this distinctive race, I have had more specimens from the same locality. The male usually has hyaline spots in 4 and 5 and usually two opaque spots in 1a. On the hindwing in some specimens there are one or two spots below the central patch. To the female the same applies, but the spots are larger, sometimes appearing as an almost continuous band from costa to 1a. One specimen has an extra spot on costa above subapicals. On the hindwing there are usually two spots below the central patch. Beneath in both sexes the colour is very much paler than in the other races and the spots of the hindwing may be brown dots or larger rings with pale centres.

It is found in spring and autumn. My dates are 2nd October to 25th November and 22nd February to 4th April. The larvae feed on a different plant to the other Victorian race. It is figured, 1927, Pl. xxvi, figs. 17, 18.

**H. DONNYSA AURANTIA** Waterh., 1927. This is the Tasmanian race and the markings above are very much deeper in colour than any of the other races. The patch on the hindwing is bright orange and sometimes there are one or two spots below it. At an altitude it has only one brood in January and February, but at the sea coast it probably has two broods. The larvae no doubt feed on *Gahnia* as I have caught it settled on this plant on Mt. Wellington. It is figured, 1927, Pl. xxvi, figs. 5, 21, 22.

**H. DONNYSA DILUTA** Waterh., 1932. This race was described from Mundoo I., near Goolwa, S. Aust. Ten specimens were caught there by Mr. F. M. Angel in March, 1907, flying about *Gahnia trifida*. At that time I doubt if more than five other specimens of *donnysa* were known from South Australia. Since then, thanks to the efforts of F. M. Angel, F. E. Parsons and M. W. Mules, over 100 specimens are in the Australian Museum from many localities and they possess numerous specimens themselves. From an examination of these specimens three races are now indicated from South Australia. With this Mr. Angel concurs and has arrived at the same distribution from the available

material as I have done. As better specimens are now available, I would add that *diluta* is as variable as the other races, paler in colour, both above and beneath, than races from an altitude and rarely has any spots below the patch of the hindwing. The sex mark in the male is duller and slightly wider than the typical race. On the underside there is generally a pinkish suffusion.

I would place specimens from Kingston and Robe with this race as well as a male from Tintinara sent me by Mr. Parsons. It is found in spring and autumn.

**H. DONNYSA FLAVIA, n. subsp.** This is the yellowish race from the coast near Adelaide and is somewhat like the race *flavescens* from Victoria. Male. Above, pale brown with basal half more or less covered with yellow scales; forewing with three pale subapicals, a small pale spot 5, darker spots in cell and 2 and 3, all hyaline, two opaque spots in 1a, sex mark dull black; hindwing with large central orange patch and often two spots below this and one above. The underside usually has a pinkish tint and the markings of the hindwing may be brown rings with pale centres or brown dots. The female is considerably larger and the spots larger and elongated, especially those in 2 and 3; on the hindwing most specimens have two spots below the orange patch and many a spot above it.

The holotype male is from a series from West Beach (Angel, 9.x.1938) and I have others very similar to it from near Henley Beach (Parsons). It is a variable race, the spot in 5 is sometimes absent and that in 4 may be present or absent. Some females have the yellow suffusion very extended. The larvae feed on *Gahnia trifida* and although the food-plant is abundant, seem to confine themselves to certain patches. The spring brood occurs from September to November and is on the wing six weeks before the race from the Ranges. The autumn brood is found in March and April and has the yellow suffusion more restricted.

**H. DONNYSA DELOS, n. subsp.** This is the fine dark race from the Mt. Lofty Ranges. I have selected the holotype from a series from Mt. Lofty (Mules, Nov. 1933). Male. Above, dark brown, large cell spot with a silky sheen, three paler subapicals, spots in 2 and 3, hyaline, opaque spot in 1a; hindwing with central patch paler and rarely with one or two spots below it. Beneath more or less pale brown with markings of hindwing usually brown dots, but cell spot often a brown ring with pale centre. Female much larger, spots larger and more markedly silky. A greater number of specimens have one or two spots below the patch of hindwing.

This race occurs in the Mt. Lofty Ranges at about 1,000 ft., wherever *Gahnia psittacorum* occurs. It has been recorded from 31st October to 6th December from Aldgate, Bridgewater, Mylor and Woodside. I would also place here specimens from Mt. Compass and Second Valley. Mr. Angel agrees with this. This is a very dark race compared with the previous one and very different from it. The spots below the central patch of the hindwing which are a feature of the previous race are not so often present in this. Some of the specimens are very large.

**H. DONNYSA ALBINA**, Waterh., 1932. This is the race from S.W. Australia, typically from Bunbury. It is separated from the others by the subapicals and spots in 2 and 3 of the forewing being whiter than the other races. I have had further specimens from Mr. Whitlock who has taken this race at Bunbury from 13th October to 10th December and from 27th February to 19th April.

**H. DONNYSA GALENA** Waterh., 1927. This is another yellowish race bred by me from pupae found on a species of *Gahnia* at Geraldton, W. Aust. It is figured, 1927, Pl. xxvi, figs. 9, 10, 13, 14.

From what I have set out above it will be seen that *H. donnysa* is a very remarkable and variable species. The amount of material to hand makes the limitations of the races somewhat difficult, as in some cases individuals of one race approach another. Some of the races would by some entomologists be considered distinct species. However, when seen in the cabinet they are easily recognized. It is quite possible that further races will be found in localities other than those mentioned above.

In addition to the friends mentioned above who have sent me specimens, I have to thank Mr. F. M. Angel for material help with the South Australian races and Mr. G. Lyell with the Victorian races.

## NOTES ON THE APHIDIDAE IN AUSTRALIA. I.

TWO APHIDS NEW TO NEW SOUTH WALES.

(HEMIPTERA: APHIDIDAE.)

By E. H. ZECK.

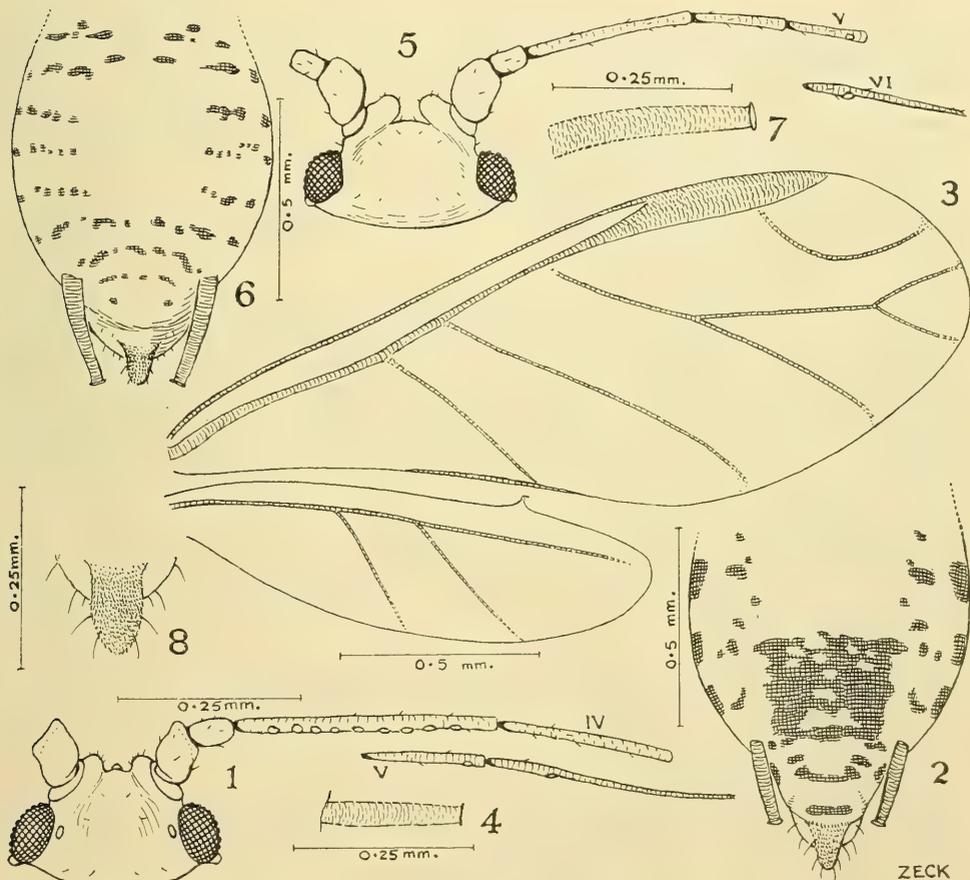
(Seventeen Text-figures.\*)

[Read 30th July, 1941.]

The main object of this paper is to record the occurrence in Australia of two aphids, *Myzus ornatus* Laing and *Rhopalosiphum lahorensis* (Das).†

*MYZUS ORNATUS* Laing. Figs. 1-8.

This aphid was described by Laing (1932) from specimens found infesting violets in Devon, England.



ZECK

Figs. 1-8.—*Myzus ornatus* Laing. Alate viviparous female. 1, Head and antenna; 2, Abdomen; 3, Wings; 4, Cornicle. Apterous viviparous female. 5, Head and antenna; 6, Abdomen; 7, Cornicle; 8, Cauda.

\* The figures were prepared from specimens mounted in Berlese's fluid, as modified by Swan (1936).

† This species is now considered to be identical with *Rhopalosiphum rufomaculatum* (Wilson) and is found in the U.S.A. on chrysanthemums.

Essig (1938) recorded and redescribed it. Specimens were first collected by him in Berkeley, California, on *Dipsacus fullonum* during April, 1936, and later he obtained them in Belgium on *Hedera helix* in gardens and afterwards in greenhouses on *Crotolaria anagyroides*, *Achyranthes* sp., *Lantana* sp. and *Acotropium peruvianum*. In 1937, Essig visited England, and there ascertained that Laing had collected the species on a considerable number of host plants, including *Salvia* and *Chrysanthemum* in various parts of the country. Essig records having taken specimens there himself on *Richardia rehmanni*, *Panax lancasteri* and *Buddleia orientalis* in greenhouses and on the young shoots of *Ulmus campestris*, *Urtica dioica*, *Geum urbanum*, *Lapsana communis*, *Salvia* sp., *Scabiosa* sp., *Teesdalia nudicalis*, apple and dandelion out of doors. On his return to California, he found this aphid on *Fuchsia elegans* and *Potentilla* sp., and records specimens being taken on *Ranunculus repens*, cultivated strawberry and heliotrope.

Mason (1940) gave a redescription and listed its hosts, which included some thirty-nine species of plants and gave its distribution as England, Scotland, Netherlands and California.

#### Brief Description.

*Alate Viviparous Female*.—Pale yellowish to greenish; head, thorax and antennae dusky; cornicles, cauda and anal plate pale dusky; abdomen with dusky central marking and smaller lateral markings; eyes red. Length (avg.) 1.4 mm.

*Apterous Viviparous Female*.—Pale yellowish to greenish; abdomen with small brownish lateral and dorsal markings; antennae pale, V and VI slightly dusky; eyes red; cornicles, cauda and anal plate slightly dusky. Length (avg.) 1.1 mm.

*Hab.*—Ryde, New South Wales, 12.v.1941 (Nance Zeck).

*Host.*—*Coleus* sp., grown indoors.

The mature aphids were found as more or less isolated individuals on the leaves, with a few progeny and not in colonies.

#### RHOPALOSIPHUM LAHORENSIS (Das). Figs. 1-9.

This aphid was described by Das (1918) from specimens found infesting cultivated chrysanthemums in Lahore, India, and for this species he erected the genus *Stephensonia*, which has since been considered by aphidologists to be congeneric with *Rhopalosiphum* Koch. P. v. d. Goot, in a footnote to Das' description (1918), doubted whether the characters of this aphid warranted a new genus and seemed to consider it might have been placed in the genus *Siphocoryne* Pass. and, indeed, in the second part of Das' paper containing the plates (Pl. xviii) it is placed as *Siphocoryne lahorensis* (Das).

Takahashi (1921) recorded this aphid in Formosa, on *Artemisia vulgaris* var. *indica* and *Siegesbeckia orientalis*, and again on the same plants in 1923. In 1924, he recorded it attacking *Chrysanthemum* sp.; and in 1931, he listed *Neaphis viridis* Nevsky as a synonym.

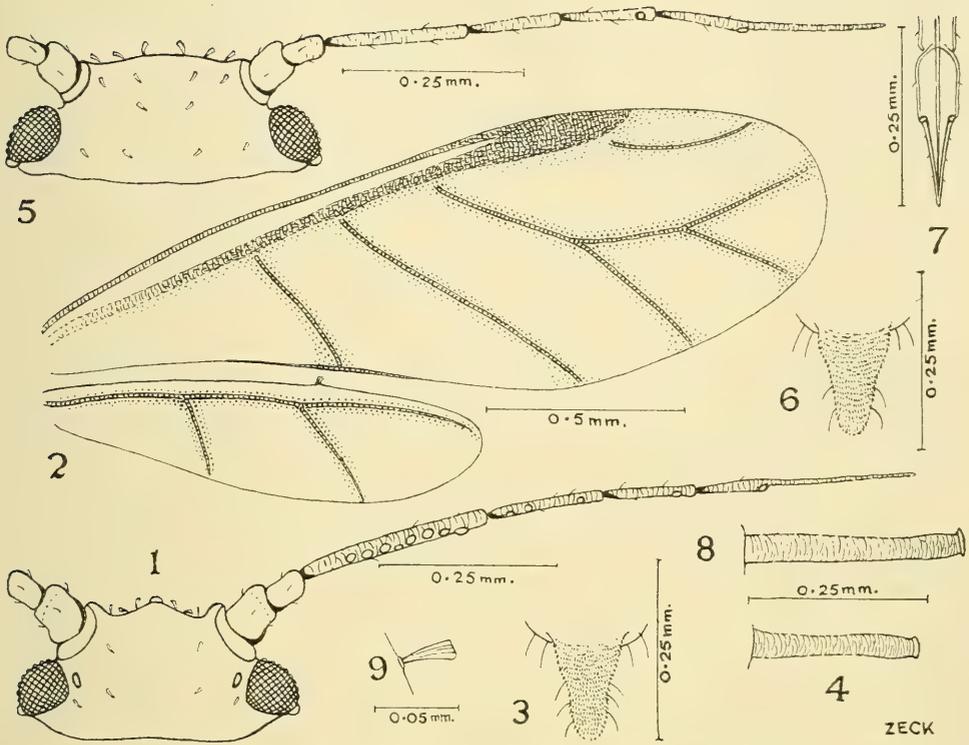
Willcocks (1922) recorded its occurrence in Egypt, where it was found infesting chrysanthemums. He stated that it appeared to be a rare species.

Hall (1926) again recorded its occurrence in Egypt on chrysanthemums, and stated: "Fairly common on chrysanthemums from the middle of March to the middle of June and again in November."

Theobald (1928) recorded it as being new to England, where it was found infesting chrysanthemums, and in the following year (1929) he again recorded it there.

#### Brief Description.

*Alate Viviparous Female*.—Shiny; head and thorax dark, almost black; antennae, except segments I, II and base of III black; eyes bright red; abdomen bright green with a few small, dark, lateral markings; cornicles, cauda and anal plate dusky, a dark marking between the cornicles; veins dark, with clouded borders, stigma dusky. Length (avg.) 1.5 mm.



Figs. 1-9.—*Rhopalosiphum lahorensis* (Das). Alate viviparous female. 1, Head and antenna; 2, Wings; 3, Cauda; 4, Cornicle. Apterous viviparous female. 5, Head and antenna; 6, Cauda; 7, Tip of rostrum; 8, Cornicle; 9, Spatulate body hair.

*Apterous Viviparous Female*.—Bright green, shiny; antennal segments I, II and III pale, IV dusky, V and VI black; eyes bright red; cornicles, cauda and anal plate dusky; a few small lateral markings on abdomen. Length (avg.) 1.7 mm.

*Hab.*—Ryde, New South Wales, 20.v.1941 (E. H. Zeck).

*Host.*—*Chrysanthemum* sp., out of doors.

This species was found mainly on the under surfaces of the leaves and to a lesser extent on the flower heads. Alate forms were not numerous in the colonies observed. Three other species of aphids, *Macrosiphum sanborni* Gill., *Myzus persicae* (Sulz.) and *Aphis gossypii* Glov., were found intermingled with it.

*Acknowledgements.*

I desire to thank Messrs. W. A. Rainbow and Frank H. Taylor, both of whom have been most generous in their assistance in making literature available to me.

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## MISCELLANEOUS NOTES ON AUSTRALIAN DIPTERA. VIII.

## SUBFAMILY LOMATIINAE.

By G. H. HARDY.

(Four Text-figures.)

[Read 30th July, 1941.]

The subfamily Lomatiinae was omitted from the revision of Australian Bombyliidae by Dr. F. H. S. Roberts (These PROCEEDINGS, liii, 1928, 90-144, 413-455, and liv, 1929, 443-583), but he made certain advances in his studies. Subsequently Dr. F. W. Edwards gave a new understanding in a paper which appeared in the *Encyclopedie Entomologique, Dipt.*, vii, 1934, 81-112, access to which is not easily obtained in Australia.

Edwards, who had examined many of the types, showed that earlier attempts to arrange species of *Comptosia* were not successful, and put forward a temporary plan of arranging them into groups and subgroups in accordance with certain structures and colouration. He gave subgeneric rank to two major divisions, and these prove stable, though his lesser groups fail to interpret affinities. Nevertheless his subgenus *Comptosia sensu stricto* rearranged, is formed by two natural groups, *Comptosia* and *Alyosia*, but for taxonomic purposes three groups are formed in this paper.

The Roberts collection and other specimens in the Queensland Department of Agriculture, those of the Queensland Museum, my own collection and sundry others, were taken into account for purposes of the present study. The forty-three species thus found comprise thirty-three species in common with most of the forty given by Edwards. There are, however, six names unplaced and ten species unnamed. One name proves to be preoccupied and Edwards wrongly attributed two names to the sexes of another species; for these, two new names are given below.

The type locality of the Diptera described by Macleay is regarded as being Sydney, and the evidence for this is discussed at the end of this paper.

*Key to Genera of Lomatiinae.*

- |  |                           |
|--|---------------------------|
| 1. Metapleura with a tuft of soft hairs .....                | 2                         |
| Metapleura bare .....  | 3                         |
| 2. Tibiae devoid of bristles .....                           | <i>Docidomyia</i> White   |
| Bristles present on intermediate and posterior tibiae .....  | <i>Doddosia</i> Edwards   |
| 3. Anal vein sinuous; alula large .....                      | <i>Oncodosia</i> Edwards  |
| Anal vein straight; alula small or absent .....              | 4                         |
| 4. Radial vein very strongly reflexed to moderately so ..... | <i>Comptosia</i> Macquart |
| Radial vein curved, but not or only slightly reflexed .....  | <i>Lomatia</i> Meigen     |

*Key to Species of Comptosia.*

- |  |                                   |         |
|--|-----------------------------------|---------|
| 1. Alula variable in development, but definitely separated from the axillary area by a distinct incision. Male with eyes contiguous, or if slightly separated, then no hairs occur on the strip between them ..... | Subgenus <i>Comptosia</i> Edwards | .... 2  |
| Alula not developed, the straight border of the wing flows into the edge of the axillary area without an incision to mark the boundary .....   | Subgenus <i>Aleucosia</i> Edwards | .... 18 |

Subgenus *COMPTOSIA* Macquart (restricted by Edwards).

- |   |                           |        |
|---|---------------------------|--------|
| 2. Wings uniformly deep brown, rarely varying to a lighter tone within the cells. Radial loop deep and the vein $M_2$ usually with the apical part (portion lying beyond the discal cell) diverted away from the direction of the basal part (which borders the median cell below), by an angle of 30 degrees, but there are two exceptions. Abdomen black, sometimes with red, but never with light-coloured hair-bands .. | <i>fascipennis</i> -group | .. 3   |
| If wings be intensely and uniformly brown, then the radial loop is very shallow (about as deep as wide). Normally varying colour intensity to clear, and invariably the median vein is diverted by 30 degrees .....   | <i>basilis</i> -group     | .... 7 |

Wings never intensely brown throughout, and the vein  $M_3$  lies in the same direction as the basal part, at most slightly diverted, but considerably less so than 30 degrees. Always without the radial cross-vein and with scutellum black . . . . . *ocellata*-group . . . . 14

COMPTOSIA FASCIPENNIS-group.

3. Costa of male conspicuously tuberculated. Interradial cross-vein present. Abdomen partly, scutellum wholly red. Hairs on frons black, on face white or yellow . . . . . 4
- Costa of male not or not noticeably tuberculated. Without an interrarial cross-vein. Scutellum black and abdomen entirely or mainly so . . . . . 5
4. Eyes of male contiguous for a considerable distance and both sexes with white apically on the wings . . . . . *fascipennis* Macquart
- Eyes of male contiguous for a shorter distance and only the male with white apically on the wings . . . . . *lateralis* Newman
5. Wings of both sexes with white subapically. Third median vein not diverted. Hair on frons all black in male, some white in female; on face white to yellowish . . . . .
- . . . . . *nigriscens* Newman
- Without white on wings . . . . . 6
6. Third median vein diverted by 30 degrees. Hair on frons black, on face white or yellowish . . . . . *sobria* Walker
- Third median vein not diverted. Yellow hair of face extends to frons . . . . . *brunnea* Edwards

COMPTOSIA BASILIS-group.

7. With an interrarial cross-vein between fourth and fifth radial veins, in addition to the normal one. Costa tuberculated on male. Abdomen with a light median stripe . . . . .
- . . . . . *vittata* Edwards
- At most only the normal interrarial cross-vein present . . . . . 8
8. Costa tuberculated in male. Interradial cross-vein present and the wings with white apically. Scutellum red and the basal segment of the abdomen with a thin band of light hairs . . . . . 9
- Costa in male not tuberculated. Interradial cross-vein absent . . . . . 10
9. Wing veins densely fumed along their length; some conspicuous spots also present . . . . .
- . . . . . *decedens* Walker
- Wing veins only slightly less densely fumed and no spots present . . . . . *basilis* Walker
10. Radial loop deep, the wings well marked with white apically. Each abdominal segment with a pale band . . . . . 11
- Radial loop shallow and the wings rather uniformly suffused light brown . . . . . 13
11. Wings with the anterior border and the broad subapical band brown . . . . . *quadripennis* Walker
- Wings similar and in addition with a basal area broadly brown . . . . . 12
12. Frons and face with white hairs . . . . . *bancrofti* Edwards
- Hairs on frons black, on face creamy-white . . . . . *biguttata* Edwards
13. Male only with white on wings. Scutellum and abdomen black . . . . . *edwardsi* n.n.
- Both sexes without white on wings. Scutellum red, abdomen red at sides . . . . . ? *rubifera* Bigot

COMPTOSIA OCELLATA-group (= ALYOSIA Rond.).

14. Wings with white in the central field as well as apically. Frons black above, golden lower and on face. Vein at lower border of median cell marked with fuscous, as also the extreme tip of wing . . . . . *ocellata* Newman
- Similar, but vein bordering median cell below and extreme tip of wing entirely without fuscous . . . . . *gemina* n.p.
- White on wings only at the apex and sometimes female without this white . . . . . 15
15. Wings rather uniformly brown except over two or three cells at anal area; this varies to being shadowed along the veins. Abdomen uniformly black . . . . . 16
- Wings with a distinct subapical band and the costal area also brown, but the colour varies in intensity. Abdomen banded with a line of light hairs on each segment . . . . . 17
16. Hair on face glistening white, the colour slightly extending to frons where otherwise black hairs occur . . . . . *apicalis* Macquart
- Hair on face dull yellowish, which colour surrounds antennae, otherwise black on frons. Antennal arista unusually thin and dilated at apex . . . . . *walkeri* Edwards
17. Hair on face and frons glistening white but may be largely or partly yellow . . . . .
- . . . . . *wilkinsi* Edwards
- Hair on face and surrounding antennae yellow, otherwise on frons black . . . . . *mortoni* Macquart

Subgenus ALEUCOSIA Edwards.

18. With fuscous spot at interrarial cross-vein; never with spots at apex of the median and anal veins . . . . . 19
- If with a spot at the interrarial cross-vein, then also spots occur at the apex of the median and anal veins. Normally without these, but spots may occur around the discal cell, and the interrarial cross-vein is frequently absent . . . . . 20

19. Abdomen with a median stripe. Yellow hairs on face and surrounding antennae, otherwise black on frons ..... *maculosa* Newman  
 Abdomen without the median stripe ..... *fulvipes* Bigot
20. Costal border marked with fuscous which does not reach the base of the fourth radial vein.  
 Spots present or absent ..... 21  
 Costal border marked with fuscous which reaches the base of the fourth radial vein .. 27  
 Fuscous marking generally distributed ..... 30
21. Interradial cross-vein present, very rarely absent ..... 22  
 Interradial cross-vein always absent ..... 25
22. Fuscous area of costa not reaching wing tip ..... *tricellata* Macquart  
 Fuscous area of costa reaching wing tip, the exceptions rare and apparently limited to  
*C. corculum* ..... 23
23. East Australian species on which the spots are always present on wing ..... 24  
 West Australian species on which the spots of wing are usually present .. *corculum* Newman
24. From Mt. Wellington, Tasmania; with frons broader than that of the mainland form  
 ..... *tripunctata* Edwards  
 From the mainland; with frons narrower than that of the Tasmanian form .....  
 ..... *calopthalma* Thomson
25. Wings with spots ..... *atherix* Newman  
 Wings without spots ..... 26
26. First basal cell completely fuscous ..... *hemiteles* Schiner  
 First basal cell clear at apex ..... *costalis* Edwards
27. Costa on male strongly bowed apically; both basal cells entirely fuscous. Abdomen banded  
 and legs black ..... *partita* Walker  
 Costa normal, legs reddish ..... 28
28. Vein closing apex of discal cell clouded ..... 29  
 Vein closing apex of discal cell without the marking ..... *dorsalis* Walker
29. With the fuscous marking not only clouding the interradian cross-vein, but also extending  
 towards apex of the cell; fuscous marking also at base and apex of cell between third  
 and fourth radial veins ..... *cuneata* Edwards  
 Without the extension of the fuscous marking on the interradian cross-vein, and with an  
 additional marking in the cell between third and fourth radial veins .. *angusta* Edwards
30. The whole wing uniformly fuscous, except a light streak which lies in the radial field  
 ..... *serpentiger* Walker  
 Wings mottled; in addition to the usual wing spots, others lie at the apex of all veins.  
 Costal area fuscous over basal part, less intensely so over apical half. Two inter-  
 radial cross-veins lie side by side, strongly converging towards costa .... *plena* Walker

## Genus COMPTOSIA Macquart.

*Comptosia* Macquart, *Dipt. exot.*, ii (1), 1840, 80. *Lygira* Bigot, *Ann. Soc. ent. Fr.*, (3) vi, 1858, 574; *ibid.*, (6) i, 1881, 22; *nec Lygira* Newman.

*Lygira* was intended for Newman's *Ligyra*, which Bigot was the first to regard as being identical with *Comptosia*, but Edwards concluded that it takes precedence over *Hyperalonia* Rondani. As there is only one specific name standing under *Lygira*, it is proposed to retain the genus as a synonym of *Comptosia* so as to simplify references.

Edwards is in error in stating that I had overlooked the fact that *Ligyra* takes precedence over *Hyperalonia*. I was reluctant to remove the name until the position was assured, as Newman may have had quite a different species under the genus to that of the genotype quoted, which I had identified as *Hyperalonia*, without having seen the type.

## Subgenus COMPTOSIA (Macquart).

Edwards, *Encycl. Ent. Dipt.*, vii, 1934, 87. *Neuria* Newman, *Entomologist*, i, 1841, 220.

Edwards gave five group names, mostly covering complexes, and here they are rearranged to form three groups only. The *ocellata*-group corresponds to *Alyosia* Rondani, and makes a homogeneous unit that stands apart from the other two adopted.

## COMPTOSIA FASCIPENNIS-GROUP.

Group A (*fascipennis*-group) Edwards, in part. Group B (*fasciata*-group) Edwards.

## COMPTOSIA (COMPTOSIA) FASCIPENNIS Macquart.

*Comptosia fascipennis* Macquart, *Dipt. exot.*, ii, 1840, 81; Hardy, *Proc. Roy. Soc. Tasm.*, 1921, 54; *ibid.*, 1924, 79. *Comptosia (Comptosia) fascipennis* Edwards, *Encycl. Ent. Dipt.*, vii, 1934, 87.

There are three species that run to couplet 4 of the key, the third is apparently unnamed and differs from the present species by both sexes having no white on the wing. New South Wales and South Australia.

COMPTOSIA (COMPTOSIA) LATERALIS Newman.

*Neuria lateralis* Newman, *Entomologist*, i, 1841, 220; Walker, *Ins. Saund.*, Dipt., 1852, 167; Schiner, *Reise Novara*, Dipt., 1868, 131. *Comptosia lateralis* Hardy, *Proc. Roy. Soc. Tasm.*, 1921, 58; Hardy, *Proc. Linn. Soc. N.S.W.*, lviii, 1933, 414. *Comptosia (Comptosia) lateralis* Edwards, *Encycl. Ent. Dipt.*, vii, 1934, 88. *Anthrax insignis* Walker, *List Dipt. Brit. Mus.*, ii, 1849, 266. *Anthrax ducens* Walker, *Ins. Saund.*, Dipt., 1850, 176; 167 (*Neuria*). *Comptosia ducens* Hardy, *Proc. Roy. Soc. Tasm.*, 1921, 58. *Comptosia rufoscutellata* Jaennicke, *Abh. senckenb. naturf. Ges.*, vi, 1867, 345; Pl. 43, fig. 9; Hardy, *Proc. Roy. Soc. Tasm.*, 1921, 61. *Neuria grandis* Schiner, *Reise Novara*, Dipt., 1868, 132. *Comptosia albofasciata* Thomson, *Eugenies Resa*, Dipt., 1869, 484; Hardy, *Proc. Roy. Soc. Tasm.*, 1921, 58.

A common species in New South Wales.

COMPTOSIA (COMPTOSIA) NIGRICENS Newman.

*Anthrax fasciata* Fabricius, *Syst. Antl.*, 1805, 118 (preoccupied); Wiedemann, *Dipt. exot.*, 1821, 150; Wiedemann, *Auss. zweifl. Ins.*, i, 1828, 321; Walker, *List Dipt. Brit. Mus.*, ii, 1849, 267. *Neuria fasciata* Walker, *Ins. Saund.*, Dipt., 1852, 167; Schiner, *Reise Novara*, Dipt., 1868, 129. *Comptosia fasciata* Hutton, *N.Z. Dipt.*, 1881, 24; Hardy, *Proc. Roy. Soc. Tasm.*, 1921, 57; *ibid.*, 1923, 79. *Comptosia (Comptosia) fasciata* Edwards, *Encycl. Ent. Dipt.*, vii, 1934, 89. *Comptosia nigricens* Newman, *Entomologist*, i, 1841, 221.

The name given by Fabricius is preoccupied by Meigen (*Klass. Beschr. zweifl. Ins.*, i, 1804, 200), and the type was not examined by Edwards, who depended upon a male named by Walker. New South Wales.

COMPTOSIA (COMPTOSIA) SOBRIA Walker.

*Anthrax sobria* Walker, *List Dipt. Brit. Mus.*, ii, 1849, 269. *Neuria sobria* Walker, *Ins. Saund.*, Dipt., 1852, 167. *Comptosia sobria* Hardy, *Proc. Roy. Soc. Tasm.*, 1921, 59. *Comptosia (Comptosia) sobria* Edwards, *Encycl. Ent. Dipt.*, vii, 1934, 91. *Comptosia bicolor* Macquart, *Dipt. exot.*, suppl. 4, 1850, 114; Pl. 10, fig. 17. *Neuria bicolor* Schiner, *Reise Novara*, Dipt., 1868, 131. *Anthrax subsenex* Walker, *Trans. ent. Soc. Lond.*, iv, 1857, 144. *Lomatia subsenex* Hardy, *Proc. Roy. Soc. Tasm.*, 1921, 52. *Comptosia subsenex* Hardy, *ibid.*, 1923, 80.

Both Walker's types were found to be identical by Edwards, who adds Macquart's species without comment. New South Wales.

COMPTOSIA (COMPTOSIA) BRUNNEA Edwards.

*Comptosia aurifrons* Hardy, *Proc. Roy. Soc. Tasm.*, 1921, 59; *nec* Macquart, *nec* Edwards. *Comptosia extensa* Hardy, *ibid.*, 1923, 80; *nec* Walker. *Comptosia (Comptosia) brunnea* Edwards, *Encycl. Ent. Dipt.*, vii, 1934, 90; fig. 1.

The valid name for this species is in doubt. I believe it to be *C. aurifrons* Macquart, a name which Edwards applies to a north Queensland species that could not have reached Macquart. The type has not been seen and there are several views concerning its identity. Edwards applied a new name to this species, contrasting it with *C. extensa* from Western Australia. There is an allied species which has the scutellum red apically, face with orange hairs in place of yellow, and the venation has the median vein diverted. New South Wales and South Australia.

COMPTOSIA BASILIS-GROUP.

Group C (*pracargentata*-group) Edwards, in part.

COMPTOSIA (COMPTOSIA) VITTATA Edwards.

Edwards, *Encycl. Ent. Dipt.*, vii, 1934, 89; fig. 3.

A very distinctive southern species, recorded from Victoria and South Australia, but apparently seldom found.

## COMPTOSIA (COMPTOSIA) DECEDENS Walker.

*Anthrax decedens* Walker, *List Dipt. Brit. Mus.*, ii, 1849, 271. *Neuria decedens* Walker, *Ins. Saund.*, Dipt., 1852, 167. *Comptosia (Comptosia) decedens* Edwards, *Encycl. Ent. Dipt.*, vii, 1934, 88.

This Western Australian species is probably conspecific with *C. basilis*, of which the venation is said to differ by the third median vein, "almost continuing the direction of the first section", and yet also is compared with that of *C. vittata*. This is a contradiction in the description and both forms agree with *C. vittata* in having the diversion to about 30 degrees.

## COMPTOSIA (COMPTOSIA) BASILIS Walker.

*Anthrax basilis* Walker, *List Dipt. Brit. Mus.*, ii, 1849, 267. *Neuria basilis* Walker, *Ins. Saund.*, Dipt., 1852, 167. *Comptosia basilis* Hardy, *Proc. Roy. Soc. Tasm.*, 1923, 80. *Comptosia (Comptosia) basilis* Edwards, *Encycl. Ent. Dipt.*, vii, 1934, 89.

There is another species allied here, but without the tuberculations on the costa, the scutellum is red and the abdomen has a pale transverse line on the basal segment. Western Australia.

## COMPTOSIA (COMPTOSIA) QUADRIPENNIS Walker.

*Anthrax quadripennis* Walker, *List Dipt. Brit. Mus.*, ii, 1849, 268. *Neuria quadripennis* Walker, *Ins. Saund.*, Dipt., 1852, 167. *Comptosia quadripennis* Hardy, *Proc. Roy. Soc. Tasm.*, 1921, 59. *Comptosia (Comptosia) quadripennis* Edwards, *Encycl. Ent. Dipt.*, vii, 1934, 92.

Queensland and South Australia.

## COMPTOSIA (COMPTOSIA) BANCROFTI Edwards.

Edwards, *Encycl. Ent. Dipt.*, vii, 1934, 93; fig. 9.  
Queensland.

## COMPTOSIA (COMPTOSIA) BIGUTTATA Edwards.

Edwards, *Encycl. Ent. Dipt.*, vii, 1934, 93; fig. 8.  
Queensland and New South Wales.

## COMPTOSIA (COMPTOSIA) EDWARDSI, new name.

*Comptosia (Comptosia) praeargentata* Edwards, *Encycl. Ent. Dipt.*, vii, 1934, 91; fig. 10; *nec* Macleay. *Comptosia (Comptosia) aurifrons* Edwards, *ibid.*, 91; *nec* Macquart.

*Synonymy*.—I have no hesitation in regarding Edwards' two forms as being conspecific, but his single specimen from Brisbane must be excluded as this belongs to an allied species in which the white of the wings is missing in both sexes. Macleay described *Anthrax praeargentata* from King's collection, and for reasons given at the end of this paper, it appears that King's Diptera have been almost entirely captured in the Sydney district. Similarly it is impossible for the present species to have reached Macquart, whose material did not come from further north than Brisbane; hence his name must apply to some other form.

*Hab.*—North Queensland: Kuranda, Cairns, Gordonvale and Meringa. A single specimen (male, 1.xii.1931, J. H. Buzacott) was reared from the larva at Meringa, and it is a well-known fly of the sugar-fields.

In addition to the above, five more species are known; one near *C. edwardsi* has the white on the wings of both sexes, and this character is entirely lacking on the others, which are similarly related. Two have the scutellum red; one of these also has the abdomen red at the sides and is marked in the key as being possibly *C. rubifera* Bigot. The other two have the scutellum and abdomen all black, one having the frons with orange hairs, the other black.

## COMPTOSIA OCELLATA-GROUP.

*Alyosia Rondani*, *Arch. per la Zool.*, iii, 1863, 54; Becker, *Ann. Mus. Zool. St. Petersb.*, xvii, 1912, 465. Group D (*apicalis*-group) Edwards, in part. Group E (*ocellata*-group) Edwards.

All described species have white on the wings at least in the male, but two others are entirely without this character, and have mixed black and white hairs on the frons and glistening white ones on the face.

COMPTOSIA (COMPTOSIA) OCELLATA Newman.

*Neuria ocellata* Newman, *Entomologist*, i, 1841, 221; Walker, *Ins. Saund.*, Dipt., 1852, 167. *Anthrax ocellata* Walker, *List Dipt. Brit. Mus.*, ii, 1849, 268. *Comptosia ocellata* Hardy, *Proc. Roy. Soc. Tasm.*, 1921, 55. *Comptosia (Comptosia) ocellata* Edwards, *Encycl. Ent. Dipt.*, vii, 1934, 95; fig. 12. *Comptosia maculipennis* Macquart, *Dipt. exot.*, suppl. 1, 1846, 116; White, *Proc. Roy. Soc. Tasm.*, 1916, 201. *Anthrax inclusa* Walker, *List Dipt. Brit. Mus.*, ii, 1849, 268. *Comptosia (Comptosia) inclusa* Edwards, *Encycl. Ent. Dipt.*, vii, 1934, 95; fig. 19.

*Synonymy*.—All three specific names were based on specimens from Tasmania, where only one variable species is known. I have not seen specimens from New South Wales and Queensland, which States were subsequently added to the distribution.

COMPTOSIA (COMPTOSIA) GEMINA, new name.

*Anthrax cognata* Walker, *Ins. Saund.*, Dipt., 1852, 177; 167 (*Neuria*); preoccupied. *Comptosia (Comptosia) cognata* Edwards, *Encycl. Ent. Dipt.*, vii, 1934, 95; fig. 13.

Walker used the name twice; in the first instance (*List Dipt. Brit. Mus.*, ii, 1849, 264) he applied it to an African Bombyliid. To the present species must be referred all records of *C. ocellata* from Western Australia, in which State only this one is known.

COMPTOSIA (COMPTOSIA) APICALIS Macquart.

*Comptosia apicalis* Macquart, *Dipt. exot.*, suppl. 3, 1846, 35; Pl. 3, fig. 13; Hardy, *Proc. Roy. Soc. Tasm.*, 1921, 59. *Alyosia apicalis* Rondani, *Arch. per la Zool.*, iii, 1863, 54. *Neuria apicalis* Schiner, *Reise Novara*, Dipt., 1868, 132. *Comptosia (Comptosia) apicalis* Edwards, *Encycl. Ent. Dipt.*, vii, 1934, 92.

New South Wales.

COMPTOSIA (COMPTOSIA) WALKERI Edwards.

Edwards, *Encycl. Ent. Dipt.*, vii, 1934, 94; fig. 11.

The type locality is not known, but a second specimen is recorded from Stradbroke I., Queensland, and further material before me comes from the same area, Bribie I. and Brisbane, all specimens being males.

From Tooloom comes a very close ally, several specimens taken *in copula*, and here the female is without the white on the wing. Except the Brisbane specimen, all recorded here were captures by Mr. H. Hacker. Edwards' type was identified as being *praeargentata* Macleay. Under that name is a specimen "in the cabinet of the Entomological Club" by Newman, and Walker may have secured the identification from this source.

COMPTOSIA (COMPTOSIA) WILKINSI Edwards.

Edwards, *Encycl. Ent. Dipt.*, vii, 1934, 94; fig. 17.

In the type locality, Groote Eylandt, two species are so much alike that they are liable to be confused, and Mr. N. B. Tindale has secured a series of both. One of these belongs to the genus *Doddosia*, and the other is the present species. The latter is dimorphic in regard to wing marking, and the former is variable. The two males before me of *C. wilkinsi*, marked allotype and paratype male respectively, are in the Roberts' collection together with four females, and represent part of a larger series; the others have not been seen by me. The male of *C. wilkinsi* has the wing markings much deeper brown than those of the female, and in addition, there is an obvious fascia, interrupted, near the base; the interruption is caused by the whole of the second basal cell being clear.

COMPTOSIA (COMPTOSIA) MORETONI Macquart.

*Comptosia moretonii* Macquart, *Dipt. exot.*, suppl. 5, 1855, 77; Pl. 3, fig. 15. *Comptosia (Comptosia) moretoni* Edwards, *Encycl. Ent. Dipt.*, vii, 1934, 94; fig. 18.

This Queensland fly, from the Moreton Bay district (Brisbane) is also recorded from north Queensland by Edwards, but I have only seen southern specimens.

Subgenus ALEUCOSIA Edwards.

Edwards, *Encycl. Ent. Dipt.*, vii, 1934, 95.

Five points that tend towards isolating this group from subgenus *Comptosia*, are given by Edwards, and a sixth may be added by referring to the face and frons colouration, which is rather uniformly dark or dingy. There is also a strong propensity for venational abnormalities to occur, and most markedly so in the radial field.

Edwards makes four groups, but two of these are somewhat complex and are better united. The *corculum*-group contains mainly species so intergrading in their characters that originally they were regarded as variations, and were united under the one name "*sylvana*", it being believed that Fabricius had described one of them under the name *Biblio sylvanus*; this is now known to be a *Ligyra*. The name "*sylvana*" has no standing in this connection, and was based principally upon *C. calopthalma* Thomson. The same species has long stood under the name *corculum* in Australian collections, and this probably misled White. Edwards again was led into error, as he had only a few Museum specimens to guide him, whereas *C. corculum* of Western Australia is a very variable form known to me from long series of specimens in various collections. The other species of which I have collected series, prove more consistent in characters, except the Mt. Wellington species, which varied widely in the characters which Edwards selected for distinguishing it. Each species so far isolated seems to have a more or less confined distribution, with no overlapping except in the case of *C. hemiteles*, which covers areas where *C. calopthalma* occurs. I think, now, all the described forms are adequately isolated, and the only species of the complex which I have not found is *C. tricellata* Macq., described from Tasmania, but it might be an abnormal form of *C. tripunctata* Edwards, which is liable to variations. Edwards saw the types, two females, in bad condition.

COMPTOSIA MACULOSA-group.

Group A (*maculosa*-group) Edwards.

COMPTOSIA (ALEUCOSIA) MACULOSA Newman.

*Neuria maculosa* Newman, *Entomologist*, i, 1841, 221. *Comptosia (Aleucosia) maculosa* Edwards, *Encycl. Ent. Dipt.*, vii, 1934, 96; fig. 2.

A Western Australian species which Edwards also records from South Australia.

COMPTOSIA (ALEUCOSIA) FULVIPES Bigot.

*Comptosia fulvipes* Bigot, *Ann. ent. Soc. Fr.*, lxi, 1892, 359. *Comptosia (Aleucosia) fulvipes* Edwards, *Encycl. Ent. Dipt.*, vii, 1934, 96.

For locality, only "Australia" is quoted, but Bigot's flies all seem to be from the eastern side. The species is quite unknown to me, and Edwards only saw the type.

COMPTOSIA CORCULUM-group.

Group B (*corculum*-group) Edwards.

COMPTOSIA (ALEUCOSIA) TRICELLATA Macquart.

*Comptosia tricellata* Macquart, *Dipt. exot.*, suppl. 2, 1847, 53; Pl. 2, fig. 6; *nec* Schiner, *nec* Hardy. *Comptosia (Aleucosia) tricellata* Edwards, *Encycl. Ent. Dipt.*, vii, 1934, 98.

The only species seen by me that agrees with the wing marking confirmed by Edwards from the type, is a variation of *C. corculum*, but this could hardly be identical.

COMPTOSIA (ALEUCOSIA) CORCULUM Newman.

*Neuria corculum* Newman, *Entomologist*, i, 1841, 221; Walker, *Ins. Saund.*, Dipt., 1852, 167; *nec* White, *nec* Hardy. *Atherix corculum* Walker, *List Dipt. Brit. Mus.*, ii, 1849, 269. *Comptosia (Aleucosia) corculum* Edwards, *Encycl. Ent. Dipt.*, vii, 1934, 99; fig. 15. *Comptosia (Aleucosia) cincta* Edwards, *ibid.*, 99.

Edwards' two forms are conspecific and the species is variable in wing markings. Western Australia.

## COMPTOSIA (ALEUCOSIA) TRIPUNCTATA Edwards.

*Comptosia corculum* Hardy, *Proc. Roy. Soc. Tasm.*, 1917, 66; White, *ibid.*, 1916, 203 (suppositious only); *nec* Newman. *Comptosia sylvana* form *tricellata* Hardy, *ibid.*, 1927, 57. *Comptosia tricellata* Hardy, *Proc. Linn. Soc. N.S.W.*, lviii, 1933, 414. *Comptosia (Aleucosia) tripunctata* Edwards, *Encycl. Ent. Dipt.*, vii, 1934, 98.

Unless the quoted locality "Tasmania" be incorrect, the species described by Edwards can only be the one limited to Mt. Wellington. At the apex of the first basal cell, there is a varying amount of clear area, ranging from quite wide to almost obsolete, the whole cell then being covered with brown, the hardly noticeable spot or dot left being easily overlooked. There is a discrepancy in the description concerning "pubescence in the lateral angle of the eye yellow" which doubtfully applies; the colour is nearer white and appears slightly yellow under artificial light. The yellow occurs on *corculum*, *costalis* and *atherix*, and white on all the rest of the species before me.

## COMPTOSIA (ALEUCOSIA) CALOPHTHALMA Thomson.

*Neuria tricellata* Schiner, *Reise Novara*, *Dipt.*, 1868, 131; *nec* Macquart. *Comptosia calophtalma* Thomson, *Eugenies Resa*, *Dipt.*, 1869, 485. *Comptosia sylvana* Hardy, *Proc. Roy. Soc. Tasm.*, 1921, 55; *nec* Fabricius. *Comptosia (Aleucosia) calophtalma* Edwards, *Encycl. Ent. Dipt.*, vii, 1934, 99; fig. 25.

New South Wales. Edwards adds Victoria and Queensland, recording two males in the British Museum from the Moreton Bay district, but it is possible that an error has been made by inexactness of locality. Some typical species of New South Wales extend into Stradbroke I., and it is possible that they came from there; Moreton Bay district records in literature all refer to the mainland, and include Brisbane. Stradbroke I. is a distinctive faunal zone for Diptera, containing species which seem to run into northern New South Wales.

## COMPTOSIA (ALEUCOSIA) ATHERIX Newman.

*Neuria atherix* Newman, *Entomologist*, i, 1841, 222; Walker, *Ins. Saund.*, *Dipt.*, 1852, 167. *Comptosia (Aleucosia) atherix* Edwards, *Encycl. Ent. Dipt.*, vii, 1934, 97. *Comptosia geometrica* Macquart, *Dipt. exot.*, suppl. 2, 1847, 53; Pl. 2, fig. 7; White, *Proc. Roy. Soc. Tasm.*, 1916, 202; Hardy, *Proc. Linn. Soc. N.S.W.*, lviii, 1933, 414. *Neuria geometrica* Walker, *Ins. Saund.*, *Dipt.*, 1852, 167. *Alyosia geometrica* Rondani, *Arch. per la Zool.*, iii, 1863, 54. *Comptosia sylvana* form *geometrica* Hardy, *Proc. Roy. Soc. Tasm.*, 1921, 57. *Atherix obscura* Walker, *Ins. Saund.*, *Dipt.*, 1852, 176; 167 (*Neuria*).

Newman's type is recorded from South Australia, those of Macquart and Walker are from Tasmania. Edwards has seen the latter two, but makes no mention of Newman's, and this identity needs confirmation. I have seen no mainland specimens of this common Tasmanian species.

## COMPTOSIA (ALEUCOSIA) HEMITELES Schiner.

*Neuria hemiteles* Schiner, *Reise Novara*, *Dipt.*, 1868, 132. *Comptosia sylvanus* form *hemiteles* Hardy, *Proc. Roy. Soc. Tasm.*, 1921, 57. *Comptosia hemiteles* Hardy, *Proc. Linn. Soc. N.S.W.*, lviii, 1933, 414. *Comptosia (Aleucosia) hemiteles* Edwards, *Encycl. Ent. Dipt.*, vii, 1934, 98.

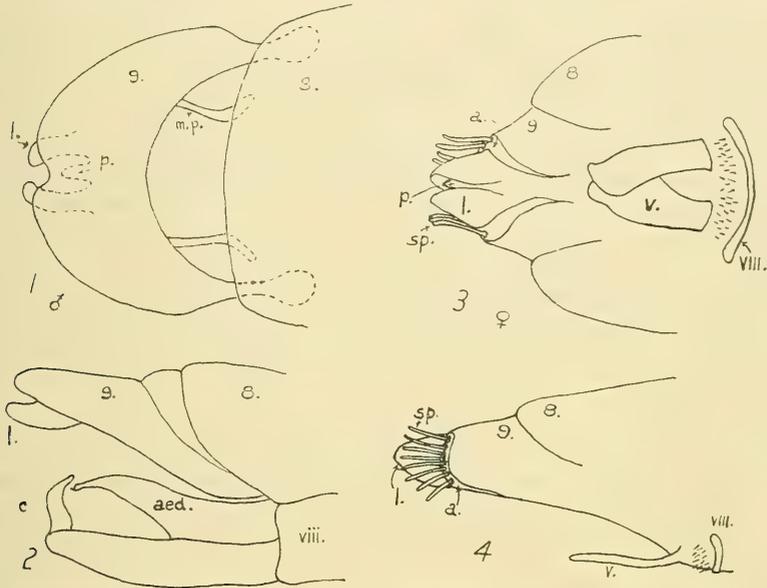
The known distribution covers New South Wales to the Toowoomba-Stanthorpe region of Queensland. The near ally, *C. costalis* Edwards, occurs widely over the mainland area of the Moreton Bay district. There is only the marking of the wing to distinguish between the two, but this proves consistent with distribution. The present form is the first spring Bombyliid to appear on the wing in the Sydney district, as far as I know, and is quickly followed by *C. calophtalma* Thomson, which lasts longer on the wing.

## COMPTOSIA (ALEUCOSIA) COSTALIS Edwards.

Edwards, *Encycl. Ent. Dipt.*, vii, 1934, 99; fig. 14.

This fly is the second of the family to appear in the Brisbane district, about the middle of August, and is abundant through the early spring. The figures given of the terminalia (Figs. 1-4) are identical with those of other species of the genus so far

examined. On the male they twist on the longitudinal axis and may be found turned to any position from erect to 180 degrees, and during copulation are inverted, the sexes flying with the male dragged behind the female and facing rearwards. The claspers are hinged to swing from the vertical and slightly sloping forwards position, to the horizontal rearwardly directed position. The supports, at the apex of which the claspers stand, are fused along the median line below, so as to form a single unit, instead of two separate ones found everywhere in the Asiloidea except in Bombyliidae. The aedeagus,



Figs. 1-4.—*Comptosia (Aleucosia) costalis* Edwards. Fig. 1.—Terminalia of the male, dorsal view. Fig. 2.—Terminalia of the male, lateral view. Fig. 3.—Terminalia of the female, ventral view. Fig. 4.—Terminalia of the female, lateral view. *a.*, acanthophorites; *aed.*, aedeagus; *c.*, clasper; *l.*, lamella; *m.p.*, median plate; *p.*, anal papilla; *sp.*, spine; *v.*, ventral valve; 8 and 9, eighth and ninth tergite; viii, eighth sternite.

which lies above this complex structure, is of the usual Asiloidean type. The anal papilla is flanked by two membranous fat-filled lamellae that represent the dorsal lamella, divided and moved downwards to take this lateral position; the ventral lamella is missing. The whole structure (proctiger) is placed subapically, below an emargination of the apical tergite. As far as can be determined, two widely separated ridges of chitin represent the median plate. The ninth (apical) tergite has two arms embedded below the eighth, and a membrane between is so arranged as to allow the whole terminalia to be retracted and mainly concealed within the eighth segment.

The female has acanthophorites fused to the ninth tergite, making one unit, and the proctiger is apically placed and of the same form as that of the male. A median plate has not been detected, but the ventral valves form a pair of flat plate-like structures that protect the gonopore. The eighth sternite is reduced to a transverse bar, an area of membrane between it and the ventral valves being heavily studded with minute bristly spines.

#### COMPTOSIA (ALEUCOSIA) PARTITA Newman.

*Neuria partita* Newman, *Entomologist*, i, 1841, 221; Walker, *Ins. Saund.*, Dipt., 1852, 167. *Comptosia (Aleucosia) partita* Edwards, *Encycl. Ent. Dipt.*, vii, 1934, 97; fig. 16.

A very distinctive form which has the apical half of the costa bowed forward, and in other ways mis-shapen in the male. Western Australia.

#### COMPTOSIA DORSALIS-GROUP.

Group C (*dorsalis*-group) Edwards. Group D (*plena*-group) Edwards.

## COMPTOSIA (ALEUCOSIA) DORSALIS Walker.

*Anthrax dorsalis* Walker, *List Dipt. Brit. Mus.*, ii, 1849, 269. *Neuria dorsalis* Walker, *Ins. Saund.*, Dipt., 1852, 167. *Comptosia dorsalis* Hardy, *Proc. Roy. Soc. Tasm.*, 1921, 59. *Comptosia (Aleucosia) dorsalis* Edwards, *Encycl. Ent. Dipt.*, vii, 1934, 100; fig. 22. Western Australia.

## COMPTOSIA (ALEUCOSIA) CUNEATA Edwards.

Edwards, *Encycl. Ent. Dipt.*, vii, 1934, 100; fig. 23. Western Australia.

## COMPTOSIA (ALEUCOSIA) ANGUSTA Edwards.

Edwards, *Encycl. Ent. Dipt.*, vii, 1934, 100; fig. 24. Western Australia.

## COMPTOSIA (ALEUCOSIA) SERPENTIGER Walker.

*Anthrax serpentiger* Walker, *List Dipt. Brit. Mus.*, ii, 1849, 270. *Comptosia (Aleucosia) serpentiger* Edwards, *Encycl. Ent. Dipt.*, vii, 1934, 101; fig. 21. Western Australia.

## COMPTOSIA (ALEUCOSIA) PLENA Walker.

*Anthrax plena* Walker, *List Dipt. Brit. Mus.*, ii, 1849, 270. *Neuria plena* Walker, *Ins. Saund.*, Dipt., 1852, 167. *Comptosia plena* Hardy, *Proc. Roy. Soc. Tasm.*, 1921, 57; 1923, 79. *Comptosia (Aleucosia) plena* Edwards, *Encycl. Ent. Dipt.*, vii, 1934, 101; fig. 16. Western Australia.

*Species of Unknown and Doubtful Identity.*

Those species recorded above have all been identified in Australian collections, except two, *C. fulvipes* Bigot and *C. tricellata* Macquart, and the approximate position is known in these cases. Attempts to establish the identity of the following seven have not been successful:

(1). *anthracina* Thomson, *Eugenies Resa*, Dipt., 1869, 485 (*Comptosia*). It is not a *Comptosia*, but probably belongs to *Lomatia*.

(2). *aurifrons* Macquart, *Dipt. exot.*, suppl. 4, 1850, 113; Pl. 10, fig. 16 (*Comptosia*). I believe this to be *C. brunnea* Edwards, but Edwards applied the name to a species which could not have reached Macquart. The type has not been seen.

(3). *extensa* Walker, *Ent. Mag.*, ii, 1835, 473 (*Anthrax*). No locality is given, but Western Australia was added at a later date. Edwards refers the name to a species I have not seen.

(4). *murina* Newman, *Entomologist*, i, 1841, 221 (*Neuria*). Unknown to all subsequent authors, and apparently the type, from South Australia, has been lost.

(5). *praeargentatus* Macleay, in King's *Narrative Surv. Coast Australia*, 1827, 468 (*Anthrax*). Several authors have attempted to identify this species, but none seems successful.

(6). *rubifera* Bigot, *Ann. Soc. ent. Fr.*, (6) i, 1881, 23 (*Lygira*). Edwards states that the type resembles *fascipennis* Macq., but is without the white fascia in the wing. This agrees with the unnamed species mentioned above, but the description does not seem to belong there. In the key, couplet 13, another species is marked as possibly Bigot's form.

(7). *stria* Walker, *List Dipt. Brit. Mus.*, ii, 1849, 267 (*Anthrax*). This evidently belongs to the *basilis*-group and cannot be placed by me without more data than Edwards gives; he compared it with *C. sobria* Walk.

*The Diptera described by Macleay.*

Macleay described eight flies in King's "Narrative of the survey of the intertropical and western coasts of Australia", 1827, under the title "A catalogue of the insects collected by Captain King, R.N.". The flies constitute about four per cent. of the total insects described, and are as follows:

*Stratiomys hunteri* is an *Odontomyia* not found north of New South Wales and reaches Tasmania; it is common in Sydney.

*Asilus inglorius* is a *Neoaratus*, abundant in Sydney, reaches Brisbane, but not certainly known north of this, records probably being confused with allied forms since described.

*Tabanus guttatus* Donovan is a *Scaptia* that does not occur beyond one hundred miles north of Brisbane, and is typical of Sydney.

*Tabanus cinerescens* reaches the Northern Territory, but is common in Sydney.

*Pangonia roei* remains unrecognized. It was named in manuscript by King himself, and his fellow officer, J. S. Roe, may have supplied it from some other source, the name being a tribute to the donor.

*Anthrax praeargentata* is certainly *Comptosia*, but of doubtful identity.

*Anthrax bombyliiformis* is *Ligyra sylvanus* Fab., widely distributed and abundant in Sydney and Brisbane.

*Musca splendida* Donovan is a *Rutilia*, typical of Sydney, but records show it has a wide distribution.

The six species that are recognized in the above list form a group that anyone would be likely to gather in Sydney, the district where King spent the longest periods of his stay in Australia. The more typical northern Diptera are not represented, except perhaps by *Tabanus cinerescens* and *Ligyra sylvanus*. The latter, at least, would coincide in occurrence with King's survey. None are typical of the area and limited there, such as was found amongst the flies collected by Banks when on Cook's voyage. It seems very doubtful if King collected any flies when in Queensland.

*Anthrax praeargentata* Macleay, judging from description alone, could be *Comptosia edwardsi* n.n., in conformity with Edwards' suggestion, but against this view is the fact that the species is known to occur during months when King was not in Queensland waters. This prohibits any possibility of King having secured it.

## NOTES ON AUSTRALIAN LYCAENIDAE. PART VIII.

ON OGYRIS ZOSINE HEW. AND O. GENOVEVA HEW.

By G. A. WATERHOUSE, D.Sc., B.E., F.R.E.S.

[Read 27th August, 1941.]

Sufficient evidence is now available to show that the above names represent two distinct species and not, as has been thought for a long time, the male and female respectively of the same species. A list of the principal references is given.

Hewitson, 1854, described and figured both species, giving no more precise locality than Australia. In 1862 he figured the underside of a specimen from the British Museum as the female of *zosine*. This specimen is a male of *genoveva*. In 1863, he still considered this specimen as a female. Kirby, 1879, in his list of the Hewitson Collection, states it contained one *zosine* and two *genoveva*. In 1936 I saw in London every specimen of the two species mentioned by Hewitson; these are now all in the British Museum.

Miskin, 1883, under the name *O. genoveva*, described and figured male and female with a purple variety of the female. Unfortunately he did not state if both female forms were taken in both the localities he mentions. This is the first time any suggestion was made that either of these species had two female forms.

Bethune-Baker, 1905, revised the genus *Ogyris* and described two new races of *zosine* and said the type form came from Townsville and was more sombre in colouring than specimens from the south. He figured the male genitalia without stating the locality of his specimen, but his figure appears to be the genitalia of a Townsville specimen.

Waterhouse & Lyell, 1914, mis-spelt the name "*zosine*", described two new races and gave evidence that the types of both species came from Brisbane.

Bethune-Baker, 1916, replied to our remarks and endeavoured to show we were in error. He made several statements as to what Hewitson had done which cannot be substantiated from Hewitson's papers nor the specimens. As I had not then seen the holotypes nor the attached labels, which Bethune-Baker did not quote, I did not reply.

Tindale, 1923, agreed with what we had published in 1914, gave some good figures and described another race. He almost came upon the truth as he figured a second form of the male from Brisbane. This was the true *zosine*.

The position, prior to 1935, on which every one seemed to agree was, following Miskin, 1883, that we had a species with a dimorphic female and that *zosine* and *genoveva* were male and female of the same species. Then in May, 1935, Mr. L. Franzen told me he considered there were two distinct species at Brisbane. He had always found small dark purple males and purple females in the one batch of larvae and pupae and never the large violet-purple male and the blue-green female associated with them. He convinced me that he was correct. At that time I had very few specimens from the Brisbane district; he, however, gave me material to take to London in 1936 to compare with the holotypes in the British Museum.

An examination of the holotype male *zosine* and the holotype female *genoveva* showed that both had a Hewitson label "Austl. Strang.". Knowing Hewitson's habit of always abbreviating, this can only mean that they were from Frederick Strange, who reached England in 1852 with a large natural history collection for sale, including many butterflies. Strange did not collect many miles north of Moreton Bay (Brisbane), and there are other specimens in the Hewitson Collection with the same label which could only have come from Brisbane. Both holotypes agree better with Brisbane specimens I

had with me than with those from many other localities. Indeed, except for age they could be considered identical. I am satisfied that my previous conclusion (1914) that both types came from Brisbane was correct. In 1852 the British Museum purchased from Strange twenty-two Lepidoptera from Moreton Bay, including a male *zosine*. The fixing of Townsville as the type locality of *zosine* by Bethune-Baker, 1905, was not based on any logical grounds. Townsville males are very much paler than the holotype and it is doubtful if there was any settlement or even collecting north of Moreton Bay before Queensland was made a separate colony in 1859.

I was pleased to find that the *Ogyris* in the British Museum were arranged according to my views and not those of Bethune-Baker. Mr. N. D. Riley went through his paper with me and agreed that several of his statements were without any justification, and that I was correct in considering the holotypes had come from Brisbane.

I returned from England convinced that the two species were distinct. I made a careful examination of the numerous specimens in my collection at the Australian Museum and in the collections of my friends in order to get the ranges of both and assign to each species the race names that had been given. I examined the male genitalia and although I found differences, I could not at first reconcile them. It seemed that at Townsville both species occurred. Two females, a blue and a dull purple, were well known from there, but only the dull purple male. This male was obviously a race of *zosine* from Brisbane. The genitalia also confirmed this. On making a further close examination of Townsville specimens and comparing them with those from other localities, I found a character that I should have noticed before. All the females from Townsville, both blue and purple, had their hindwings more drawn out towards the anal angle and were distinctly narrower than any female from the southern States. I then made a series of measurements of the hindwings at right angles and reduced these to a common basis, with the result that all Townsville females agreed with Brisbane purple females and not with females of *genoveva*. This showed that all Townsville specimens were *zosine* and there it had two forms of female. I had thought previously that *genoveva* had the two forms of female. When I now see the specimens in the cabinets I wonder why this character was not seen earlier.

Dr. C. P. Ledward and Miss Smales have made a careful investigation into the life-histories of the two species at Burleigh Heads, S.Qd. The larvae are slightly different and are attended by different species of *Camponotus*. The larvae and pupae of *zosine* are not found in the ants' nests, but under stones, bark, in tree cracks or in curled leaves on the ground. The larvae and pupae of *genoveva* are always found in the ants' nests, usually underground and the empty pupal shells are torn to pieces by the ants. The pupae of *zosine* are duller black with abdomen slightly mottled, more noticeable after emergence, empty shells being often found. The pupae of *genoveva* are uniformly black.

The hooks of the genitalia are sharply bent in *zosine* while those of *genoveva* are bent in an even curve. The clasps also show differences.

As far as is at present known *zosine* is a coastal species from Richmond River, N.S.W., to Cooktown; also at Port Darwin. The exception is specimens taken at Clermont, Qd., by Mr. E. J. Dumigan. The other species *genoveva* has not yet been found on the coast north of Brisbane, but is found in the Main Divide as far north as Duaringa. It is a coastal and inland species in New South Wales, Victoria and South Australia.

These are a very interesting pair of similar species which overlap, as far as is known, only over a short part of their range. It now becomes necessary to sort out the various subspecific names that have been given to the two species. There are other pairs of similar species that overlap such as *Trapezites iacchus* and *T. eliena*, which by some are considered the same species, but here the overlap is much greater.

#### OGYRIS ZOSINE Hewitson, 1854.

The holotype is a male in the British Museum and, as I have shown, from Brisbane. Like most Brisbane males, it is small and dark purple. The figure of Hewitson is good. The specimen from the British Museum Collection figured by Hewitson in 1862 as the female is a male *genoveva*. In 1863 he still considered this a female. Kirby, 1879,

gives one *zosine* in the collection, i.e., the holotype. Therefore Bethune-Baker, 1916, was wrong when he said Hewitson associated the purple female with it. This purple female in the collection was never mentioned by Hewitson and was placed in the No. 1 position over the name *genoveva*, the holotype female being in the No. 2 position. This accounts for the two Hewitson specimens mentioned by Kirby. I have little doubt that Hewitson considered this purple female as the male of *genoveva*.

The typical race is found from Ballina, N.S.W., to Brisbane. The males are dark purple. All females so far are bright rich purple, and the pale spot of the forewing is not so large as in *genoveva* from the same district. The female is figured by Miskin, 1883, as *genoveva*, var. a. A synonym of the female is *zenobia* Waterh. and Lyell, 1914. Both sexes are figured by Tindale, 1923, p. 346, text-figs. A and B. The female is figured, Waterhouse, 1932, Pl. xxv, 1B. The ants attending the larvae at Burleigh Heads are *Camponotus claripes* Mayr.

The race from the north is *typhon* Waterh. and Lyell, 1914. The holotype is in the Australian Museum with blue female and purple female (*iberia*) all from Townsville. Thanks to the late F. P. Dodd this race is well represented in collections. The male is much duller purple than that from Brisbane. Of twenty females from Townsville before me, fourteen are blue of varying shades and six are dull purple. The pale spot of forewing is smaller. It is figured, Waterh. and Lyell, 1914, fig. 403 ♂, 425 ♀ blue, 420 ♀ purple (*iberia*) and Tindale, 1923, Pl. xxix, fig. 15 blue, fig. 14 purple. Males from Mackay, Clermont, Herbert River, Cooktown and Port Darwin are all very similar to those from Townsville, but those from Cairns are darker purple. Of females I have seen fewer specimens, one blue from Mackay, three blue and one purple from Clermont, three blue from Cooktown and six blue from Darwin. From near Cairns I know of twenty dark purple females and only one blue. This latter is a darker blue than those I have from Townsville. It seems that blue females are commoner in drier areas and purple in wetter ones. More females are required from localities in Queensland.

O. ZOSINE ZOLIVIA, n. subsp. This is a remarkably large race caught and bred by Mr. T. H. Guthrie on Hayman and Whitsunday Islands, Qd. in March and April, 1935. All the specimens are much larger than those from other localities. The male above is dark purple, not so deep as in *zosine* nor so dull as in *typhon*, and has broad black margins; beneath it is paler than in *zosine* but not so pale as in *typhon*. The female above is black with restricted purple basal areas and the paler cream spot of forewing is between veins 3 and 6. Beneath mottled as in the other races. Mr. Guthrie took a number of specimens and all the females were purple as well as those he saw flying. I caught a purple female on Lindeman I. and saw another.

#### OGYRIS GENOVEVA Hewitson, 1854.

The holotype is a female in the British Museum and, as I have shown above, from Brisbane. Hewitson's figure is fairly good, but he describes the colour as silvery-blue and figures it with a greenish tint which agrees better with the holotype. In 1862 he recorded another female and figured the underside of a male as the female of his *zosine*. Both specimens were received at the British Museum at the same time in 1857, from Moreton Bay. Kirby, 1879, gives two *genoveva* in the Hewitson Collection. No. 1 is the purple female which Hewitson never mentioned and which, I believe, he considered the male of *genoveva*. No. 2 is the holotype.

The male is quite a different colour to *zosine* above, having a decided violet tint of varying degrees. The female has much broader hindwings. The basal colour has a varying greenish tint according to the angle at which it is viewed. I have never seen a specimen approaching the pale silvery-blue of Townsville females of *zosine*. The extent of colour on the hindwing is very variable. There may be two spots of colour on either side of veins 2, 3 and 4 near the termen; these spots may be joined to the basal area by colour along the veins and reach their greatest extent in the holotype female of the race *splendida*. The cream spot of forewing is wider than in *zosine*.

The eggs are laid on *Loranthus* or in a crack or under bark on the host tree some distance from the *Loranthus*. I suggest that when the young larvae hatch, they are taken by the ants to their food or may even be taken to the nests and there fed by the ants. It is remarkable how often as many as forty larvae and pupae are found in the

one ants' nest. Probably the ants collect the young larvae from several trees and bring them to the one nest. When the larvae are older they are guided to and from their food by the ants, which in south Queensland and New South Wales are usually *Camponotus nigriceps*. The pupae are uniformly dull black and after emergence the pupal shells are torn to pieces by the ants. This explains why pupal shells of this species are so rarely found.

This species does not show as much geographical variation as *zosine*. The chief differences above in the males are the different tints of violet-purple and the width of the dark margins. In the females the cream patch of the forewing becomes wider and longer as we come from north to south and there is an increase of basal colour. However, when the following races are seen together in the cabinet the distinctions are more apparent.

The typical race is from Brisbane, where some very large specimens have been bred. To these Bethune-Baker, 1905, gave the unnecessary name *magna*. Waterhouse and Lyell, 1914, figs. 398 ♀ and 407 ♂ undersides are from specimens marked *magna* by Bethune-Baker at the time he wrote his paper. Besides the information on the label of the holotype, females from Brisbane I took to London agreed better with it than those from any other locality.

The male above is rich dark violet and has the dark margins narrower than the other races. The female has the basal areas bluish-green and sometimes there are spots near the termen of hindwing. The cream spot of forewing extends from vein 7 to below 3 on the upperside, but to 2 on the underside. This race seems to be rarer than formerly and is known from Brisbane to Burleigh Heads. The female is figured as *zosine* by Tindale, 1923, Pl. xxix, fig. 13. A comparison of this figure with figs. 14 and 15 of *O. zosine typhon* on the same plate shows at once the difference in shape of the two species.

*O. GENOVEVA DUARINGA* Bethune-Baker, 1905. This race is slightly smaller than the above. The male is paler violet with narrow margins. The female has the basal areas much bluer than the other races and the cream spot extends from 7 to below 3 on the upperside and to 2 on the underside. The blue of the hindwings sometimes extends along veins 2, 3 and 4 almost to join spots on either side of these veins close to the termen. In one specimen the colour is almost as extensive as in the holotype *splendida*.

This race was described from a long series in the Tring Museum from near Duaringa, Qd., amongst which are no purple females. Thanks to the late Lord Rothschild, two pairs of the series are before me and there are others in Australia from the same locality. The male and female are figured by Miskin, 1883, but his figure of var. a is the purple female of *zosine* probably from Brisbane. Specimens from near Milmerran bred by Mr. J. Macqueen have most females with a decided blue tint and belong here.

*O. GENOVEVA GELA*, *n. subsp.* This is the New South Wales race, typically from St. Mary's, near Sydney, where before the trees were cut down I bred it in considerable numbers. The male is smaller than *genoveva*, brighter in colour and the dark margins are broader. In the female the basal areas are greener and not very extensive, spots near the termen of hindwing being rarely present. The cream spot of forewing is broad and extends from vein 7 nearly to 2 on the upperside and to 2 on the underside, and above 7 there is sometimes a whitish bar. It is figured as *araxes* male, Waterh. and Lyell, 1914, fig. 428. I am including here specimens from near Scone and Murrurundi as well as those from several Sydney localities.

*O. GENOVEVA ARAXES* Waterh. and Lyell, 1914. This is the Victorian race typically from Dimboola. It is a still smaller race. The male is a different paler shade of violet purple and the margins are broader. The female is greenish-blue and the colour is not very extensive. The cream spot is broad, extending from above vein 7 to 2 above and to 2 below with a white bar above 7. The spot is not so deeply indented inwardly as in the northern races. Specimens from Horsham agree with this as no doubt do those from near Melbourne, which I have not yet seen.

*O. GENOVEVA GENUA*, *n. subsp.* This is the race found in the Mt. Lofty Ranges near Adelaide. The specimens are somewhat larger than the previous race. The male has the dark margins broader than the previous race and the general colour is darker, more like specimens from New South Wales. The female has the bluish-green more restricted.

The cream patch is broad and of an even width, inwardly almost straight. It extends from above vein 7 to 2 where in most cases it is sharply cut off; on the underside it also extends to 2 and almost to the costa where it is white.

O. *GENOVEVA SPLENDIDA* Tindale, 1923. This was described from a single female from Mt. Painter, Flinders Range, S. Australia. In this the metallic-blue areas are much increased, especially on the hindwing, where the colour reaches the termen enclosing three irregularly defined black spots in 3, 4 and 5. There is also a small streak of colour in 7 of the forewing. Mr. Mules has a somewhat similar female from Cradock, which is close to the Flinders Range. It is smaller and the metallic areas are not so extensive, but it has a few metallic scales near the apex of the forewing.

In addition to those who have sent me specimens as mentioned, I have to thank Mr. J. Macqueen, Dr. Ledward and Miss Smales for many important notes.

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## NITROGEN FIXATION AND CELLULOSE DECOMPOSITION BY SOIL MICRO-ORGANISMS. III.

CLOSTRIDIUM BUTYRICUM IN ASSOCIATION WITH AEROBIC CELLULOSE-DECOMPOSERS.

By H. L. JENSEN, Macleay Bacteriologist to the Society.  
(From the Department of Bacteriology, University of Sydney.)

(Two Text-figures.)

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### Introduction.

It has been shown already by Pringsheim (1909) that butyric acid bacilli are able to grow in association with anaerobic cellulose-decomposing bacteria and thus to fix elementary nitrogen by consuming the breakdown products of the cellulose which they cannot utilize directly. The cultures of cellulose-decomposing bacteria used by Pringsheim were in all probability not pure. More recently, Krishna (1928) and Vartiovaara (1938) observed nitrogen fixation in combined pure cultures of cellulose-decomposing fungi and *Clostridium butyricum* (syn. *Cl. pasteurianum*), the fungi presumably acting as protective aerobes as well as providing the clostridia with organic nutrients in the form of hydrolysis products of cellulose. Pure cultures of cellulose-decomposing organisms other than the few species of fungi studied by Krishna and Vartiovaara do not appear to have been tested for their ability to support growth of anaerobic nitrogen-fixing bacteria. Great differences may exist in this respect, since the metabolism of the numerous aerobic cellulose-decomposers shows a wide range of variation (Jensen, 1940*b*). Experiments in this direction have therefore been carried out, as a sequel to previous investigations (Jensen, 1940*b*; Jensen and Swaby, 1941).

### Methods.

The following cellulose-decomposing organisms (Jensen, 1940*b*) were tested: one strain (G) of *Cytophaga*, three strains of *Cellvibrio*, one strain (G) of "*Cellulobacillus*", and three strains of *Corynebacterium*, besides a few fungi and actinomycetes. The same strain of *Clostridium butyricum*, freshly isolated from garden soil, was used in all experiments. Pure cultures grew only in hydrogen- or nitrogen-atmosphere, and fixed in nitrogen-free glucose solution 3.0–3.5 mgm. N per gm. of glucose fermented; a stimulating influence of small concentrations of sodium molybdate on the fixation could not be detected, as claimed by Bortels (1936).

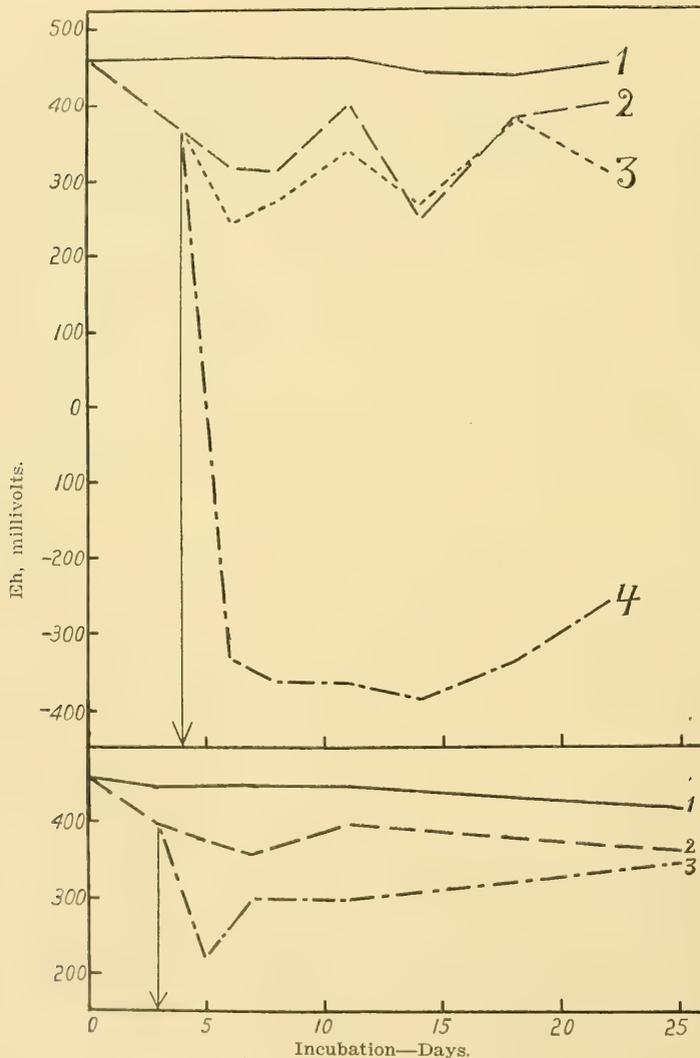
The general method of cultivation was to start growth of the cellulose-decomposing organisms and then to superinoculate the cultures with *Cl. butyricum*, either from a young glucose-broth culture or from a slope culture on soil extract-glucose-agar. The culture vessels were either test tubes or flat-bottomed round flasks of 50 to 250 c.c. capacity. Cellulose was supplied as filter paper—Whatman No. 1, except in a few cases where natural plant materials were used. The basal nutrient solution contained:  $K_2HPO_4$  0.1%,  $MgSO_4$  0.05%,  $NaCl$  0.02%,  $FeCl_3$  0.01%,  $Na_2MoO_4$  0.001%,  $CaCO_3$  0.5%, besides small amounts of nitrogen as  $(NH_4)_2SO_4$  or yeast extract. Although sterile calcium carbonate was added separately after sterilization, it was sometimes found that the solution had lost a small quantity of  $NH_4$ -N during autoclaving. All cultures were incubated at 28–30°C. The methods for determination of nitrogen and residual cellulose were the same as previously used (1940–41).

### EXPERIMENTAL.

As an approach to the problem, the ability of *Cl. butyricum* to develop in association with cellulose-decomposers was first tested qualitatively. Ordinary test tubes with a strip of filter paper in approximately 10 c.c. of nutrient solution were inoculated first

with the cellulose-decomposers and then, when the paper was visibly attacked, with the clostridia, after which they were incubated further and watched for gas evolution. At intervals, duplicate tubes were taken out and the oxidation-reduction potential as well as the reaction measured electrometrically as previously described (Jensen and Swaby, 1941).

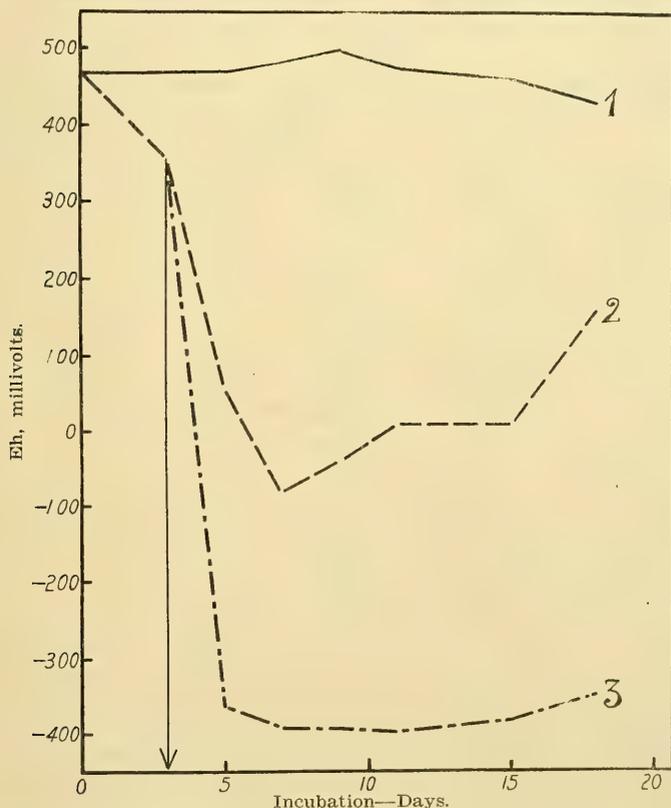
1.—*Cellvibrio (vulgaris?)*, strain G2, was grown in solution with 10 mgm.  $\text{NH}_4\text{-N}$  per 100 c.c., alone and together with *Cl. butyricum* or *Azotobacter chroococcum*, which were both introduced after 4 days' growth of the cellvibrios. *Azotobacter* produced only a trace of growth, as observed previously (Jensen, 1940*b*), but the tubes inoculated with clostridia, after 24 hours already showed a vigorous gas evolution which persisted for more than 3 weeks. The results of the Eh-measurements, averaged and corrected to pH 7.0, are shown in Fig. 1, which also gives the results of a similar experiment with *Cytophaga*. The cellvibrios, alone or in association with *Azotobacter*, cause only slight



Text-fig. 1.—Oxidation-reduction potentials in pure and combined cultures of *Cl. butyricum* and cellulose-decomposing bacteria. Upper set of curves: 1, sterile medium; 2, *Cellvibrio* G2; 3, *Cellvibrio* G2 + *Azotobacter*; 4, *Cellvibrio* G2 + *Cl. butyricum*.—Lower set of curves: 1, sterile medium; 2, *Cytophaga*; 3, *Cytophaga* + *Cl. butyricum*. (Arrows indicate time of inoculation with *Cl. butyricum*.)

and irregular lowerings of the Eh-values, but the combined cultures of *Cellvibrio* and *Cl. butyricum* show, coinciding with the onset of fermentation, an abrupt decline of the oxidation-reduction potential to the level characteristic of obligate anaerobic bacteria, viz., Eh = -0.35 to -0.40 volt; not until the end of the incubation period, when the gas production begins to slacken, does a small rise of Eh take place. Another experiment with medium containing 0.4% crude xylan instead of filter paper gave a similar result: Eh = -0.401 volt 24 hours after inoculation with *Cl. butyricum*. Unlike *Cellvibrio*, the strictly specific cellulose-decomposing *Cytophaga* did not support any active fermentation or growth of the clostridia, although the associated cultures did show a slight decrease of Eh, conceivably due to introduction of reducing compounds with the inoculum. In several other trials, *Cytophaga* again failed to support growth of the clostridia. This striking difference between *Cellvibrio* and *Cytophaga* may be connected with an essential difference in their metabolism: *Cellvibrio* attacks the cellulose by ectoenzymatic hydrolysis, as shown by the formation of clear zones on cellulose agar and the accumulation of reducing sugars under certain conditions, whereas *Cytophaga* seems to oxidize the entire cellulose-molecules, which are partially transformed into a mucilage of largely unknown constitution (Walker and Warren, 1938). The experiments thus suggest that *Cl. butyricum*, unlike *Azotobacter*, can intercept the hydrolysis products formed by *Cellvibrio*,\* but cannot ferment the mucilage which is almost the only organic by-product formed by *Cytophaga*.

2.—*Corynebacterium*, strain Vb, and *Cl. butyricum* were grown in solution with 1% yeast extract. The clostridia were introduced after 3 days' growth of the corynebacteria,



Text-fig. 2.—Oxidation-reduction potentials in pure and combined cultures of *Corynebact. Vb.* and *Cl. butyricum*. 1, sterile medium; 2, *Corynebact. Vb.*; 3, *Corynebact. Vb.* + *Cl. butyricum*. (Arrow indicates time of inoculation with *Cl. butyricum*.)

\* The assumption lies close at hand that the first product of hydrolysis may be cellobiose, which according to Koch and Seydel (1911) is not directly available to *Azotobacter*.

and vigorous fermentation was seen after 24 hours. The results of the Eh-determinations are seen in Fig. 2. The cultures of *Corynebacterium* alone show a somewhat stronger reduction than in an earlier experiment under similar conditions (Jensen and Swaby, 1941), but the associated cultures of *Corynebacterium* and *Cl. butyricum* show, as in the previous experiment, a sudden and persistent fall of Eh to nearly -0.40 volt.\*

Similar experiments were conducted with a spore-forming organism (*Bacillus* G) and a *Botryosporium*-like fungus ("P"). The results were somewhat erratic; growth of the clostridia took place in some cases only, and was then accompanied by a fall in Eh to the same level as mentioned above. These organisms seem less apt than the cellvibrios and the corynebacteria to create a favourable environment for the clostridia, possibly because they attack the cellulose more slowly and therefore are less active in lowering the oxygen tension of the medium.

The actual gains of nitrogen and losses of cellulose were determined in subsequent experiments. In the first of these, *Cellvibrio* G2 was grown alone and together with *Cl. butyricum* and/or *Azotobacter chroococcum*. The medium consisted of 0.5 gm. filter paper and 50 c.c. basal solution with 2.5 mgm.  $\text{NH}_4\text{-N}$ , in 100 c.c. flasks. After 3 or 5 days' growth of *Cellvibrio*, the nitrogen-fixing bacteria were introduced, *Azotobacter* as a loopful of suspension of cells from agar culture, *Cl. butyricum* as 2 drops of glucose-broth culture per flask. The *Clostridium*-cultures showed a slow but steady gas formation after 24 hours. The growth of *Azotobacter* was very feeble in association with *Cellvibrio* alone, but quite appreciable together with the clostridia. Nitrogen and residual cellulose were determined after approximately 3 and 5 weeks. The results are shown in Table 1.

TABLE 1.

*Nitrogen Fixation in Combined Cultures of Cellvibrio vulgaris, Clostridium butyricum, and Azotobacter chroococcum.*

Inoculum.	Incubation, Days.	Cellulose, Gm.		Nitrogen, Mgm.	
		Per Culture.	Loss.	Per Culture.	Gain.
Control (tripl.) .. .. .	0	0.478		2.18	
<i>Cellvibrio</i> .. .. .	20	0.360	0.118	2.12	(-0.06)
	34	0.313	0.165	2.27	(0.09)
<i>Cellvibrio</i> + <i>Clostridium</i> .. .. .	19 (5+14)	0.347	0.131	2.86	0.68
	33 (5+28)	0.309	0.169	3.34	1.16
<i>Cellvibrio</i> + <i>Azotobacter</i> .. .. .	21	0.375	0.103	2.32	(0.14)
	35	0.326	0.152	2.41	0.23
<i>Cellvibrio</i> + <i>Clostridium</i> + <i>Azotobacter</i>	21 (3+18)	0.373	0.105	3.02	0.84
	36 (3+33)	0.312	0.166	4.16	1.98
Average gain of N, mgm. per gm. of cellulose decomposed:					
<i>Cellvibrio</i> + <i>Clostridium</i> , 19 d.: 5.2 mgm.					
33 d.: 6.9 mgm.					
<i>Cellvibrio</i> + <i>Clostridium</i> + <i>Azotobacter</i> , 21 d.: 8.0 mgm.					
36 d.: 11.9 mgm.					

All data averages of duplicates, except initial control and *Cellvibrio* + *Clostridium*, 33 days (triplicate).

As found before (Jensen, 1940b), there is no gain of nitrogen in the pure cultures of *Cellvibrio*, and also in the presence of *Azotobacter* the increases seem too small to be significant. The association of *Cellvibrio* and *Cl. butyricum* shows a definite nitrogen fixation, and this becomes still stronger in the combined cultures of all three organisms. A survey of the losses of cellulose shows the remarkable fact that cellulose decomposition is not much influenced by the presence of nitrogen-fixing bacteria and is most rapid during the first three weeks of the experiment, whereas

\* A similar effect of clostridia on Eh in cellulose media is reported by Vartiovaara (1938).

the nitrogen fixation continues with undiminished vigour. In the cultures of *Cellvibrio* + *Clostridium* the maximal gain of nitrogen per gm. of cellulose decomposed approaches 7 mgm., which is comparable to the yields of 3.4 to 10.4 mgm. observed by Pringsheim (1910). When it is borne in mind that a not negligible proportion of the cellulose must have been consumed by the cellvibrios, it becomes evident that the process of nitrogen fixation must in these associated cultures be far more efficient than that of pure cultures in sugar solutions, as pointed out already by Pringsheim. In the presence of *Azotobacter* the yield of fixed nitrogen even rises to nearly 12 mgm., obviously because *Azotobacter* has recourse to the fermentation products of the clostridia (butyric and acetic acid, butyl alcohol, etc.). The fact that only small quantities of cellulose are lost during the last two weeks of incubation, while the nitrogen fixation shows no corresponding decline, points to a still greater economy in this second stage, but since the actual amounts of nitrogen and cellulose are small and only duplicate determinations were made, no definite conclusions can be drawn. The experiment was therefore repeated with 5 replicates. Inoculum of the clostridia was given as suspension of cells from agar culture, thereby avoiding the introduction of some nitrogen with the broth.\* Tests with two other strains of *Cellvibrio* were included in this experiment. The results are seen in Table 2.

TABLE 2.  
*Nitrogen Fixation in Combined Cultures of Clostridium butyricum and Different Strains of Cellvibrio.*

Inoculum.	Incubation, Days.	Cellulose, Gm.		Nitrogen, Mgm.	
		Per Culture.	Loss.	Per Culture.	Gain.
Control .. .. .	0	0.478	—	2.48	—
<i>Cellvibrio</i> G2 .. . . .	39	(a) 0.375	0.103	(a) 2.72	0.24
		(b) 0.388	0.090	(b) 2.60	0.12
	21 (5+16)	(c) 0.374	0.104	(c) 2.75	0.27
		(d) 0.380	0.098	(d) 2.60	0.12
		(e) 0.373	0.105	(e) 2.57	0.09
<i>Cellvibrio</i> G2 + <i>Clostridium</i> .. . . .	45 (5+40)	(a) 0.284	0.194	(a) 3.32	0.84
		(b) 0.264	0.214	(b) 2.87	0.79
	45 (5+40)	(c) 0.291	0.187	(c) 3.41	0.93
		(d) 0.278	0.200	(d) 3.63	1.15
		(e) 0.296	0.182	(e) 3.15	0.67
<i>Cellvibrio</i> 17 + <i>Clostridium</i> .. . . .	35 (5+30)	0.359	0.119	2.68	0.20
<i>Cellvibrio</i> G4 + <i>Clostridium</i> .. . . .	35 (5+30)	0.377	0.101	2.47	(-0.01)

Averages of duplicates, except *Cellvibrio* G2 + *Clostridium*.

The gains of nitrogen in the cultures of *Cellvibrio* G2 and the clostridia during the first period are in this case quite small, equivalent to less than 2 mgm. per gm. of cellulose lost. After 45 days the gains become appreciable, and the loss of cellulose is nearly doubled; it is also considerably higher than in the cultures of *Cellvibrio* alone. The yield of fixed nitrogen per gm. of decomposed cellulose is rather variable, from 1.8 to 5.7 mgm. in the individual cultures, but is significantly higher than after 21 days, as shown by Student's *t*-Test for comparison between two means (Fisher, 1935):

	Lowest.	Highest.	Mean ( $\bar{x}$ ).	S( $x-\bar{x}$ ) <sup>2</sup> .
21 days .. . . .	0.86	2.59	1.67	2.3665
45 days .. . . .	1.82	5.75	4.11	8.9066

\* This amount, however, was, when determined separately, found not to exceed 0.1 mgm. per 2 drops of broth.

With  $n = 8$ , we find  $t = 3.250$ , and  $P = 0.02-0.01$ . The difference is clearly significant, and there can thus be no doubt that the efficiency of nitrogen fixation increases with the age of the cultures; this may be due partly to removal of the  $\text{NH}_4\text{-N}$  originally present, partly perhaps to disturbance of the normal oxidative metabolism of the cellvibrios due to the low oxidation-reduction potential in the associated cultures (cf. Vartiavaara, 1938). The cultures of the two other *Cellvibrio*-strains showed a very sluggish gas evolution which had almost ceased after 3-4 weeks; the gains of nitrogen are not significant. There is thus a considerable variability in the aptitude of different cellvibrios to support growth of *Cl. butyricum*; this may have some connection with the fact that when the various strains of *Cellvibrio* were tested for production of reducing sugars from cellulose in sealed tubes (Jensen, 1940), strain G2 gave a vigorous, and the other two a faint, reaction, which suggests a less abundant secretion of cellulose-splitting ectoenzyme by these two strains.

In the next experiment the cellulose-decomposing corynebacteria were tested. The medium consisted of 0.5 gm. filter paper and 50 c.c. of basal solution with 1% yeast extract. In the first series, only *Corynebact. Vb* was employed; the cultures were grown in 100 c.c. flasks, with 2 drops of broth culture of *Cl. butyricum* as inoculum after 2 days' growth of the corynebacteria. The cultures in the second series were grown in  $20 \times 3$  cm. test tubes, and three species of *Corynebacterium* were tested; for comparison, cultures with *Cellvibrio* G2 and *Az. chroococcum* were included; inoculum of clostridia was given as cell suspension from agar-slope culture 2 days after inoculation with the cellulose-decomposers. Table 3 gives the results.

TABLE 3.  
*Nitrogen Fixation in Combined Cultures of Corynebacteria and Clostridium butyricum.*

Inoculum.	Incubation, Days.	Cellulose, Gm.		Nitrogen, Mgm.	
		Per Culture.	Loss.	Per Culture.	Gain.
Series I: round flasks.					
Control .. .. .	0	0.478	—	1.80	—
<i>Corynebacterium Vb</i> (single) ..	23	0.378	0.100	1.62	(-0.18)
	36	0.395	0.083	1.77	(-0.03)
<i>Corynebacterium Vb</i> + <i>Clostridium</i>	23	0.346	0.132	2.24	0.44
	33	0.256	0.222	2.22	0.42
	50	0.274	0.204	2.20	0.40
Series II: test tubes.					
Control .. .. .	0	0.478	—	1.77	—
<i>Corynebacterium Vb</i> + <i>Clostridium</i> ..	35	0.287	0.191	1.94	(0.17)
<i>Corynebacterium 3</i> + <i>Clostridium</i> ..	35	0.318	0.160	1.92	(0.15)
<i>Corynebacterium Va</i> + <i>Clostridium</i> ..	36	0.376	0.102	1.86	(0.09)
<i>Cellvibrio G2</i> + <i>Clostridium</i> ..	38	0.425	0.053	1.84	(0.07)
<i>Corynebacterium 3</i> + <i>Azotobacter</i> (single) .. .. .	30	0.352	0.126	3.11	1.34
<i>Corynebacterium Vb</i> + <i>Azotobacter</i> (single) .. .. .	30	0.340	0.138	3.27	1.50

Averages of duplicates unless otherwise stated.

Inoculation with *Cl. butyricum* gave rise to gas evolution in all cultures of the corynebacteria, and appears in the first series to have stimulated the cellulose decomposition, but the gain of nitrogen is small and not increasing after the first 23 days, and in the second series it is altogether insignificant in all three corynebacteria. *Cellvibrio* grew poorly in this medium, and neither visible growth of the clostridia nor nitrogen fixation took place. The control experiments with *Azotobacter* and corynebacteria show the same efficiency of fixation as found previously (Jensen and Swaby, 1941), viz., 10-11 mgm. N per gm. of cellulose lost. It appears that the metabolic by-products of the corynebacteria are indeed favourable nutrients for

*Azotobacter*, but not for *Cl. butyricum*; even if the small gains of nitrogen in the first series of Table 3 are considered significant, the efficiency would only correspond to some 2-3 mgm. N per gm. cellulose lost.

Various other aerobic cellulose-decomposers were tried next. The fungi and actinomycetes did not support any growth of the clostridia in solution with (NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub> or yeast extract in open flasks or test tubes (although this had occasionally been observed in the preliminary trials), even with addition of reduced iron. The influence of an alternating atmosphere of ordinary air and N<sub>2</sub>-gas was therefore tried (cf. Vartiavaara, 1938). Test tubes with 0.5 gm. filter paper and 50 c.c. basal solution + 1% yeast extract were inoculated with *Trichoderma koningi*, the unknown fungus "P", *Actinomyces* sp. (*violaceus*?), and *Micromonospora* sp.; after 5 days' growth the cultures were inoculated with *Cl. butyricum*. No fermentation was visible after a further 7 days; the cultures were then placed in N<sub>2</sub>-atmosphere in a Fildes-McIntosh jar and incubated for another 20 days. During this time there began a slight evolution of gas which continued when the tubes were again placed in atmospheric air; this gas production was strongest in *Trichoderma*-cultures, but was in all cases weak. A few control cultures of the cellulose-decomposers were left in atmospheric air. Another series of experiments in the same medium was carried out with a spore-forming organism previously described as *Bacillus* G (Jensen, 1940); it attacked the cellulose very slowly, and was therefore allowed to grow for 3 weeks before inoculation with *Cl. butyricum* (from agar culture) and/or *Az. chroococcum*. A steady but very slow gas formation arose in the *Clostridium*-cultures and persisted throughout the incubation, which was continued for another 9 weeks.

As seen from Table 4, which gives the results of both series of experiments, the decomposition of cellulose is in all cases weak, and nitrogen fixation is insignificant or nearly so, except perhaps in the cultures of *Bacillus* G together with both *Clostridium* and *Azotobacter*.

TABLE 4.

*Nitrogen Fixation in Combined Cultures of Clostridium butyricum and Various Aerobic Cellulose-decomposers.*

Series I: <i>Cl. butyricum</i> + <i>Bacillus</i> G.				
Inoculum.	Incubation, Days.	Loss of Cellulose, Gm.	Nitrogen, Mgm.	
			Per Culture.	Gain.
Control .. .. .	0	—	1.82	—
<i>Bacillus</i> G .. .. .	78	0.027	1.89	(0.07)
"  " + <i>Azotobacter</i> (single) .. .. .	78	0.046	2.00	(0.18)
"  " <i>Cl. butyricum</i> (triplicate) .. .. .	84	0.099	1.85	(0.03)
"  " + "  " + <i>Azotobacter</i> (triplicate) .. .. .	84	0.060	2.16	0.34
Series II: <i>Cl. butyricum</i> + fungi and actinomycetes.				
Inoculum.	Incubation, Days.	Loss of Cellulose, Gm.	Total N, Mgm.	
Control .. .. .	0	—	1.88	
<i>Trichoderma</i> (single) .. .. .	43 d. in atm. air.	0.058	1.77	
"  " + <i>Cl. butyricum</i> (single) .. .. .	47 d. (12 d. air + 20 d. N <sub>2</sub> -gas + 15 d. air)	0.084	2.14	
Fungus "P" (single) .. .. .	42 d. in atm. air.	0.105	1.91	
"  " + <i>Cl. butyricum</i> .. .. .	48 d. (12 d. air + 20 d. N <sub>2</sub> -gas + 16 d. air).	0.064	2.14	
<i>Actinomyces</i> (single) .. .. .	43 d. in atm. air.	0.070	1.89	
"  " + <i>Cl. butyricum</i> .. .. .	47 d. (12 d. air + 20 d. N <sub>2</sub> -gas + 15 d. air).	0.083	1.97	
<i>Micromonospora</i> + <i>Cl. butyricum</i> .. .. .	48 d. (12 d. air + 20 d. N <sub>2</sub> -gas + 16 d. air).	0.092	2.00	

Averages of duplicates unless otherwise stated.

The utilization of natural cellulosic materials instead of filter paper was tried next. Since it had been observed that the various cellulose-decomposing organisms except *Cytophaga* could all attack hemicellulose in the form of crude xylan, this compound was also tested. *Cellvibrio* G2 was grown together with *Cl. butyricum* in two different media: the first consisted of 35 c.c. of basal solution with 1% crude xylan and 1.0 mgm.  $\text{NH}_4\text{-N}$ ; in the second the xylan was replaced by 0.5 gm. finely ground wheat-straw. The culture vessels were 50 c.c. round flasks, and one drop of broth culture of *Cl. butyricum* was used as inoculum after three days' growth of *Cellvibrio*. Evolution of gas resulted, but did not continue for more than a couple of weeks. Table 5 gives the results.

TABLE 5.  
*Nitrogen Fixation in Combined Cultures of Cellvibrio vulgaris and Clostridium butyricum on Hemicellulose and Straw.*

Series.	Inoculum.	Incubation, Days.	Nitrogen, Mgm.		Gain of N per gm. of Material Supplied.
			Per Culture.	Gain.	
Hemicellulose 0.35 gm. crude xylan.	Control (dupl.) .. ..	0	0.98	—	—
	<i>Cellvibrio</i> (single) .. ..	10	0.85	(-0.13)	—
		25	0.96	(-0.02)	—
	<i>Clostridium</i> (single) .. ..	7	1.13	(0.15)	—
		22	1.11	(0.13)	—
<i>Cellvibrio</i> + <i>Clostridium</i> (tri- plicate) .. ..	3+7	1.32	0.34	1.0	
	3+22	1.58	0.60	1.7	
Straw, 0.5 gm.	Control (dupl.) .. ..	0	1.82	—	—
	<i>Clostridium</i> (single) .. ..	3+21	2.08	(0.26)	} 0.5 (?)
		3+35	2.07	(0.25)	
	<i>Cellvibrio</i> + <i>Clostridium</i> (tri- plicate) .. ..	3+21	2.25	0.43	0.9
		3+35	2.33	0.51	1.0

*Cl. butyricum* alone produced no visible growth in the xylan medium, but caused a slight fermentation in the straw medium; the gains of nitrogen are in both cases doubtful, especially in the former. The combined cultures of *Cellvibrio* and *Clostridium* show a small gain of nitrogen in both media; the fixation process seemed to be comparatively efficient, since the appearance of the cultures showed plainly that only a small proportion of the organic material, especially of the straw, had been used up. The experiment was repeated with a few other organisms; finely ground, water-extracted dry material of *Paspalum dilatatum*, containing 1.38% Total-N, was also tested. In the first series the medium consisted of 1.0 gm. straw and 100 c.c. basal solution with 1.0 mgm.  $\text{NH}_4\text{-N}$  in 250 c.c. round flasks. After 4 days' growth of the cellulose-decomposers, 4 drops of broth culture of *Cl. butyricum* were added; this inoculum was included in the initial control determination of nitrogen. The residue of dry insoluble matter in the straw was determined at the termination of the experiment as well as initially, by acidification with dilute HCl, filtering through a dry and tared filter, washing with distilled water, and drying at 98°C.; the residue was then added to the filtrate and washings, and total nitrogen determined. The second medium consisted of 0.5 gm. *Paspalum*-material and 30 c.c. basal solution in 50 c.c. flasks; one drop of broth culture of *Cl. butyricum* was added after 2 days' growth of the cellulose-decomposers. *Azotobacter* was also tested in a few cultures. The results are seen in Table 6.

All cultures in the straw-medium, also of *Cl. butyricum* alone, showed within 24 hours after inoculation with the clostridia a vigorous fermentation which gradually subsided and had almost ceased when the experiment was concluded. The two fungi

TABLE 6.

*Nitrogen Fixation in Combined Cultures of Cl. butyricum and Aerobic Cellulose-decomposers on Wheat Straw and Paspalum-hay.*

Inoculum.	Incubation, Days.	Dry Residue, Gm.	Nitrogen, Mgm.	
			Per Culture.	Gain.
Control .. .. .	0	0.764	3.19	—
<i>Cl. butyricum</i> .. .. .	40	0.770	3.05	(-0.14)
„ „ + <i>Cellvibrio</i> G2 .. .. .	40	0.736	3.67	0.48
„ „ + <i>Actinomyces</i> .. .. .	40	0.722	3.29	(0.10)
„ „ + <i>Trichoderma</i> .. .. .	40	0.744	3.38	(0.19)
„ „ +Fungus "P" .. .. .	40	0.762	3.38	(0.19)

Series II: 0.5 gm. H<sub>2</sub>O-extr. *Paspalum*-hay.—Incubated 28 days.

Inoculum.	Total N, Mgm.	Inoculum.	Total N, Mgm.
Control, initially .. .. .	6.25	<i>Trichoderma</i> (1) .. .. .	6.13
<i>Cl. butyricum</i> .. .. .	5.87	„ + <i>Azotobacter</i> (1) .. .. .	6.02
<i>Cellvibrio</i> G2 .. .. .	6.18	„ + <i>Cl. butyricum</i> .. .. .	6.25
„ „ + <i>Cl. butyricum</i> .. .. .	5.99	„ + „ „ + <i>Azotobacter</i> .. .. .	6.62
„ „ + „ „ + <i>Azotobacter</i> .. .. .	6.34		

Averages of duplicates, except those marked (1), which represent single cultures.

and the actinomyces produced a good growth, but only the cultures of *Cellvibrio* + *Cl. butyricum* showed a significant, although small, gain of nitrogen. The loss of insoluble constituents in the straw was in all cases comparatively slight, since it did not exceed 6% of the initial amount, whereas of the filter paper cellulose some 20% to 40% was decomposed in a similar length of time (Tables 1-2). It must be admitted, indeed, that in the cultures of the fungi and the actinomyces the actual losses are somewhat larger than they appear, since the residues contain a certain amount of synthesized mycelial substance, but generally it seems clear that the lignified cellulose and hemicelluloses in the straw are much less readily attacked than the filter paper cellulose or the artificially prepared xylan, at least by the organisms here examined, and under conditions of nitrogen shortage.\* The efficiency of nitrogen fixation in the *Cellvibrio*-cultures cannot be directly calculated, since we do not know how big a proportion of the water-soluble constituents of the straw has been used up. Assuming complete utilization, however, the minimum would be:  $0.48 / (0.953 - 0.736) = 2.2$  mgm. N per gm. dry matter lost. In the experiment with *Paspalum*-hay there was a gas evolution in all *Clostridium*-cultures, quite strong at first but gradually disappearing; only the combination of *Trichoderma*, *Clostridium* and *Azotobacter* gives rise to a significant, but small, gain of nitrogen.

#### Conclusions.

These and previous investigations show that the simplest microbial associations by which nitrogen may be fixed at the expense of cellulose are the following:

1. *Azotobacter* + aerobic cellulose-decomposers (fungi), provided that oxygen is periodically excluded (Vartiovaara, 1938).
2. *Azotobacter* + facultative anaerobic cellulose-decomposing corynebacteria (Jensen, 1940b; Jensen and Swaby, 1941).
3. *Clostridium butyricum* + aerobic cellulose-decomposers: fungi (Vartiovaara, 1938) or cellvibrios.
4. *Cl. butyricum* + facultative anaerobic corynebacteria.

\* Cf. Olsen (1932), who found that beech and oak leaves lost from 7% to 20% of their total dry matter in 3 months, and only 15% to 36% in 10 months.

- (5. Definitely pure cultures of obligate anaerobic cellulose-decomposing bacteria have not been tested in this respect, but it is well known that *Azotobacter* as well as clostridia can fix nitrogen in association with their impure and presumably also their pure cultures.)

The nitrogen fixation by combinations (1) and (4) is slight, but in (2) and (3) its efficiency in terms of nitrogen fixed per unit of cellulose destroyed is equal, or at least comparable, to that which it is in impure mixtures of organisms (Jensen, 1940*a-b*). In all cases, however, it appears that a certain degree of anaerobiosis is necessary to bring about an active fixation. This explains fully why little or no nitrogen is fixed in well-aerated soil with addition of cellulosic materials (Jensen, 1940*a*). Even in constantly water-saturated soil with addition of straw the fixation of nitrogen by clostridia may be slight or negligible (Jensen and Swaby, 1940), probably because of the slow rate of decomposition of the lignified straw cellulose, together with the equally important fact that the highest efficiency of nitrogen fixation is not attained in the early stages of the process, whether the active microbic association consists of *Azotobacter* + corynebacteria (Jensen and Swaby, 1941) or of *Clostridium* + cellvibrios. It is therefore hardly to be expected that the nitrogen fixation in soil during brief intermittent periods of water-saturation will reach an effective stage, although the clostridia certainly can show rapid development under these conditions (Jensen and Swaby, 1940). In Australian wheat soils the conditions for co-operation between nitrogen-fixing and cellulose-decomposing organisms are generally not favourable, as previously discussed (Jensen and Swaby, 1941), but where suitable conditions prevail for longer periods, it seems likely that the nitrogen-fixing effect of the clostridia may approach or even rival that of *Azotobacter*. Further, the clostridia may be of great indirect significance by fermenting certain intermediate decomposition products of cellulose and thus rendering them available to *Azotobacter*, as suggested by the data in Tables 1, 4 and 6.

#### SUMMARY.

*Clostridium butyricum* was found able to develop in symbiosis with several aerobic cellulose-decomposing organisms, viz., *Cellvibrio*, *Corynebacterium*, "*Cellulobacillus*", fungi and actinomycetes, but not *Cytophaga*. Growth of the clostridia was accompanied by a decline in the oxidation-reduction potential to Eh = -0.35 to -0.40 volt. An appreciable quantity of nitrogen was fixed only when the clostridia were associated with one particular strain of *Cellvibrio* (*vulgaris*?); the yield of fixed nitrogen in these cultures could reach 6.9 mgm. per gm. of cellulose decomposed, and could rise to nearly 12 mgm. in combined cultures of *Clostridium*, *Cellvibrio* and *Azotobacter*, the last of which was unable to fix significant amounts of nitrogen by direct association with *Cellvibrio*. The efficiency of the process of nitrogen fixation appeared to increase with advancing age of the cultures. Hemicellulose in the form of crude xylan, and natural cellulosic materials like wheat straw and grass, could also be utilized for nitrogen fixation, but the straw and grass much less readily than filter paper cellulose.

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## SOME NEMATODE PARASITES OF AUSTRALIAN BIRDS.

By T. HARVEY JOHNSTON and PATRICIA MAWSON, University of Adelaide.

(Twenty-two Text-figures.)

[Read 30th July, 1941.]

The parasites under review include members of the Trichurata, Strongylata, Ascaridata, and Spirurata. The material has been collected by the late Dr. T. L. Bancroft of Eidsvold, Queensland; Professor J. B. Cleland of Adelaide; Dr. D. Brummitt of Adelaide; members of the Ralph Tate Society, Adelaide; and the senior author. Four of the hosts are not native Australian birds. The study has been made possible by the Commonwealth Research Grant to the University of Adelaide. Types of new species have been deposited in the South Australian Museum.

The following is a list of parasites arranged under their hosts:

- STREPERA FULIGINOSA Gould (Coorong, S. Aust.). *Acuaria streperina*, n. sp.  
 STREPERA MELANOPTERA Gould (Flinders Chase, Kangaroo I.). *Acuaria streperina*, n. sp.  
 STREPERA VERSICOLOR Lath. (Mt. Kosciusko and Sydney, N.S.W.). *Porrocaecum streperae*, n. sp.  
 CORACINA NOVAE-HOLLANDIAE Gm. (West Burleigh, Qd.). *Capillaria graucalina*, n. sp.  
 HETEROPSAR ALBICAPILLUS Blyth. (Adelaide Zoological Gardens). *Syngamus gracilis* Chapin.  
 CINCIOSOMA PUNCTATUM Lath. (Launceston, Tas.). *Porrocaecum clelandi*, n. sp.  
 OREOCINCLA LUNULATA Lath. (Bunya Mts., Qd.). *Porrocaecum clelandi*, n. sp.  
 ANTHUS AUSTRALIS Vieill. (Encounter Bay, S. Aust.). *Porrocaecum clelandi*, n. sp.  
 MYZANTHA FLAVIGULA Gould (Renmark, S. Aust.). *Porrocaecum* sp., larvae.  
 MYIAGRA RUBECULA Lath. (Stradbroke I., Qd.). *Rictularina spinosa*, n. gen., n. sp.  
 PHILEMON CITREOGULARIS Gould (Burnett R., Qd.). *Oxyspirura bancrofti*, n. sp.  
 POMATOSTOMUS SUPERCILIOSUS Vig. & Horsf. (Baradine, N.S.W.). *Seuratinema pomatostomi*, n. sp.  
 SCYTHROPS NOVAE-HOLLANDIAE Lath. (Eidsvold, Qd.). *Subulura clelandi*, n. sp.  
 PODARGUS STRIGOIDES Lath. (Perth, W. Aust.; Eidsvold, Qd.). *Subulura clelandi*, n. sp.  
 HALCYON SANCTUS Vig. & Horsf. (Milson I., N.S.W.; Stradbroke I., Qd.). *Cheilonematodum halcyonis*, n. gen., n. sp.  
 DACELO GIGAS Bodd. (Pilliga Scrub, N.S.W.). *Seuratinema magnum*, n. sp.  
 COLUMBA LIVIA Linn. (Adelaide; Melbourne). *Capillaria columbae* (Rud.) (Adelaide; Sydney; Melbourne; Brisbane). *Ascaridia columbae* (Gm.).  
 LEUCOSARCIA MELANOLEUCA Lath. (Burnett R., Qd.). *Heterakis bancrofti* Johnston.  
 FRANCOLINUS CHINENSIS Osbeck. (Sydney Zoological Gardens). *Heterakis gallinae* (Gm.).  
 ALECTURA LATHAMI Gray (Burnett River, Qd.). *Heterakis bancrofti* Johnston.  
 GALLUS DOMESTICUS (Adelaide; Melbourne; Sydney). *Heterakis gallinae* (Gm.).  
 EUPODOTIS AUSTRALIS Gray (Mt. Liebig, Central Aust.). *Cyrnea dentifera*, n. sp.  
 CACATUA LEADBEATERI Vig. (Sydney Zoological Gardens). *Heterakis gallinae* (Gm.).  
 DOMICELLA GARRULA FLAVOPALLIATA Salvad. (Sydney—from East Indies). *Ascaridia columbae* (Gm.).

## TRICHURATA.

## CAPILLARIA GRAUCALINA, n. sp. Figs. 1-2.

From *Coracina novaehollandiae* from West Burleigh, southern Queensland. A male and a female present; male 16.3 mm. long, 80 $\mu$  maximum width; female 27.3 mm. long, 110 $\mu$  maximum width. Ratio of lengths of oesophageal to intestinal regions about 1:2 in

female (9.4:17.9 mm.), and 7:8 in male (7.7:8.6 mm.). Male  $6\mu$  across head,  $70\mu$  across body at junction of oesophagus and intestine. Bursa formed by two lateral flaps overhanging posterior end of body. Cloaca subterminal. Spicule 1.8 mm. long, stout, cylindrical, ending in rounded tip. Female  $8\mu$  across head,  $65\mu$  across body at base of oesophagus,  $50\mu$  across body at level of anus; tail  $20\mu$  long. Vulva just posterior to oesophagus, its position marked by a protrusion of vagina and body wall. Eggs  $55\mu$  by  $30\mu$ , the given length including that of polar plugs.

CAPILLARIA COLUMBAE (Rud. 1819).

From *Columba livia*, from Adelaide and Melbourne. Many specimens, length agreeing with that given by Baylis (1929, 264).

STRONGYLATA.

SYNGAMUS GRACILIS Chapin 1925.

From the trachea of a white-capped starling, *Heteropsar albicapillus*, from the Adelaide Zoological Gardens. McLennan (1933) referred to the occurrence, identifying the parasite as *Syngamus trachea*.

ASCARIDATA.

SUBULURA CLELANDI, n. sp. Figs. 3-4.

From *Podargus strigoides* (type host) from Perth, Western Australia (type locality; coll. Dr. Cleland) and Eidsvold, Queensland (coll. Dr. Bancroft); and from *Scythrops novae-hollandiae* from the latter locality.

Males 8-9 mm. long, 0.24 mm. wide; females 12-15 mm. long, 0.42 mm. wide. Head with six small papillae. Lateral cuticular alae extending a short distance beyond the level of the end of the oesophagus. Buccal capsule strongly chitinized;  $60\mu$  long,  $50\mu$  wide (latter measurement including walls  $10\mu$  thick) in female. Oesophagus 1.2 mm. and 1.4 mm. long in male and female respectively; bulb longer than broad, 0.19 mm. by 0.17 mm. in female. Nerve ring around oesophagus at end of first quarter of length.

Male. Tail 0.28 mm. long, including narrow terminal whiplike portion  $85\mu$  long. Five pairs preanal and five pairs post-anal papillae arranged as in Fig. 4. Spicules equal, 0.91 mm. long, with two dorsally directed spurs at  $80\mu$  and  $40\mu$  respectively from its distal end. Sucker very poorly developed, its centre 0.42 mm. in front of cloaca.

Female. Tail 0.85 mm. long, ending as in male in whiplike part. Vulva just in front of midbody at 5.8 mm. from head (at 1:2.2 of body length).

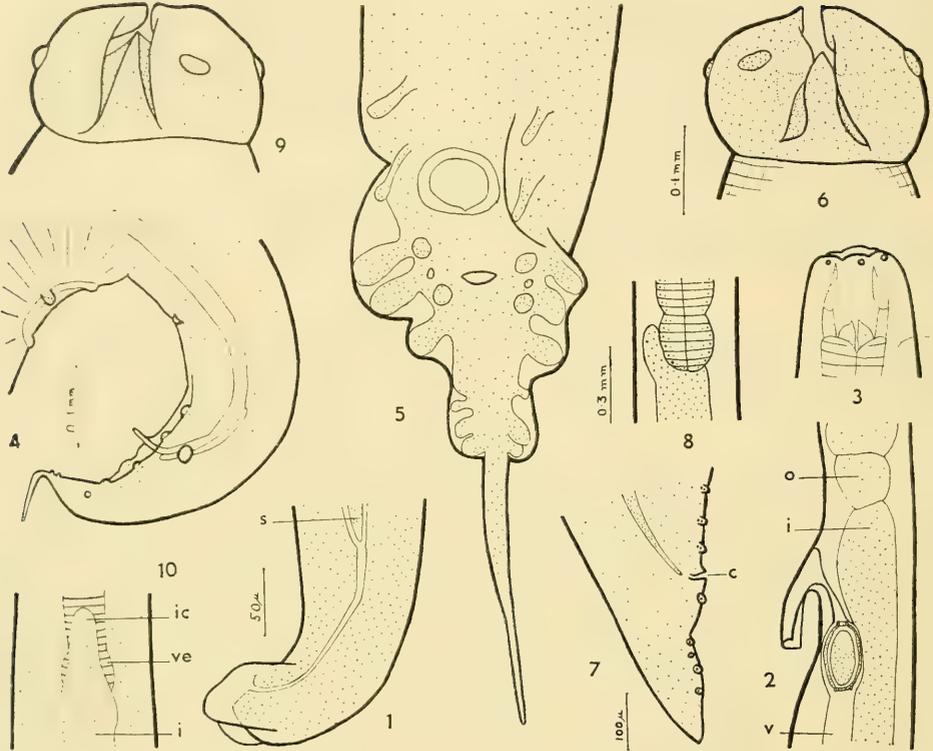
The species differs from *S. acutissima* (Molin) in its length; from *S. brumpti* Lopez Neyra in the position of the vulva, and in the length of the gubernaculum and spicules. It differs from *Subulura* sp. Justn. & Mawson (1941) from *Ninox strenua* in the size of the eggs, length of tail, and the shape of the oesophageal bulb. It is very close to *S. differens* (Sonsino), but differs in being larger and also in having relatively shorter spicules and smaller eggs.

HETERAKIS BANCROFTI Johnston 1912. Fig. 5.

Some specimens were examined from the type host, *Alectura lathamii*, from Eidsvold, Burnett R. The species is also now recorded from *Leucosarcia melanoleuca* from the same district (coll. Dr. Bancroft). Specimens from *A. lathamii* were longer than those recorded by Johnston and more papillae were seen on the male tail. The general description of the new material agrees with the earlier account. Its measurements are as follows: Female: 8-9 mm. long; oesophagus 0.85 mm. long; nerve ring 0.25 mm. from head; tail 0.9 mm. long; vulva just behind midbody; eggs  $65-70\mu$  by  $40\mu$ . Male: 5-7 mm. long; width 0.34 mm.; spicule length 1.23 mm.; distance from posterior border of sucker to cloaca 0.05 mm., and from cloaca to tip of tail 0.36 mm.; length of narrow part of tail posterior to alae 0.21 mm.; sucker  $65\mu$  across and  $53\mu$  long; caudal alae widest just anterior to sucker; eight pairs pedunculated papillae supported by alae, and three pairs sessile papillae adanally, arranged as in Fig. 5.

HETERAKIS GALLINAE (Gmelin 1790).

This common parasite was obtained from *Francoelinus chinensis* and *Cacatua leadbeateri* from the Sydney Zoological Gardens; and the domestic fowl from Adelaide, Melbourne and Sydney.



Figs. 1-2.—*Capillaria graucalina*, n. sp. 1, male tail; 2, vulvar region of female. Figs. 3-4.—*Subulura clelandi*, n. sp. 3, head; 4, male tail. Fig. 5.—*Heterakis bancrofti* Johnston, male tail. Figs. 6-8.—*Porrocaecum clelandi*, n. sp. 6, head; 7, male tail; 8, junction of intestine and oesophagus. Figs. 9-10.—*Porrocaecum streperae*, n. sp. 9, head; 10, posterior end of oesophagus. Figs. 1, 2, 3 and 5 drawn to same scale, beside 1; figs. 6, 9 and 10, beside 6. c, cloaca; i, intestine; ic, intestinal caecum; o, oesophagus; s, spicule; v, vagina; ve, ventriculus.

*PORROCAECUM CLELANDI*, n. sp. Figs. 6-7.

Material consists of male 30 mm. long, 0.72 mm. wide, from a thrush, *Oreocincla lunulata* (type host) (Bunya Mts., Queensland); a female 50 mm. long, 0.73 mm. wide, from another thrush, *Cinclosoma punctatum*, from Launceston, Tasmania; and a male 40 mm. long, 0.73 mm. wide, from a ground lark, *Anthus australis*, from Encounter Bay, S. Aust.; all material collected by Dr. Cleland. Head 0.27 mm. broad, distinctly wider than succeeding body; dentigerous ridge on each lip long, continuing on lateral flanges almost to base of lip; interlabia about two-thirds length of lips, to which they are joined internally near their tips; two papillae on dorsal lip, one on each ventral lip. Oesophagus 2.96 mm. long; intestinal caecum (seen only in specimen from *Anthus australis*) very short, 0.2 mm. long; ventriculus 0.3 mm. long. Nerve ring in type specimen 0.7 mm. from head.

Male. Tail tapering to blunt point; spicules almost equal, 0.54 mm. long; thirteen pairs preanal papillae, five pairs post-anal, arranged as in Fig. 7.

Female. Tail elongate, tapering, 0.64 mm. long; vulva at end of anterior third of body length; eggs not present. Our species differs from *P. ensicaudatum* (Zeder) and *P. cheni* Hsü (in both of which the intestinal caecum is rudimentary) in the number of post-anal caudal papillae in the male; and from the latter species in the position of the vulva. The lengths of oesophagus and spicules in *P. ensicaudatum* are not available.

## PORROCAECUM STREPERAE, n. sp. Figs. 8-9.

From intestine of *Strepera versicolor* (type host) from Mt. Kosciusko and from Sydney, N.S.W. Each collection contained one female only. Length 35-40 mm., width 0.88 mm. Head rather narrower than succeeding body. Each lip with narrow cuticular flange on either side and without dentigerous ridge. Interlabia pointed, nearly as long as lips, joined to latter internally near their tips. Oesophagus 2.2 mm. long, ending in spherical bulb (ventriculus) separated from rest by constriction. Intestinal caecum 0.1 mm. long; vulva just in front of midbody. Ripe eggs not present.

The species differs from *P. clelandi*, described above, in the absence of dentigerous ridges on the lips, and in the presence of a definite intestinal caecum, and in the size of the head relative to the body width. It differs from *P. wui* Hsü in the length of the intestinal caecum and in the absence of dentigerous ridges on the lips.

## PORROCAECUM SP. Larvae.

Two specimens from *Myzantha flavigula* from Renmark, S. Aust. (coll. Dr. Cleland). Lips undeveloped, intestinal caecum present; length 8-10 mm. The adult stage possibly occurs in a hawk.

## ASCARIDIA COLUMBAE (Gmelin 1790).

From *Columba livia* in Adelaide, Sydney, Melbourne and Brisbane; and from *Domicella garrula* var. *flavopalliata* (Syn. *Lorius flavopalliatius*), Sydney Zoological Gardens.

## SPIRURATA.

## CHEILONEMATODUM HALCYONIS, n. gen., n. sp. Figs. 11-12.

Material consists of a male worm from *Halcyon sanctus* from Stradbroke Island, Queensland; and a male and female from the same host species from Milson Island, Hawkesbury River, N.S.W.

The specimens from Milson Island were obscured by a black pigment with which they had come in contact and which had penetrated the body cavity and mouth. The worms were very fragile so that only a sublateral view of the lips could be obtained.

Male 16-18.5 mm. long, 0.65-0.7 mm. wide; female 20 mm. long, 0.68 mm. wide. Anterior end with two lips, each with median projection. Lips free on external surface but joined to interlabia internally. Interlabia present, their form not determined in lateral view. Each lip with two large papillae. Mouth leading to chitinized buccal capsule 40 $\mu$  long and 12 $\mu$  wide. Oesophagus narrow, straight, 3.1 mm. long in male, 3.5 mm. in female; anterior part rather narrower, 0.82 mm. long in male, 0.9 mm. in female. Nerve ring 0.23 mm., and excretory pore 0.35 mm. from head end.

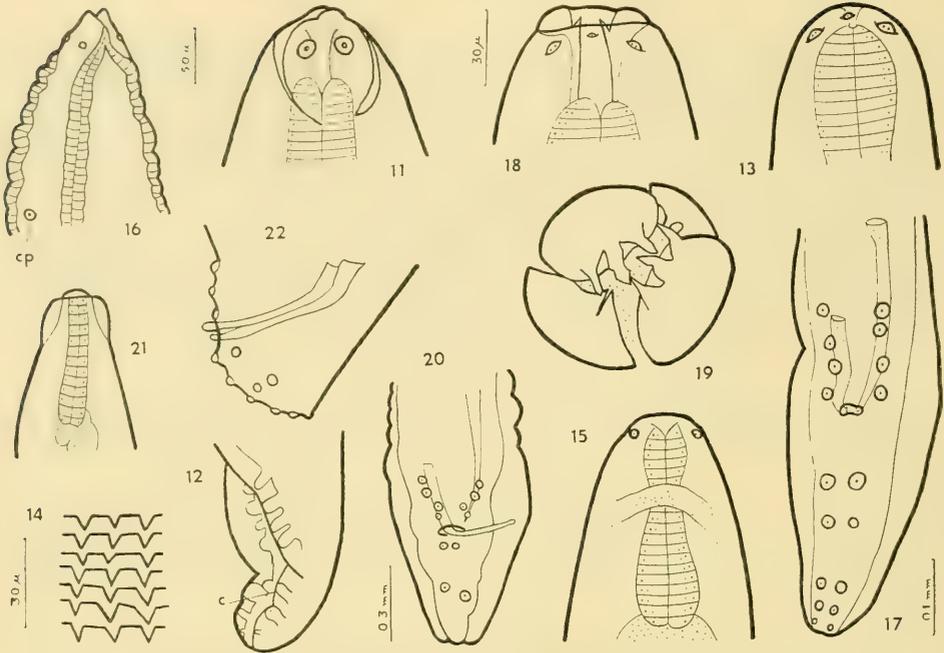
Male. Posterior end coiled; cloaca 90 $\mu$  from rounded tip; caudal alae wide; four pairs preanal and three pairs post-anal papillae in alae, and a pair sessile papillae adanally; spicules unequal; longer narrow tubular, 0.12-0.15 mm. in length; shorter spatulate, 0.07-0.08 mm.

Female. Position of anus not clearly seen, but most probably near tip of rounded tail; vulva at midbody; uteri opposed; eggs thick shelled, 26-28 $\mu$  by 45-48 $\mu$ .

The genus is probably nearest to the Habronematinae as defined by Chitwood and Wehr (1934). Since the shape of the interlabia is unknown, it is difficult to classify it definitely. It differs from the Hedrurinae in the structure of the male tail (caudal alae present, spicules unequal), but agrees in having only the four submedian papillae on the head. In the latter feature as well as in the shape of the lateral lips it differs from any known genus of *Habronematinae*. We suggest a new genus, *Cheilonematodum*, diagnosed as follows: Habronematinae?: Anterior and posterior ends rounded, anterior with two lateral lips each with a median projection; interlabia present; vestibule followed by long narrow oesophagus with two distinct parts.

Male: With wide caudal alae supporting pre- and post-anal papillae; spicules unequal; gubernaculum absent.

Female. With vulva at mid-body; opisthodelphous; eggs thick-shelled. Parasites of birds. Type species, *C. halcyonis*, n. sp.



Figs. 11-12.—*Cheilonematodum halcyonis*, n. gen., n. sp. 11, head; 12, male tail. Figs. 13-14.—*Rictularina spinosa*, n. gen., n. sp. 13, head; 14, part of cuticle of midbody. Fig. 15.—*Seuratinema magnum*, n. gen., n. sp., anterior end. Figs. 16-17.—*Acuarina streperina*, n. sp. 16, head; 17, male tail. Fig. 18.—*Oxyspirura bancrofti*, n. sp., head. Figs. 19-20.—*Cyrnea dentifera*, n. sp. 19, head, face view; 20, male tail. Figs. 21-22.—*Seuratinema pomatostomi*, n. gen., n. sp. 21, head; 22, male tail. Figs. 11, 13 and 16 to same scale, beside 11; figs. 12, 17 and 22, beside 17; figs. 15, 20 and 21, beside 20. c, cloaca; cp, cervical papilla.

*RICTULARINA SPINOSA*, n. gen., n. sp. Figs. 13-14.

From the leaden fly-catcher, *Myiagra rubecula*, from Stradbroke Island, Queensland. A female and a very young worm present. Body stout, 8.5 mm. long, 0.4 mm. maximum breadth. Head rounded, with four large submedian and two small more anteriorly situated lateral papillae. Mouth leading to funnel-shaped vestibule  $20\mu$  long; oesophagus 0.6 mm. long, swollen anteriorly and posteriorly. Nerve ring 0.2 mm. from head; excretory pore just behind that level. Cuticle strongly annulated, anterior border of each annulation overlapped by the one preceding it; each annulation with about eighty-two short, triangular, posteriorly directed hooks on its posterior border, arranged in longitudinal rows converging anteriorly and posteriorly. Vulva behind middle of body, 3.6 mm. from posterior end; tail short, conical, pointed, 0.3 mm. long. Ripe eggs not present.

The presence of hooks indicates a member of the Rictulariinae but their arrangement does not agree with that in any previously described genus. A new genus, *Rictularina*, is therefore proposed, with the following diagnosis: Rictulariinae: Head rounded, lips absent; six cephalic papillae. Cuticle strongly annulated, each ring with numerous hooks arranged in longitudinal rows, continuous over whole of body. Oesophagus short, muscular, swollen anteriorly and posteriorly. Male unknown. Female with short conical tail; vulva behind middle of body. Parasites of birds. Type species, *R. spinosa*, n. sp.

*ACUARIA (CHELOSPIRURA) STREPERINA*, n. sp. Figs. 16-17.

From *Strepera fuliginosa* (Coorong, S. Aust.; coll. Dr. D. Brummitt) and *S. melanoptera* (Kangaroo Island, obtained by the Ralph Tate Society). One female 9.5 mm. long, 0.26 mm. wide, from former host; two females 13-15 mm. long, 0.32 mm. wide, and one male 8 mm. long, 0.31 mm. wide, from *S. melanoptera*, which is the type host.

Head typical of genus; cordons prominent, continuing beyond oesophageal region before disappearing, relatively longer in female. Cervical papillae round, 0.19 mm. from head; vestibule 0.18 mm. long in female, 0.12 mm. in male; oesophagus 0.7 mm. long in male and 0.8 mm. in female.

Male. Caudal alae slightly unequal, being a little longer on same side as shorter spicule (i.e., extending about 0.55 mm. from posterior end of body); spicules unequal, 0.1 mm. and 0.26 mm. long, similar in shape, massive, tapering; four pairs preanal and five pairs post-anal papillae arranged in two longitudinal rows.

Female. Body narrowing suddenly just in front of anus; tail short, rounded, 0.23 mm. long; vulva at midbody; eggs thick-shelled, 35–37 $\mu$  by 23 $\mu$  in uterus, one in vagina 27 $\mu$  by 40 $\mu$ .

The species is very like *A. corvicola* Jnstr. & Mawson, but differs in the relative lengths of the oesophagus and cordons, and in the size of the eggs.

OXYSPIRURA BANCROFTI, n. sp. Fig. 18.

From *Philemon citreogularis*, from Eidsvold, Queensland (coll. Dr. Bancroft). Two specimens and several broken pieces present, all apparently immature. Complete worms 10.4 mm. and 12.8 mm. long, 0.23 mm. wide. Head with two lateral papillae 10 $\mu$  from anterior end, and four submedian papillae 15 $\mu$  from end. Buccal capsule 39 $\mu$  long, 12 $\mu$  wide, its strongly chitinized walls 2–3 $\mu$  thick, continuous anteriorly with a chitinized ring around mouth and bearing near its anterior end six sharply pointed teeth projecting into mouth. Oesophagus 3.6 mm. long, anterior 0.3 mm. narrower than the rest. Nerve ring 0.2 mm. from head. Tail tapering to a point, anus 0.15 mm. from tip. Vulva not observed.

In 1912 *O. acanthochaerae* was described by the senior author from another honey-eater, *Acanthochaera rufigularis*, from some poorly preserved material obtained originally by Krefft. It is difficult to compare the present specimens with that species, since the descriptions are incomplete, and on the only points at which they overlap, the worms differ (body length, positions of anus and nerve-ring, body width). The variation is not great, but pending the examination of more material from both hosts, we consider it wiser to assign the parasites from *Philemon* to a new species, *O. bancrofti*.

CYRNEA DENTIFERA, n. sp. Figs. 19–20.

From the bustard, *Eupodotis australis*, Mt. Liebig, Central Australia. Several specimens, bodies rather wrinkled and darkened. Males about 10 mm. long, females up to 16 mm. Head with four lips, the two laterals being wider; three teeth on each lateral, two each on dorsal and ventral lips. Cephalic papillae obscure, probably two on each dorsal and ventral lip and one on each lateral. Oesophagus 4.32 mm. long (in male); anterior region 0.48 mm. long, narrower than remainder. Nerve ring 0.36 mm. from head.

Male. Ventral surface of alae and tail raised into longitudinal ridges extending anteriorly for about 1.9 mm. in front of cloaca. Alae 0.8 mm. long, widest at anterior ends, narrowing to joint at posterior end of body. Spicules unequal; longer 2.7 mm. in length, narrow, with rounded tip; shorter about 0.5 mm., ending in rounded knob. Gubernaculum about 0.1 mm. long. Papillae symmetrically arranged, four pairs precloacal, a pair immediately postcloacal, and a pair half-way between cloaca and tip of tail. Tail 0.4 mm. long.

Female. Tail 0.22 mm. long, rounded. Vulva not observed. Uteri full of eggs, latter largest near middle of body, so vulva is presumably in that region. Eggs thick-shelled, 26 $\mu$  by 40 $\mu$ .

The species is nearest to *C. excisa* (Molin), from which it differs in the relative lengths of the spicules and in the size of the eggs. Teeth are not described as occurring on the dorsal and ventral lips of that species.

SEURATINEMA POMATOSTOMI, n. sp. Figs. 21–22.

From *Pomatostomus superciliosus*, from Baradine, N.S.W. (coll. Dr. Cleland). Male 8 mm. long, 0.72 mm. wide; female 22 mm. long, 1 mm. wide. Head rounded, mouth dorsoventrally elongate; no cephalic papillae. Cervical cuticle inflated in region

commencing (in male) 0.03 mm. from head end and extending to a point 0.2 mm. from head, forming a collarette around base of lips. Oesophagus cylindrical, clubshaped, short, 0.5 mm. long in male, 0.82 mm. in female. Nerve ring at level of base of cervical inflation.

Male. Spicules equal, 0.2 mm. long; tail 0.12 mm. long, conical; three pairs preanal and eight pairs post-anal papillae arranged as in Fig. 12.

Female. Tail long, tapering, rounded at tip; position of vulva not determined, but eggs most numerous near middle of body; uteri not extending into anterior quarter of body.

The species is referred to *Seuratinema* Jnstr. & Mawson (1941) in view of characters of the head and male tail; it differs from the only other species described for the genus in its smaller size and in the greater number of caudal papillae in the male.

#### SEURATINEMA MAGNUM, n. sp. Fig. 15.

From *Dacelo gigas*, from the Pilliga Scrub, north-western New South Wales (coll. Dr. Cleland). Only a very large female obtained. Body shrivelled, greatly twisted by preservation; when pulled as straight as possible length 40 mm., but probably nearer 50 mm., width 3.5 mm. Body tapering suddenly at head end, more gradually to tail. Head with two low lips, each with two submedian papillae. Oesophagus 0.8 mm. long, muscular, with constriction 0.3 mm. from its anterior end; nerve ring around constriction. Tail end shrivelled, rectum and anus not visible. Greatest development of uteri and ripest eggs found in middle of body; vulva not seen but presumably lies in that region. Uterine tubes not approaching oesophageal region. Eggs subglobular, thick-shelled, about 50 $\mu$  diameter.

The species resembles *Seuratinema* in the characters of the head, but differs in the shape of the oesophagus and in the absence of inflated cervical cuticle. In view of the condition of the material the species is assigned provisionally to that genus.

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NOTES ON THE KAMILAROI STRATIGRAPHY IN THE WESTERN COALFIELD OF  
NEW SOUTH WALES.

By J. A. DULHUNTY, B.Sc., Linnean Macleay Fellow of the Society in Geology.

(Plate ix; four Text-figures.)

[Read 27th August, 1941.]

*Introduction.*

In connexion with an investigation of the stratigraphical arrangement of the torbanite deposits in the Upper Coal Measures of the Kamilaroi Basin of New South Wales, it was found necessary to carry out a limited amount of stratigraphical work along the western margin of the basin, from the Burrigorang Valley in the south to the Goulburn Valley in the north (see Index Map, Fig. 1). The principal objects of this work were the determination of horizons representing the upper and lower stratigraphical limits of the Upper Coal Measures, the relation between the Marangaroo Conglomerate Beds and the coal-measures throughout the different districts of the Western Coalfield, and the continuity and arrangement of the principal coal-bearing horizons. Only the upper portion of the Kamilaroi is present in the western districts, consisting of Upper Coal Measures overlying Upper Marine Beds.

A considerable mass of data, obtained by the Geological Survey of New South Wales and other investigators, is available concerning the general stratigraphy of the coal-measures in the Burrigorang Valley and the Blue Mountains, and at points between Lithgow, Kandos and Rylstone. Several reports of a reconnaissance nature have been made by the Geological Survey, dealing with the Ulan-Wollar-Barigan coal-measures.

Coal-measures outcropping to the south of the Goulburn River, from Bylong to the vicinity of Sandy Hollow and as far south as Rylstone, have received but little geological attention and have not been surveyed. These coal-measures, together with those of the Ulan-Wollar-Barigan area, should assume importance when the Sandy Hollow-Maryvale railway is completed. In view of these facts and the limited amount of detailed information available concerning the Ulan-Wollar-Barigan area, it was considered essential to include in the present paper a geological map (Plate ix) showing the outcrop of Upper Coal Measure strata and associated formations along the southern side of the Goulburn River between Ulan, Rylstone and Baerami. Numerous igneous bodies in the form of flows, laccoliths, sills and necks occur between Rylstone, Barigan and Kerrabee. These are not shown on the map as their investigation does not come within the scope of the present work.

*The Marangaroo Conglomerate Beds.*

Beds of conglomerate and sandstone, known as the Marangaroo Conglomerate, have attracted much attention as an important and persistent feature occurring at or near the base of the Upper Coal Measures in the Western Coalfield. Carne (1908) described the Lithgow Coal Seam as the lowest in the Western Coal Measures, occurring immediately above the Marangaroo Conglomerate. This was found to hold good for areas lying immediately to the north and north-east of Wallerawang, but between Marangaroo and Lithgow, the Lithgow Coal Seam occurs directly beneath a thick bed of quartz-pebble conglomerate similar in every respect to the Marangaroo Conglomerate. The same difficulty arose in other districts, the coal-seam appearing sometimes above and sometimes below the conglomerate. A suggested explanation of the relation between the Marangaroo Conglomerate and the Lithgow Coal Seam was put forward by Andrews and Morrison (1926). They considered that there were two stages or members of the

Marangaroo Conglomerate separated by the Lithgow Coal Seam, the upper member being more pronounced to the south and south-east of Marangaroo Railway Siding, and the lower more pronounced to the north and north-west. This explained the apparent anomaly of the Lithgow Seam appearing above the Marangaroo Conglomerate in some places, and beneath it in others.

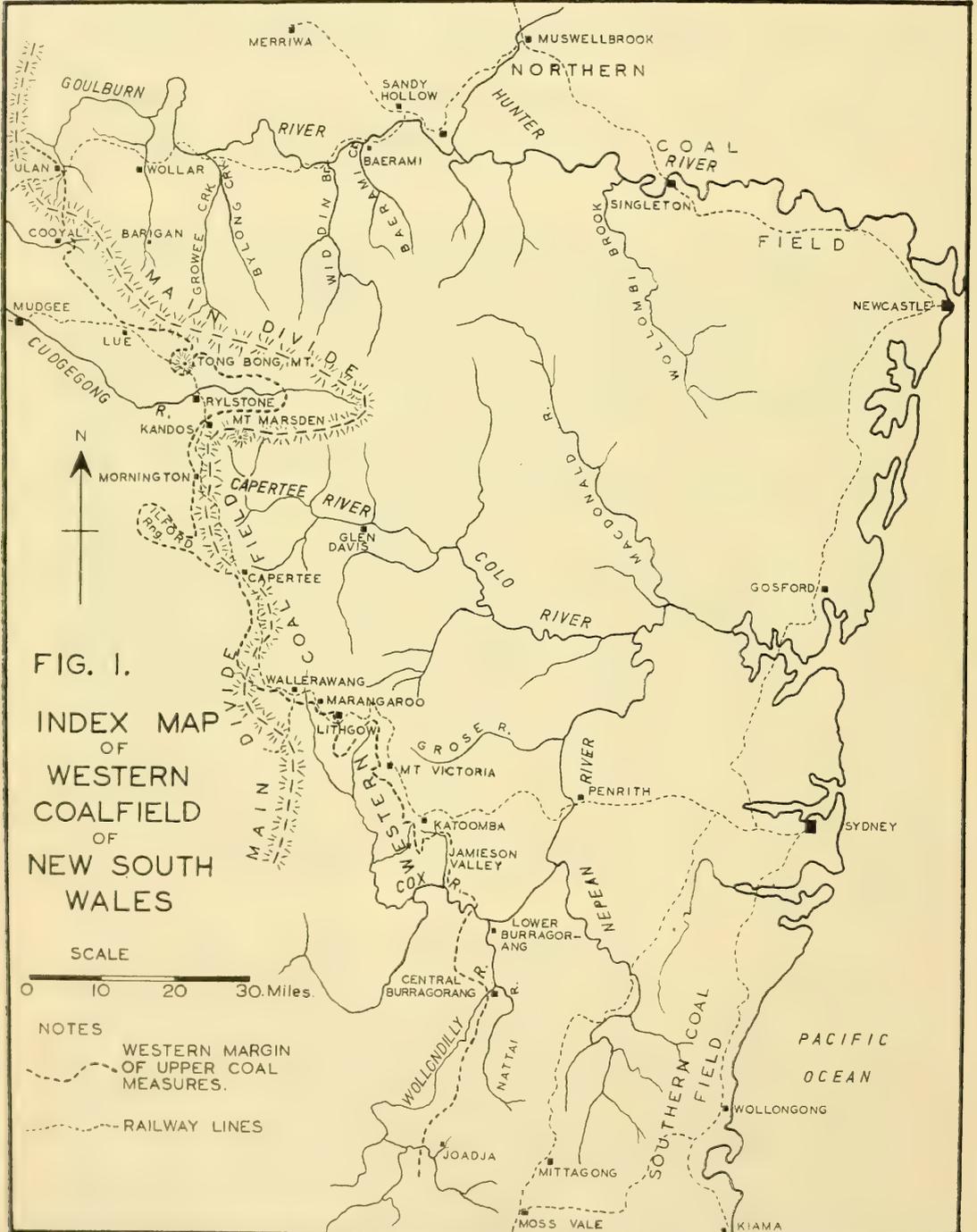


FIG. 1.  
INDEX MAP  
OF  
WESTERN  
COALFIELD  
OF  
NEW SOUTH  
WALES

Fig. 1.

For the purpose of description, the two conglomerate beds and the coal-seam will be referred to as the Marangaroo Beds. The relations between these beds have recently been examined by the writer, and the conclusions of Andrews and Morrison have been confirmed in every respect. It has been possible to establish beyond all reasonable doubt, the continuity of the beds from Ulan in the north to the vicinity of Joadja in the south, a distance of 155 miles.

The Marangaroo Beds attain their maximum development in the vicinity of Marangaroo and Wallerawang, where they represent shoreline deposits consisting of coarse quartz-pebble conglomerates. The horizon of the Lithgow Coal Seam is indicated by carbonaceous shale and mudstone in the marginal facies of the Marangaroo Beds, where they outcrop immediately to the north of the point where the main road passes over the old Marangaroo railway tunnel. These shales and mudstone increase in thickness and undergo a gradual change into coal, forming the Lithgow Coal Seam, as they pass to the east. The transition from carbonaceous shale to coal is well shown in the disused railway cuttings about 10 chains south-west from the western end of the new Marangaroo railway tunnel. The general relation between the members of the Marangaroo Beds is illustrated in Fig. 2.

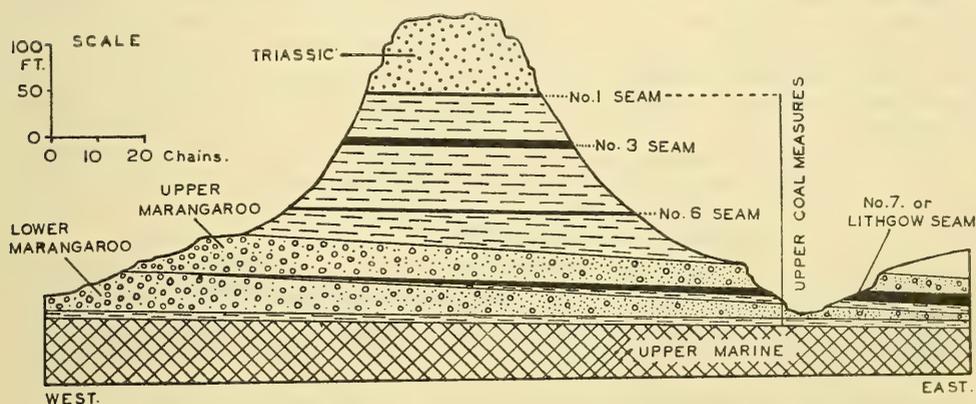


Fig. 2.—West-east section through Middle Creek Range, near the new Marangaroo railway tunnel.

The Marangaroo Beds, consisting of either the upper or lower member, and in places both, together with the Lithgow Coal Seam, constitute a remarkably persistent feature extending throughout the marginal areas of the Western Coalfield. At all places along these marginal areas, which trend from north-west to south-east, the Marangaroo Beds exhibit a rapid lithological change from conglomerate to sandstone and thin out quickly as they pass from west to east, suggesting that the present western margin of the coalfield is approximately parallel to the actual margin of the area in which the beds were deposited.

Between Wallerawang and Capertee, south of the area shown in the map (Plate ix), the lowest member of the Marangaroo Beds maintains its thickness of about 50 feet, while the upper member diminishes and eventually disappears to the north-north-west. The coal-measures outcrop in the Capertee Valley for a distance of about 20 miles east of Capertee before they dip below the level of the Capertee River to the east of Glen Davis, where the lower member of the Marangaroo Beds is present in the form of sandstone 8 to 15 feet in thickness. At places a thin sandstone bed appears above the Lithgow Coal Seam, representing the upper member. At Airly Gap and along the western escarpment of the Capertee Valley the lower member is persistent, forming a sandstone bed from 10 to 20 feet in thickness, but there is very little evidence of the upper member.

At Mornington and north-west to Tong Bong Mountain, the Marangaroo Beds are represented mainly by the lower member, underlying the Lithgow Seam. The upper member becomes more prominent in the vicinity of Mount Marsden, on the northern

side of the Capertee Valley, and continues in a northerly direction, being evident at many places round the head of the Cudgegong Valley. On the northern side of the main divide at the head of Growee Creek, which runs into Bylong Creek (see geological map, Plate ix), both upper and lower members of the Marangaroo Beds are present together with the Lithgow Coal Seam, giving the following section:

- 20 feet. Sandstone with pebbles. Upper Marangaroo.
- 5 " Coal. Lithgow Coal Seam.
- 4 " Shales.
- 8 " Sandstone. Lower Marangaroo.
- 6 " Shales. Followed by Upper Marine.

Growee and Bylong Creeks have eroded their valleys well below the base of the Upper Coal Measures, exposing up to 300 feet of Upper Marine strata. The outcrop of the Marangaroo Beds runs along the sides of these valleys, forming a well-defined feature. Between the junction of Growee and Bylong Creeks and the point at which the Bylong Creek runs into the Goulburn River, the strata assume a strong northerly dip, and the horizon of the Marangaroo Beds passes beneath the floor of the Goulburn Valley. At Wollara Station, about six miles up the Goulburn River from its junction with Bylong Creek, the Marangaroo Beds again outcrop, forming a prominent feature a little above the level of the valley-floor, which is in Upper Marine Beds. On the eastern side of the gap between the Wollar and Goulburn Valleys, through which the road and railway pass, both upper and lower members of the Marangaroo Beds are present, separated by carbonaceous shales and mudstone which occupy the horizon of the Lithgow Coal Seam, as follows:

- 15 feet. Coarse sandstone. Upper Marangaroo.
- 3 " Carbonaceous shale. Horizon of Lithgow Seam.
- 4 " Shale and mudstone.
- 20 " Sandstone. Lower Marangaroo.

In the Wollar Valley the Marangaroo Beds outcrop on either side of the creek, exposing Upper Marine strata, between Barigan and the village of Wollar. To the north of Wollar all the Kamilaroi Beds dip beneath the creek level. Limited outcrops of the Marangaroo Beds and Upper Marine strata also occur in the valley of Willpinjong Creek, a large western tributary of the Wollar Creek. In this locality the upper member is 15 feet thick and the lower about 5 feet, the two forming sandstone beds separated by the Lithgow Coal Seam, which contains some bituminous coal at this point.

In the vicinity of Ulan, on the western margin of the Upper Coal Measures, the Marangaroo Beds become conglomeratic, especially the lower member, which varies from 15 to 25 feet in thickness, and lies directly on the granite forming the basement rock of the Kamilaroi Basin in this locality. The Lithgow Seam attains the remarkable thickness of 30 feet, consisting mainly of good coal with a number of thin chert bands, and the upper member of the Marangaroo Beds is 35 feet thick and much finer grained than the lower. The typical Upper Marine Beds of sandy shale and mudstone with calcareous bands, are overlapped by the lower member of the Marangaroo somewhere between Ulan and the Willpinjong Valley.

From Ulan the margin of the Kamilaroi trends roughly south-east through Cooyal and Lue to Rylstone. About 5 miles from Ulan, Upper Marine Beds again outcrop between the Marangaroo Beds and the old Palaeozoic basement rocks. Between Cooyal and Lue, the lower member of the Marangaroo Beds outcrops strongly as a bed of sandy conglomerate from 30 to 50 feet in thickness. The Lithgow Coal Seam is very inconstant, forming up to 7 feet of coal at some places and nothing but coaly streaks in carbonaceous shale at others. The upper member of the Marangaroo is less conspicuous than the lower, being fine-grained and seldom amounting to more than 10 feet in thickness. Passing to the east from Lue towards Rylstone, the lower member loses its conglomeratic nature and becomes reduced in thickness to about 10 feet at Tong Bong Mountain. The Lithgow Seam is more persistent, with a thickness of about 5 feet of coal, and the upper member of the Marangaroo appears to cut out almost completely.

South-east from Marangaroo and Wallerawang, the lower member of the Marangaroo Beds diminishes rapidly in thickness and becomes inconspicuous in the vicinity of

Lithgow. For detailed descriptions and sections of the Marangaroo Beds and Lithgow Coal Seam in the Lithgow district, see Carne (1908), Andrews and Morrison (1926), Andrews (1928). On the western side of the valley of the Lett River both members of the Marangaroo Beds are present as sandstone occurring above and below the Lithgow Coal Seam, the upper member being 9 feet in thickness and the lower 12 feet. On the eastern side of the Lett River Valley in the vicinity of Hartley Vale, the lower member becomes less prominent and the upper member consists of sandy conglomerate overlying the Lithgow Seam. In the Grose Valley, to the east of Hartley Vale, the upper member and Lithgow Seam outcrop at several places but there is little evidence of the lower member. South of Hartley Vale in the vicinity of the Victoria Pass and Sugar Loaf Mountain, the upper member forms the roof of the Lithgow Seam and varies in thickness up to 20 feet. The lower member outcrops on the eastern side of Sugar Loaf Mountain where it is 23 feet thick, but it appears to be non-existent on the north-western side at Hartley Pass Colliery and Victoria Pass.

Between Mount Victoria and Blackheath the upper member persists as sandy conglomerate and coarse sandstone varying between 10 and 20 feet in thickness, and the lower member occurs at isolated points only. Under the western escarpment of Mount Blackheath the upper member forms 9 feet of sandstone overlying the Lithgow Coal Seam, but there is no evidence of the lower member. To the south-east of Blackheath in the vicinity of the Megalong Valley, both members of the Marangaroo Beds are present in the form of coarse sandstone containing numerous small white quartz pebbles. At the western head of Nellie's Glen the upper and lower members are 12 and 10 feet thick respectively, and the Lithgow Seam consists of about 6 feet of carbonaceous shales with bands of bituminous coal. On the eastern side of Megalong Valley, at Mort's Glen Mine, the following section is exposed at several places:

- 8 feet. Fine quartz-pebble conglomerate. Upper Marangaroo.
- 4 inches. Bright bituminous coal. Lithgow Coal Seam.
- 3 feet. Shales.
- 6 feet. Fine quartz-pebble conglomerate. Lower Marangaroo.

Considerable difficulty was experienced in following the outcrop of the Marangaroo Beds to the south-east of Katoomba, owing to the heavy covering of talus along the steep and rugged sides of the Jamieson Valley. Sufficient outcrops were obtained, however, to establish the continuation of the beds along the eastern side of the valley, and at a point about three miles from its junction with the Cox Valley, good sections are available showing both upper and lower members forming beds of pebbly sandstone, 15 and 10 feet thick, respectively, and separated by 5 feet of carbonaceous and coaly shale representing the Lithgow Coal Seam. The extension of the beds to the east, along the Cox Valley, was established by sections obtained at a number of points. At the junction of the Cox and Wollondilly Rivers, the following section was measured:

- 20 feet. Sandstone. Upper Marangaroo.
- 2 ,, Coaly shale. Lithgow Coal Seam.
- 13 ,, Shales.
- 3 ,, Black mudstone.
- 15 ,, Coarse sandstone. Lower Marangaroo.

The presence of the Marangaroo Conglomerate and Lithgow Coal Seam in the Lower Burratorang Valley was reported by Morrison and Kenny (1924) at Brimstone and Riley's Gullies on the eastern side of the valley. The writer obtained a section near Mount Kamilaroi, at the junction of the Nattai and Wollondilly Rivers, showing 10 feet of upper Marangaroo sandstone, 4 feet of coaly and carbonaceous shales representing the Lithgow Coal Seam, and 20 feet of pebbly sandstone constituting the lower Marangaroo. Further to the south-west at Higgins Creek, near Mount Tonalli on the western side of the Burratorang Valley, an exposure first recorded by Morrison and Kenny (1932) shows the Lithgow Seam consisting of 10 feet of coal, and 8 feet of conglomerate forming the lower Marangaroo.

The beds can be followed along the eastern side of the Upper Burratorang Valley, where sections were originally measured by A. J. Lambeth. The lower member of the Marangaroo Beds, varying between 10 and 20 feet in thickness, assumes a conglomeratic

nature similar to that of the types developed between Capertee and Wallerawang. The Lithgow Seam is of very variable nature, consisting of coal in some places and carbonaceous shale in others, and the horizon of the upper Marangaroo is occupied mainly by a sandstone bed from 10 to 15 feet in thickness. Much the same situation exists at the southern end of the Burragorang Valley near Bullio, where the lower member consists of a well-marked conglomerate.

The southern continuation of the Marangaroo Beds is established by a section in the Joadja Valley first reported by Carne (1903), where the Lithgow Seam, 4 feet in thickness, overlies a massive conglomerate 15 to 20 feet in thickness, constituting the lower Marangaroo. South from Joadja the lower member thins out rapidly but maintains its conglomeratic nature. A section measured at Penang Trig. Station by A. J. Lambeth shows 9 feet of heavy conglomerate, and carbonaceous shales on the horizon of the Lithgow Seam. South from Penang, the lower member has been followed to the vicinity of Emu and Black Bob's Creeks on the southern side of the Wingecarribee River.

The lower member of the Marangaroo Beds appears to extend some distance to the east from the Upper Burragorang Valley, as indicated in a section obtained by David (1889) on Iron Creek near Colo, where the Lithgow Seam, consisting of 6 feet of coal, immediately overlies a bed of conglomerate representing the lower Marangaroo.

*The Occurrence of Coal-Measures below the Marangaroo Beds near Bylong.*

Coal-measures are not known below the thin bed of shales immediately underlying the lower member of the Marangaroo Beds, with the exception of one occurrence in the Goulburn Valley, two miles up the river from its junction with Bylong Creek. At this point, below the road at the eastern end of a cutting in the steep southern bank of the river, 80 feet of coal-measure beds, including three coal seams, outcrop between the bed of the river and the lower member of the Marangaroo, as illustrated in Fig. 3. The base of the beds is not exposed, so they must be over 80 feet in thickness. The outcrop extends over a small area on the floor of the valley (see geological map, Plate ix), but

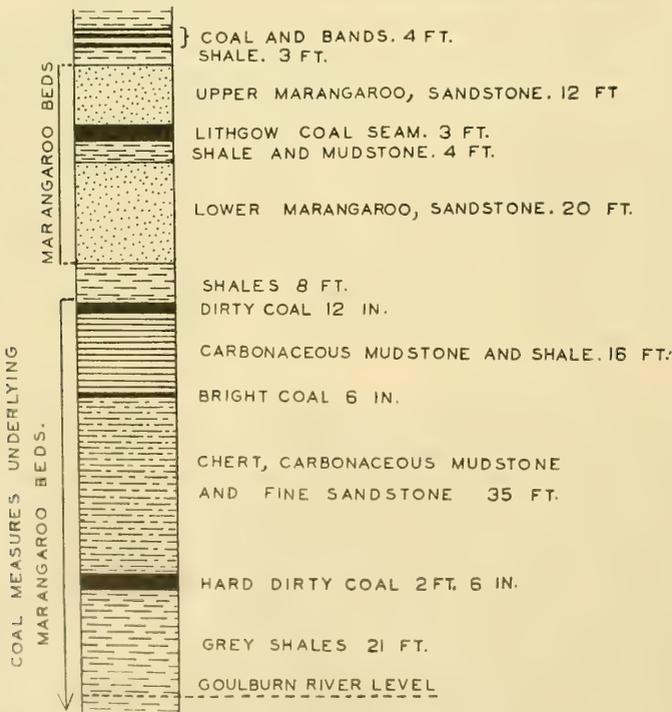


Fig. 3.—Section of coal-measures underlying Marangaroo Beds near Bylong.

cannot be traced for more than one mile to the west; here the Upper Marine again assumes its normal position below the Marangaroo Beds which evidently overlap the intervening coal-measures. To the east the strata dip beneath the bed of the river, and the Marangaroo Beds do not outcrop again in the Goulburn Valley.

These coal-measures may be a local development representing an isolated deposit, but it seems highly probable that they are the equivalent of some section of the coal-measures outcropping in the Hunter Valley, with which they may be continuous, the exposure described being on the actual margin of a unit thinning out towards the west. It is evident that the coal-measures occur between the Marangaroo Beds and the Upper Marine, and thus they cannot be equivalent to the Greta or Lower Coal Measures, but most probably represent the lower portion of the Newcastle Stage, or possibly the upper portion of the Tomago Stage of the Upper Coal Measures in the Hunter Valley. Taken in conjunction with the enormous increase in thickness of the Upper Coal Measures, amounting to about 3,000 feet, which occurs between the western districts and the Hunter Valley, the foregoing results would indicate that the horizon of the Marangaroo Beds occurs well above the base of the Upper Coal Measures in the Northern Coalfield. Furthermore the increase in thickness of the coal-measures is evidently due to the coming in of additional beds towards their base, as well as an increase in the thickness of the measures which outcrop in the western districts.

*The Upper and Lower Stratigraphical Limits of the Upper Coal Measures.*

Along the western margin of the Kamilaroi Basin, Triassic sandstone overlies beds of the Upper Coal Measures, which in turn rest on Upper Marine strata. These three formations are conformable, and considerable difficulty has been experienced in determining specific horizons representing the base and upper limits of the coal-measures. At the base of the measures the general change in sedimentation was from marine to freshwater conditions, while at the top it involved the passing from Permian to Triassic time.

Carne (1908), after considering the evidence available at that time, came to the conclusion that the Marangaroo Conglomerate, immediately overlying the Lithgow Coal Seam, should be taken as an arbitrary base of the coal-measures, representing an approximate line of division between the underlying marine sediments and the overlying freshwater beds.

As stated earlier in this paper, it has been established that there are two members of the Marangaroo, occurring immediately above and below the Lithgow Coal Seam. It has been noted by the writer that small seams of coal, usually amounting to less than 12 inches in thickness, frequently occur on top of the upper member of the Marangaroo Beds, and also just below the lower member. Those occurring below the lower member are invariably associated with carbonaceous shales which vary in thickness up to 10 feet, and contain *Glossopteris*. Below these shales occur the typical Upper Marine Beds, consisting of fine grits, sandy mudstones, calcareous shales and mudstone, and in places sandy conglomerate with angular pebbles and erratic boulders up to 18 inches in diameter. Although fossil evidence is difficult to obtain in these beds, they are certainly marine and probably fluvio-glacial, and form the topmost beds of the Upper Marine Series. At one place between Lue and the head of Cooyal Creek, the lower member of the Marangaroo is separated by 3 feet of shale from a rather remarkable tillite, consisting of a hard matrix and extremely angular fragments up to 12 inches in length.

Figure 4 is a generalized form of the sequence exposed at many places along the margin of the Western Coalfield. With the one exception described above, no shales resembling freshwater sediments or containing coal-measure fossils have been found lower than the few feet of shales occurring immediately below the lower member of the Marangaroo. The nature of the Marangaroo Conglomerates, their proximity to the Upper Marine Beds, and the fact that coal-measure shales and coal are interbedded with them, create the impression of a fluctuating transition from glacial marine to warm freshwater conditions of sedimentation. This cannot be so, however, as normal Upper Coal Measure strata occurring between the Marangaroo Beds and the Upper Marine in the Goulburn Valley, exclude the possibility of the Marangaroo Conglomerates being

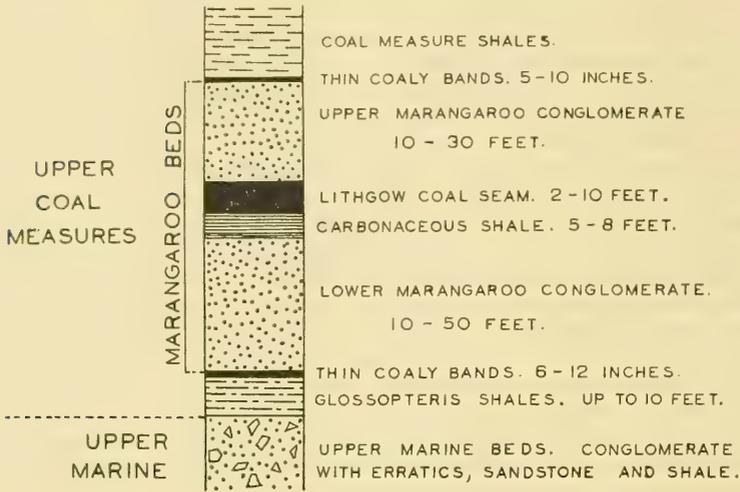


Fig. 4.—Generalized section at base of Upper Coal Measures.

passage beds. It follows that the top portion of the Upper Coal Measures, including the horizon of the Marangaroo Beds, overlaps the lower portions between the Hunter Valley and the western districts, and lies directly on the Upper Marine. This would involve a long time-break, preceding the deposition of the Marangaroo Beds, and considerable contemporaneous erosion would be expected at the top of the Upper Marine. Such erosion is suggested by the fact that the topmost beds of the Upper Marine vary from tillite to sandstone and shales, at different places along the western margin of the coal-measures. In view of the foregoing, it is evident that the thin bed of shales occurring between the lower member of the Marangaroo and the typical Upper Marine strata, must be taken as the base of the Upper Coal Measures.

The coal-measures are overlain by the Narrabeen Beds of the Triassic Series, carrying residual masses of Hawkesbury Sandstone at many places along the central western margin of the Kamilaroi Basin. The Narrabeen Beds are characterized by massive sandstone, with "chocolate shales" occurring on several horizons. The Triassic sandstone weathers into bold cliffs which contrast with the talus-slopes of the underlying coal-measures. The approximate junction between the two formations occurs at or near the base of the cliffs, but the determination of the actual horizon by means of which they may be separated presents some difficulty. As described by Carne (1908), there is no apparent break in the stratigraphical sequence from Kamilaroi to Triassic, but a time-lapse is indicated by a sudden change in the types and relative abundance of fossil flora, which occurs immediately above the top or Katoomba Coal Seam. The relation between the Upper Coal Measures and Triassic in other parts of the Kamilaroi Basin has been discussed by David (1907), Dun (1910), Harper (1915) and Raggatt (1938).

The writer has recently investigated the relationship along the western margin of the Kamilaroi Basin. From the Goulburn River in the north to the Lower Burrarorang Valley in the south, the Katoomba Coal Seam occupies a horizon near the base of the massive Triassic sandstone, which forms vertical cliffs. The depth of the coal-seam below this sandstone varies from nothing to about 70 feet. The intervening space, where present, is occupied by shales or laminated shaly sandstone. In some places these shales thin out towards the points where the coal-seam is in contact with the sandstone, while elsewhere they change gradually from shale to shaly and laminated sandstone, then finally pass into massive sandstone. Typical coal-measure fossils such as *Glossopteris* and *Vertebraria* are abundant in the beds underlying the Katoomba Seam, and in the seam itself, but they were not found in the shales and laminated sandstone immediately overlying the coal-seam, where the only fossils observed were *Phyllothea*

and fragmentary plant debris. In other parts of the Kamilaroi Basin, *Glossopteris* is said to be associated with Mesozoic flora close above the top seam (Carne, 1908).

The foregoing evidence would indicate that the change from Permian to Triassic strata occurs immediately above the Katoomba Coal Seam, but the sudden disappearance of *Glossopteris*, and the entry of Mesozoic flora at this horizon would also indicate a considerable time-break during which sedimentation ceased. This being so, it is difficult to understand the conditions which allowed the preservation of plant-material, and the early stages of coalification, to proceed over the extensive area now occupied by the top seam, with only the thinnest veneer of sediments covering it. The absence of contemporaneous erosion is particularly marked at the horizon of the coal-seam, and it seems unlikely that extensive removal of protecting sediments could have taken place during the apparent time-lapse in sedimentation between the two periods. In view of this difficulty, it seems most likely that some relatively sudden change in environmental conditions occurred after the deposition of the coal-seam, exterminating the *Glossopteris* flora almost completely. Sedimentation probably continued at a very slow rate depositing transition beds while the first Mesozoic plants made their appearance. Then the more rapid deposition which produced the massive Triassic sandstones may have caused contemporaneous erosion some distance above the coal-seam in marginal areas. This erosion could be responsible for the variation in thickness, and irregular nature of the shaly transition beds between the coal-seam and the massive sandstone.

In consideration of the foregoing evidence and discussion, the most accurate and suitable line of demarcation between Triassic and Kamilaroi Beds, for those areas north of Central Burragorang, would be a horizon immediately above the Katoomba Seam. South from Central Burragorang, to the vicinity of Joadja and Mittagong, a somewhat different situation exists. In this area the top portion of the Upper Coal Measures is missing, and the No. 3 or Dirty Seam becomes the top seam, taking the place of the Katoomba Seam in the Western Coalfield. This has been referred to in publications of the Department of Mines (Morrison and Kenny, 1924; Jones, 1925; Andrews, 1928), and substantiated by detailed work recently carried out by A. J. Lambeth in the area concerned. The writer has also followed the Dirty Seam from the vicinity of Katoomba to Central Burragorang where it forms the top seam of the coal-measures. It is important that the Dirty Seam in the Burragorang-Joadja district bears much the same relations to the Triassic as the Katoomba Seam in the Western Coalfield. Thus the time-break between the deposition of the Dirty Seam and the massive Triassic sandstone must have been much longer than that which followed the formation of the Katoomba Seam. *Glossopteris* is common in the shales occurring between the Dirty Seam and the Triassic sandstone, and it is probable that considerable contemporaneous erosion occurred before the commencement of Triassic time. It follows that the line of subdivision between Triassic and Kamilaroi in this area must be taken at the base of the massive sandstone or the highest horizon on which coal-measure fossils are found, and not necessarily at the top of the highest coal-seam.

#### *The Continuity and Arrangement of Coal-Bearing Horizons.*

In the following notes the coal-seams, and horizons on which they occur, are described in terms of their importance as stratigraphical units. For information concerning their relative importance in the coal mining industry, reference should be made to Carne (1908), Pittman (1912), Jones (1925, 1926), Andrews and Morrison (1926), and Andrews (1928).

The No. 1, or Katoomba, Seam, as already described, occupies the highest position in the coal-measures. Its horizon is well defined either by a coal-seam or by coaly bands and carbonaceous shales, and can be identified at almost all points in the western districts. The horizon occupies from 5 to 20 feet of strata, although there is seldom more than 6 feet of good coal in any one section. In the vicinity of Capertee Valley and Rylstone, splits in the seam are common. At Ilford Range, Mornington and Mount Marsden, a bed of chert splits the seam into upper and lower portions, and in the vicinity of the Ilford Range the lower portion is split by numerous bands of shale, giving a total thickness of 22 feet for the whole coal-bearing zone. The horizon is very persistent and free from washouts, and there is much less evidence of thinning and

irregularities towards the margin of the measures than in the case of some of the lower horizons. One exception to this occurs in the vicinity of Ulan, where the Katoomba horizon is missing altogether over a considerable distance to the east of the Ulan Coal Mine, having been overlapped by the Triassic. It is present, however, in the Willpinjong Valley, 8 miles to the east of Ulan, where it consists of 5 feet of coal and bands, and has been followed along the southern side of the Goulburn River to Baerami, near Sandy Hollow. As described above, in the south-western districts between Burragorang and Joadja the coal-measures above the Dirty Seam are missing. The most southerly point at which the Katoomba horizon has been observed, is in the Burragorang Valley at Mount Kamilaroi near the junction of the Nattai and Wollondilly Rivers.

The second coal-bearing horizon, or No. 2 Seam, is very inconstant and occurs only at isolated points in the western districts. It is missing altogether in the Burragorang-Joadja area, as described in the literature dealing with the absence of No. 1 Seam in that locality. It is present in the Cox Valley, a little above the junction of the Cox and Wollondilly Rivers, and has been followed to the Jamieson Valley, where it occurs 25 to 35 feet below the Katoomba Seam. It is present at Katoomba and continues intermittently to the vicinity of Lithgow, where it is 25 to 40 feet below the top seam. To the north of Lithgow there is very little evidence of the No. 2 horizon. At one or two places in the Capertee Valley thin bands of coal have been observed at from 20 to 30 feet below the Katoomba Seam, but in the coal-measures between Ulan, Bylong and Rylstone, the No. 2 Seam appears to be completely absent. Further to the east, however, in the Baerami and Widdin Valleys, a coal-seam varying in thickness up to 4 feet occurs about 35 feet below the top seam and 55 feet above the Dirty Seam, and may be equivalent to the No. 2 horizon.

The third coal-bearing horizon, on which the No. 3 or Dirty Seam is developed, is one of the most important and consistent stratigraphical units occurring in the Western Coalfield. It is marked by a zone of strata varying from 10 to 40 feet in thickness and is characterized by numerous bands of shale and chert interbedded with coal. It is possible to find this horizon at all points on the coal-measure slopes where exposures of the strata occur. It is continuous from the Burragorang-Joadja area, where it occurs at the top of the measures, to the Goulburn Valley in the north, and it has been followed east along the southern side of the Goulburn Valley and its tributaries, to Baerami. West from Wollar, the No. 3 horizon thins out considerably, and it is absent over small areas in the vicinity of the Ulan Coal Mine, on the actual margin of the coal-measures.

The No. 3 horizon usually occurs less than 100 feet below the Katoomba Seam, the average depth being about 75 feet. It has been noted that this interval does not necessarily vary as a function of the total thickness of the coal-measures. At Katoomba, No. 3 is 60 feet below the No. 1 Seam where there is a total thickness of about 300 feet of coal-measures, while at Glen Davis the interval is 63 feet with a total of 580 feet, and at Tong Bong Mountain it is 70 feet, where the coal-measures are only 240 feet in thickness.

The three coal-bearing horizons just described can be correlated with the three highest coal-seams of the Southern Coalfield. The same applies to the lowest coal-seam in the measures, known as the Lithgow Seam in the western districts and No. 7 Seam on the south coast of New South Wales. There is some difficulty, however, in correlating Nos. 4, 5, and 6 of the south coast with equivalent horizons in the Western Measures. Small and unimportant seams of coal occasionally appear on two horizons which may be equivalent to Nos. 4 and 5, but they are of no value industrially, and do not form persistent stratigraphical horizons.

The Irondale Seam or No. 6, occurring above the Lithgow Seam, is generally considered to be equivalent to No. 6 on the south coast. Its horizon is well marked and continuous in the vicinity of Lithgow, Capertee Valley and Kandos, but further to the north it is not possible to follow it continuously. Between Katoomba and Lower Burragorang the No. 6 horizon becomes indefinite, although it is believed that the middle seam of the three which occur in the Burragorang-Joadja area, is its equivalent. In the central portion of the Western Coalfield, the Irondale Seam occurs at a height

varying between 70 and 180 feet above the Lithgow Seam, and at a depth of 80 to 200 feet below the Dirty Seam. Its relative position is reasonably constant, the variation in the above figures being due to differences in the thickness of the measures between the Dirty and Lithgow horizons.

The No. 7, or Lithgow, Seam is an important stratigraphical horizon. Its relationship to the Marangaroo Conglomerates at the base of the coal-measures, and typical increase in thickness as it passes away from the marginal areas of the coal basin, are described above. The No. 7 horizon occupies from 5 to 20 feet of strata, consisting of coal, carbonaceous shale and mudstone. At many places near the margin of the measures, the horizon bears only carbonaceous shale and mudstone with coaly bands, although an important coal-seam is present in several districts, amounting to 10 feet in the vicinity of Lithgow and the exceptional thickness of 30 feet at Ulan. The coal-seam, where present, almost invariably occurs at the top of the No. 7 horizon, immediately underlying the upper member of the Marangaroo Beds.

From Ulan to Bylong, the Lithgow Seam gradually decreases in thickness from 30 to 2 feet, thus forming a rather striking exception to the usual thickening of the seam as it passes to the east away from the margin of the measures. To the south-east from Ulan, the coal-seam on the No. 7 horizon rapidly decreases in thickness and assumes an irregular nature between Cooyal and Rylstone, some exposures showing only a few inches of coal and others as much as 8 feet. From Rylstone to Bylong the seam is also irregular, seldom amounting to more than 6 feet of coal, and consisting of nothing but carbonaceous mudstone in many places.

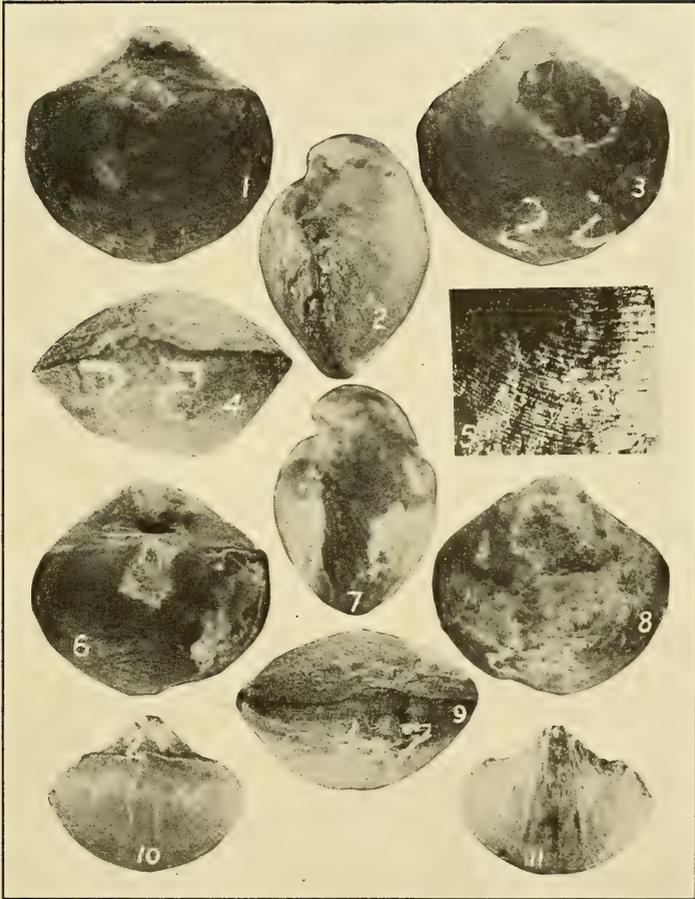
#### *Acknowledgements.*

In conclusion the writer wishes to acknowledge helpful discussion with members of the Geological Survey of New South Wales and the staff of the Department of Geology, University of Sydney, in connexion with the preparation of this paper.

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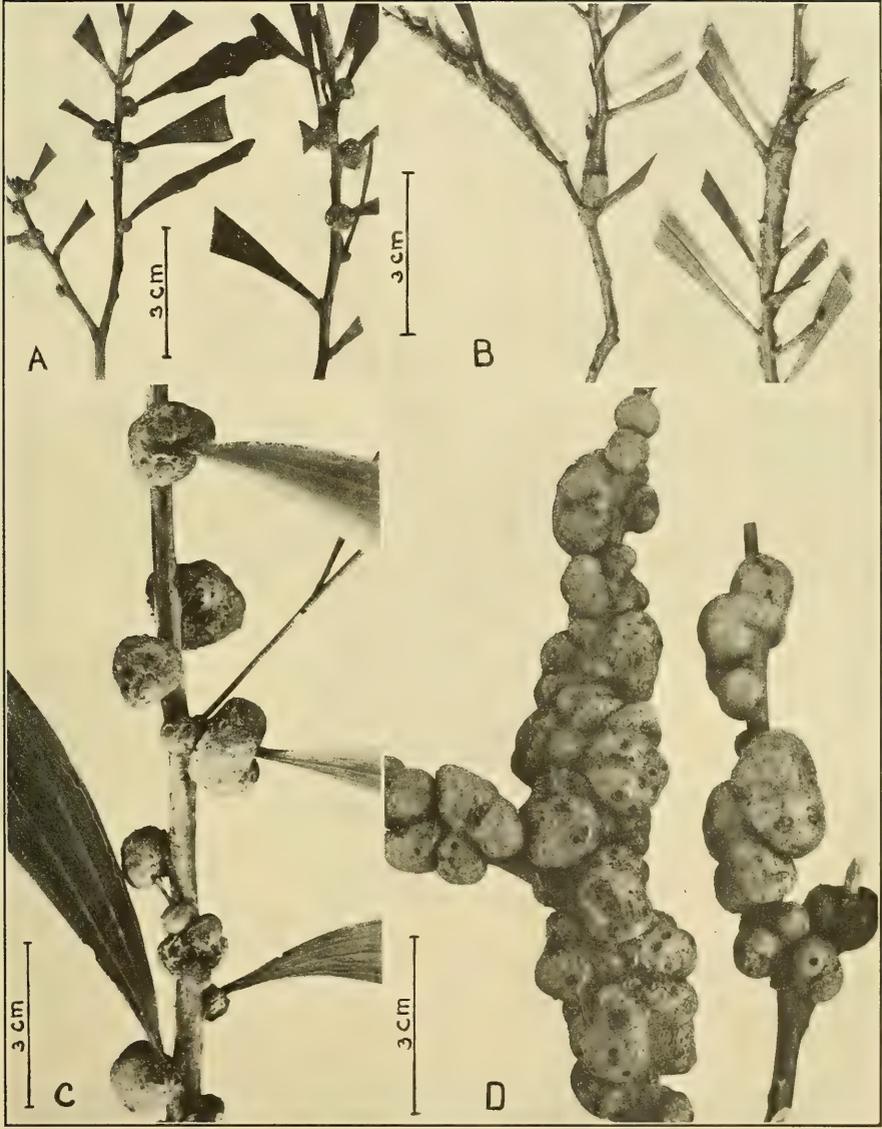
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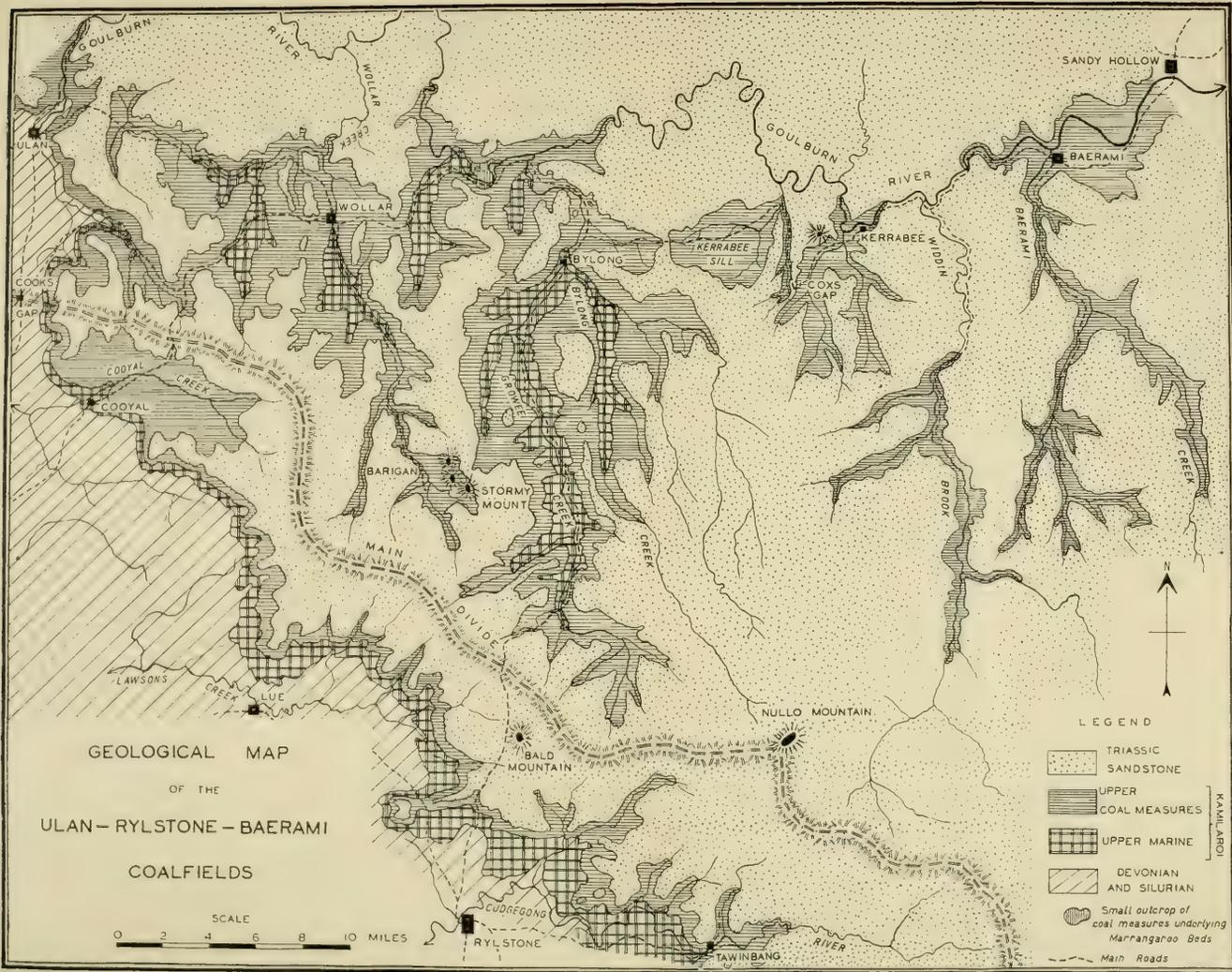
*Spirinella caecistriata.*





Galls on *Acacia implexa* and *A. Maidenii* caused by *Trichilogaster maideni*.





GEOLOGICAL MAP  
OF THE  
ULAN-RYLSTONE-BAERAMI  
COALFIELDS

SCALE  
0 2 4 6 8 10 MILES

LEGEND

- TRIASSIC SANDSTONE
- UPPER COAL MEASURES
- UPPER MARINE
- DEVONIAN AND SILURIAN
- Small outcrop of coal measures underlying Marrangaroo Beds
- Main Roads

KAMU AROI



## AUSTRALIAN RUST STUDIES. VI.

COMPARATIVE STUDIES OF BIOTYPES OF RACE 34 OF PUCCINIA GRAMINIS TRITICL.

By W. L. WATERHOUSE and I. A. WATSON, The University of Sydney.

(Plate xi.)

[Read 29th October, 1941.]

*Introduction.*

Physiological specialization is now known to occur frequently in parasitic fungi. It reaches a high development in the plant rusts. The determination of physiological races within the cereal rusts has received a great deal of attention in many countries, based largely on methods developed at the Minnesota Agricultural Experiment Station by Stakman and Levine (1938). Using this technique, more than two hundred races of wheat stem rust have been determined.

In Australia, in work which has extended over the past twenty years, nine races have been found (Waterhouse, 1939). Since 1929 approximately 98% of the isolates examined have proved to be race 34, a rust which is also well known in other countries. In this determination work, and in studies of race 34, it was early found (Waterhouse, 1929) that changes in the environmental conditions caused marked variations in the reactions shown by certain of the differential hosts that are normally used. In particular, the varieties Arnautka, Mindum and Spelmars at temperatures of 70–75°F. exhibited reactions of type 3 and type 4, but at about 55°F. the reactions were flecks. That is to say, what was race 34 at the higher temperatures became race 56 at the lower. Other varieties exhibit changes in reaction of this same nature. The culture used in these studies is the one which was first found in November, 1925. It has since been maintained in the uredospore stage, and is the one referred to herein as the standard Australian biotype.

## INVESTIGATIONS IN U.S.A.

Recently it became possible to make comparisons between the Australian race 34 and an American culture of the same designation. One of us (I.A.W.) had opportunities of carrying out the investigations whilst working under Dr. E. C. Stakman at the Minnesota Agricultural Experiment Station.

*(a). Tests with Fixed Crossbred Wheats.*

During the spring and summer of 1939, a number of rust resistant selections were tested in the rust nursery at St. Paul, Minnesota. These included derivatives of Kenya wheats and others which owe their resistance to the variety of *Triticum durum* named "Gaza". All had been selected and tested for their rust resistance in the plant-house and under field conditions in New South Wales where race 34 was present. Of thirty-one lines, five segregated for resistance and susceptibility. Race 34 was isolated from susceptible pustules in segregating lines.

If independent genetic factors were responsible for resistance to the U.S.A. and the Australian biotypes of race 34, it would be impossible to select consciously, lines that are resistant to both biotypes, although such lines could be isolated by chance. There was no evidence that two different genes control resistance to the two biotypes, especially since so few discrepancies occurred in the tests that were made.

*(b). Tests with F<sub>3</sub> Lines.*

Fifty-five F<sub>3</sub> lines of the cross Dundee 985\* × Kenya 745 and thirty of the cross Federation 107 × Kenya 745 were selected at random. The progeny of each single F<sub>2</sub> plant was divided into three parts. One part was sown and inoculated at St. Paul in the seedling stage with a U.S.A. culture of race 34. A second part was sown in the

\* Varieties carry the Sydney University Accession Number.

field at St. Paul and exposed to an epiphytotic caused by several races of stem rust. The third part was sent to the University of Sydney, where the seedlings were inoculated with the standard culture of the Australian race 34.

In Table 1 are given the results of the seedling inoculations in the two countries.

TABLE 1.  
Reactions of  $F_3$  lines and the parents of two crosses, Dundee 985  $\times$  Kenya 745 and Federation 107  $\times$  Kenya 745, when inoculated with the two biotypes of race 34 of *Puccinia graminis* Tritic.

	F <sub>3</sub> Reactions to U.S.A. Biotype.								Origin of Culture.	Parents.		
	Dundee 985 $\times$ Kenya 745.				Fed. 107 $\times$ Kenya 745.					Dundee 985.	Kenya 745.	Fed. 107.
	Res.	Seg.	Susc.	Total.	Res.	Seg.	Susc.	Total.				
Reactions to the Australian Biotype—												
Res. ..	10			10	9			9	United States. Australia.	3+	; and 2	4
Seg. ..		31		31		15		15		3	;	3+
Susc. ..			14	14			6	6				
Total ..	10	31	14	55	9	15	6	30				

It is clear that the same gene was found to govern seedling resistance to both cultures, irrespective of whether Kenya 745 was crossed with Federation 107 or Dundee 985. Parental varieties showed slight differences, all three indicating that the U.S.A. culture of this race is more virulent than the standard Australian culture. The  $F_3$  results show that one and the same gene governs resistance to both cultures of race 34. The seedling reactions at St. Paul showed complete correlation with the mature plant behaviour in the field there.

(c). Tests with Inbred Ryes.

In 1929 a number of selfed single plants of rye were selected in Australia on the basis of their field reaction to Australian race 34. Progenies have been tested each year, grown on and selfed. The selections came from the varieties "March" and "Petkus Rug". Their usefulness as differentials of *P. graminis Secalis* has already been demonstrated (Waterhouse, 1938). The reactions of these lines to the Australian race 34 are stable, some being resistant, others susceptible.

Table 2 gives the results of testing thirty-one of these lines, whose reactions to the Australian culture were known, with a U.S.A. biotype of race 34.

TABLE 2.  
Reactions of thirty-one inbred lines of rye to two biotypes of race 34 of *P. graminis* Tritic.

Inbred.	Origin of Rust Culture.		Inbred.	Origin of Rust Culture.	
	United States.	Australia.		United States.	Australia.
R <sub>2</sub>	;	3	R <sub>18</sub>	3	3
R <sub>3</sub>	x=and ;	3	R <sub>19</sub>	3	3
R <sub>4</sub>	; and 1+	3	R <sub>20</sub>	x	3
R <sub>5</sub>	1+	3	R <sub>21</sub>	3	3
R <sub>6</sub>	; and 1+	3	R <sub>22</sub>	3	3
R <sub>7</sub>	; and 1+	3	R <sub>23</sub>	3	3
R <sub>8</sub>	;	3	R <sub>24</sub>	;	2=
R <sub>9</sub>	x=, ; and 1	3	R <sub>25</sub>	;	2=
R <sub>10</sub>	;	3	R <sub>26</sub>	;	x
R <sub>11</sub>	x	3	R <sub>27</sub>	;	x
R <sub>12</sub>	3	3	R <sub>28</sub>	;	x
R <sub>13</sub>	3	3	R <sub>11</sub>	x	;
R <sub>14</sub>	3	3	R <sub>42</sub>	3 and x	;
R <sub>15</sub>	3	3	R <sub>43</sub>	;	;
R <sub>16</sub>	3	3	R <sub>44</sub>	x+, ; and 1	;
R <sub>17</sub>	3	3			

It is apparent that selection over a period of years, either for resistance or susceptibility to one biotype of race 34, does not necessarily insure that the selection so made will give the same reaction with another collection of the same race. Whereas the same genetic factor was concerned in the reactions shown by the Kenya 745 cross-breds, in the inbred ryes different factors govern the resistance to the two biotypes of race 34.

(d). *Tests on Standard Differentials.*

Arising out of the finding (Waterhouse, 1929) that the Australian race 34 gives the reactions of race 56 at low temperatures at Sydney, a study was made to find out how closely a U.S.A. culture of race 34 resembled race 56 at low temperatures at Minnesota.\*

Two random isolates, one representing race 34 and the other race 56, were made from the United States Department of Agriculture field survey material. Each was increased on Little Club and the experiment made during the autumn of 1939, when two suitable average temperatures were available. The lower temperature varied between 53.6°F. and 68°F., with an average of 58°F., and the higher varied between 64°F. and 77.5°F., with an average of 70.5°F. At each of these two temperatures three light intensities were used. The highest intensity of 1,600 foot candles was the average when plants were exposed to sunlight on the greenhouse bench. A medium intensity of 500 foot candles and a low intensity of 300 foot candles were obtained by placing the seedlings beneath cages covered by two and four thicknesses respectively of 80-mesh cheesecloth.

Plants of Kota, Arnautka, Mindum, Spelmars, Kubanka, Acme, Einkorn, Hope, and Thatcher were inoculated, when two inches high, by the brush method. Notes were taken fifteen days after inoculation. The results are set out in Table 3.

It is clear that in general the lower temperature tends to depress the severity of the rust attack, and browning, previously reported by Hart and Allison (1940), occurs on some varieties at the higher temperatures. Despite a reduction in severity of reaction, however, Arnautka, Mindum and Spelmars do not approach the fleck reactions with U.S.A. race 34 as reported for the Australian race 34 at similar temperatures. There is therefore no possibility of confusing the U.S.A. races 34 and 56 even at low temperatures.

INVESTIGATIONS IN AUSTRALIA.

Thanks to the courtesy of the Matson Navigation Co., whose officials refrigerated a collection of uredospores of U.S.A. race 34 whilst *en route* to Australia, a culture from Minnesota became available for studies carried out in Sydney. Side by side comparisons of the reactions shown by the American and Australian rusts thus became possible.

At the outset the two cultures were checked for their reactions on the usual set of differentials at a temperature of about 75°F. on the plant-house bench at the University of Sydney. During May and June, 1940, preliminary comparisons were made of the two cultures, and in July and August the studies were carried out in greater detail.

For purposes of the experiment, two different temperatures and two different exposures to light were used. Because of limitations of space, only some of the twelve usual differentials were employed, each pot containing fifteen to twenty seedlings. Some fluctuations occurred in the temperatures during the tests, but the average readings were 75°F. in the one house and 55°F. in the other. Artificial light was provided for the long day series.

The results are summarized in Table 4.

It will be seen that there are striking differences between the two biotypes, as measured by the reactions shown by the differentials. Typical reactions are illustrated in Plate xi. The U.S.A. race 34 is much more virulent. On Kota, the Australian race at 75°F. gives somewhat stronger reactions, but on the durums the differences are very marked in the other direction. The resistant reactions on Arnautka, Mindum and Spelmars at the low temperature are in agreement with the observations previously reported, and regularly found year after year during the winter months where the

\* Grateful acknowledgement is made to Mr. W. Q. Loegering for help in conducting this experiment.

TABLE 3.  
*Reactions of varieties of wheat to two races of P. graminis Trifoci at two temperatures and three light intensities.*

Variety.	High Temperature.						Low Temperature.					
	Light Intensity and Race No.						Light Intensity and Race No.					
	High.		Medium.		Low.		High.		Medium.		Low.	
	34	56	34	56	34	56	34	56	34	56	34	56
Kofa ..	3-b	3, 4-	3=b	3-, 3+	3=b	3	3-	3	3=b, 3	3=, 3+	3=	3=, 3
Arnautka ..	3, 4	0, 1, 1,	3, 4-	0; 1	3	0; 1=	3-, 3	0; 1	3, 3+	0; 1	3=, 3	0;
Mindum ..	4	0; 1	3, 4	0; 1	3, 3+	0; 1=	3	0; 1	3-, 3++	0; 1	3=, 3	0; 1
Spelnaars ..	4+	0; 1	3, 4	0; 1	3, b=	0; 1	3=, 3+	0; 1	3, 3++	0; 1	3-, 3	0;
Kubanka ..	3, 4 b=	3, 4	3	3, 4	3	3-, 3	3	3	3-, 3++	3-, 3++	3=, 3	3=, 3
Acme ..	3, 4 b	3+, 4	3 b	3 b	3=b	3	3+	3=, 3	3, 3+	3= 3+	3=, 3	3=, 3
Einkorn ..	0; 1=	0; 1	0; 1-	0; 1=	0;	0;	0; 1	0; 1++	0; 1	0; 1++	0;	0; 1-
Hope ..	3, 4	1+, 2-	3, 4	1, 2=	3, 3+	0; 2-	3	0; 1++	3-, 3++	0; 1++	3, 3+	2=
Thatcher ..	x+b	x+	x+ b-	x++	3 b	3, 3+	x=	x-	x-	x-	x=	x-

b represents browning.

b = represents faint browning.

TABLE 4.

Reactions of two biotypes of race 34 of *P. graminis Tritici* on wheat differentials, when tested side by side at two temperatures and two light exposures.

Variety.	Temperature 75° F.				Temperature 55° F.			
	18 Hours Light.		6 Hours Light.		18 Hours Light.		6 Hours Light.	
	U.S. 34.	Aust. 34.	U.S. 34.	Aust. 34.	U.S. 34.	Aust. 34.	U.S. 34.	Aust. 34.
Kota .. ..	2+	3+	2	3	2+	2	2-	2=
Arnautka .. ..	4	3+	3	3- and x-	3++	3, 1 and ;	3-	3=, 1 and ;
Mindum .. ..	4	3+ and x+	3	3- and x-	3++	1 and ;	3-	1 and ;
Spelmars .. ..	4	3+ and x+	3	3- and x-	3++	1 and ;	3-	1 and ;
Kubanka .. ..	3 and 3 <sup>c</sup>	3 <sup>c</sup> and x	3- <sup>c</sup>	x-	3 and x	x-	x-	x=
Acme .. ..	3 and 3 <sup>c</sup>	3 <sup>c</sup> and x	3- <sup>c</sup>	x-	3 and x	x	x-	x=

standard Australian race is used, as well as in cases where other isolates of Australian race 34 have come up for observation.

Comparisons of the two biotypes showed that there were differences in the colour of their uredosori. On the Ridgway Colour Standards the U.S.A. biotype is "Burnt Sienna of Plate II", whilst the Australian biotype is "Sanford's Brown of Plate II". For long we have had marked colour differences between *different* physiological races, some of which have already been reported (Waterhouse, 1929), and from the standard Australian culture of race 34, a very light colour variant (Ridgway Standard "Light Cadmium of Plate IV") has arisen on three different occasions during the past fifteen years. Its reactions on the differential hosts have been similar to those of the parent culture.

Not only in colour have differences been found in different isolates of Australian race 34. Thus on the variety "Barwang", which gives type 3+ reactions with the standard culture, an isolate which came from South Australia gave flecks, and yet when tested on the twelve differentials, it gave typical race 34 reactions.

Passing reference may also be made to results which will be reported in fuller form later. Cultures derived from barberries inoculated with race 34 have received considerable study. In them, it has been found that isolates that gave similar reactions of race 34 at 75°F. differ in their response to lower temperatures, as measured by their resistant reactions on differentials like Arnautka, Mindum and Spelmars.

Again, it has been found that comparisons at 70-75°F. of the U.S.A. and the Australian biotypes on such varieties as Marouani, D5, Nodak, Pinet, Trigo Africano, Egypt 75 and Greece 18, reveal marked differences in the reactions shown. The implications of this in respect of a programme of breeding for rust resistance are very important.

This position is similar to that which occurs in *Puccinia triticina*, where it has been shown (Waterhouse, 1929) that Australian isolates tested on the eight normal differentials give similar reactions. But if further tested on a variety like "Thew", one isolate may give a completely resistant, and another a completely susceptible reaction. That is to say, two different rusts are involved. Size differences between their uredospores have been demonstrated, and also differences in their prevalence at different times during the season. The fact that there are really two rusts obviously has an important bearing on the problem of breeding for resistance.

It is certain that if more differential varieties were added to the twelve now generally used to determine races of *P. graminis Tritici*, many more races could be isolated. Aamodt (1934) has given the formula for calculating the number of races

possible with any one group of varieties, disregarding the mesothetic reaction. The advisability of thus increasing the number of stem rust differentials, however, is questionable for general practice. For special purposes it may be desirable.

#### Conclusion.

These results show that the normal method of sorting out physiological races by means of the reaction shown on certain differential hosts that have been empirically selected, does not necessarily sort out entities that are identical. Physiological races which bear the same designation may be different. Thus the U.S.A. race 34 is not the same as the Australian race 34. Clearly physiological races do not represent the final stages in the analysis of a rust culture. A term is necessary to define these entities. "Isolates" would cover the requirement, but has a rather wider application than is wanted. It is believed that the term "biotype" as suggested by Christensen and Rodenhiser (1940) for the smut fungi adequately describes these entities. A biotype, then, is a single individual or group of individuals having the same genetic constitution. In the case of *P. graminis*, two isolates may or may not be the same biotype. Where hybridization on *Berberis* sp. is common, it may be expected that a physiological race will comprise a number of biotypes; but under Australian conditions where barberries are not frequently infected, race 34 probably comprises relatively few biotypes, which have arisen mainly in the asexual stage.

#### SUMMARY.

Comparisons, on a cultural basis, have been made between a culture of *Puccinia graminis Tritici* isolated in U.S.A. and a standard Australian culture of the same race, first at St. Paul, Minnesota, and secondly at the University of Sydney.

##### 1. At St. Paul:

- (a). Fixed Australian crossbreeds gave no reliable proof that the biotypes are different.
- (b).  $F_3$  lines from two crosses which had been tested in Australia with race 34 showed similar reactions when tested with a U.S.A. biotype of this race.
- (c). Inbred ryes of known reactions to the Australian biotype gave quite different reactions when tested with the U.S.A. biotype.
- (d). Differential varieties recorded as showing a changed reaction to race 34 in Australia, owing to a lowered temperature, did not thus change when tested with the U.S.A. biotype.

2. At the University of Sydney, side by side comparisons of the two biotypes were made under varying conditions of temperature and light:

- (a). Differential varieties, previously reported to give a change in reaction with a lowered temperature, did thus change when tested with the Australian biotype, but did not with the U.S.A. biotype.
- (b). Colour differences are discernible between the two biotypes.
- (c). On certain varieties not included in the set of differentials, the two biotypes show different reactions.

#### Acknowledgments.

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#### EXPLANATION OF PLATE XI.

Leaves of Mindum showing (A) the susceptible reactions to the U.S.A. biotype and (B) the resistant reactions to the Australian biotype of race 34 of *P. graminis Tritici*. The plants were exposed to 18 hours' light at a temperature of 55°F. In each, two leaves show the upper and two the lower surfaces of the leaves. Nat. size  $\times$  2.

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## MICROBIOLOGICAL INVESTIGATIONS ON THE DEW-RETTING OF FLAX.

By H. L. JENSEN, Macleay Bacteriologist to the Society.

(From the Department of Bacteriology, University of Sydney.)

(Plate x; two Text-figures.)

[Read 24th September, 1941.]

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*Introduction.*

The so-called "retting" of flax and other textile plants consists in a biological decomposition of the pectic substances that constitute the middle lamellae of the cell walls in the parenchymatous tissue; this decomposition renders the bundles of fibre separable from the rest of the tissues. Retting may be achieved by steeping the flax straw in water, either in rivers or ponds, or more rationally in tanks under controlled conditions. The biological agents in these systems of "water-retting" are chiefly anaerobic bacteria (varieties of *Clostridium butyricum*, and related forms), the nature and activities of which have been studied extensively.\* A quite different treatment is known as "dew-retting". This is brought about by placing the flax straw in a thin layer on a grass- or stubble-field, where it is exposed to the attack of aerobic micro-organisms, and may last from one to several weeks, depending, of course, on factors like the temperature and the amount of moisture provided by dew and rain. Dew-retting cannot be readily controlled like tank-retting, and yields, as a rule, a less valuable product; nevertheless it is practised to a considerable extent, especially in East European countries.

Our knowledge concerning the micro-organisms responsible for dew-retting is incomplete, and rests upon only a few pieces of research. Behrens (1902) found that the dew-retting of hemp was caused by filamentous fungi, particularly *Cladosporium herbarum* and *Rhizopus nigricans* (syn. *Mucor stolonifer*); at low temperatures the latter was replaced by *Mucor hiemalis*. Flax could also be retted by *Cladosporium*; the dark colour of dew-retted fibre was ascribed to the pigmented mycelium of this fungus. Haumann (1902) isolated many bacteria and fungi from dew-retted flax, and stated that *Cladosporium herbarum* was the most frequent among the fungi. He also concluded, on the basis of pure-culture tests, that dew-retting could be caused by any micro-organism, but that the fungi were generally more active than the bacteria. Behrens (1903) criticized these results as due to a faulty technique of sterilization, and found that aerobic bacteria, with the exception of *Bacillus asterosporus* and certain varieties of *Bacillus mesentericus*, were unable to ret. Ruschmann (1923) did not find *Rhizopus nigricans* or *Mucor hiemalis* on flax straw, and regarded *Cladosporium herbarum* as the all-important agent in dew-retting. *Mucor plumbeus* was described as a new retting fungus, but this as well as *Rhizopus nigricans* was suppressed by *Cladosporium herbarum* in mixed culture. The presence or absence of various other fungi as well as yeasts and bacteria seemed to be of no consequence. The very variable quality of dew-retted flax was ascribed, *inter alia*, to the fact that *Mucor* and *Rhizopus* under favourable conditions will produce a more light-coloured and pliable fibre than *Cladosporium*, which also has a tendency to cause mechanical damage to the fibre. Very recently Ruschmann and Bartram (1940) have stated that *Alternaria tenuis* is active in dew-retting as well as in subsequent fibre-destruction.

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\* On the biology of retting in general, see Thaysen and Bunker (1927).

In Australia, the conditions imposed by the Second World War have led to a great and rapid increase in the cultivation of flax, and a large proportion of the crop must be dew-retted, since the number of sites where tank-retting plants can be established is limited by the problem of water supply. A preliminary investigation of the organisms active in dew-retting under Australian conditions has therefore been undertaken.

*The Organisms Present on Dew-retted Flax.*

The organisms active under laboratory conditions were first studied. The method was essentially the same as that used by Behrens (1902) and Ruschmann (1923): 10 to 12 pieces of clean flax straw, about 8 cm. long, were placed side by side on clean microscopic slides, which were moistened with a few drops of distilled water and placed on a layer of wet sand in large Petri dishes; each dish thus formed a humid chamber for 6 straw-covered slides, which could be taken out for examination and returned at will. The fungi which developed during incubation could be observed directly under a low-power microscope with oblique illumination. At intervals the pieces of straw were picked off a slide, plate cultures were made on acid-glucose agar for the fungi, and on neutral glucose-yeast-extract agar for the bacteria; the straw was tested for retting, and the slides were stained (Gram + erythrosine) for observation of the organisms adhering to them. The degree of retting was judged mainly by the "loose-core" test (Munro, 1939); afterwards, the straw was dried at 98°C. and the fibre separated from the shives by breaking and rubbing of the dry straw. All these experiments, as well as the subsequent pure-culture tests, were made on material from the same batch of flax straw (Liral Crown, from Colac Flax Mill, Victoria).

Incubation at different temperatures gave the following results:

At 10°C. there appeared after 4-5 days a dense mycelium of a *Mucor* which was gradually, during the next 2-3 weeks, replaced by small dark patches of *Cladosporium herbarum* mixed with an *Alternaria*; the dark spore-chains of the latter appeared very conspicuous under direct microscopic examination. Here and there the straw also showed some growth of a green *Penicillium*, and small drop-like colonies of bacteria and pink yeasts. The stained slides showed after 2 and 3 weeks an abundance of small Gram-negative, non-spore-forming bacteria, besides fungal hyphae and spores. The straw was partially retted after 14, and fairly well retted after 21 days; the fibre was strong, but dark olive-grey. The *Mucor* (an atypical form of *Mucor racemosus*), *Cladosporium herbarum*, *Penicillium* sp. and two strains of bacteria were isolated.

At 24°C. the straw showed after 2 days some growth of *Rhizopus nigricans*; this became abundant after 3 to 7 days, together with *Cladosporium* and *Alternaria*. After 2 weeks the growth of *Rhizopus* had largely receded, and there was now a conspicuous growth of *Stachybotrys* sp., the black conidial heads of which covered large parts of the straw with a finely granular layer. The straw was partially retted after 7, and well retted after 14 days; the fibre was dark grey. After 20 days the straw was distinctly over-retted, to judge by the obvious weakness of the fibre when the straw was broken. *Stachybotrys* sp. (*atra*?) and a black sterile mycelium were isolated.

At 28-30°C. there appeared also during the first 4 to 7 days a copious growth of *Rhizopus nigricans*, which was gradually replaced by *Alternaria* and *Stachybotrys*; a green *Aspergillus* and a *Macrosporium* were also visible. Agar-cultures showed mainly colonies of *Aspergillus glaucus*, with admixture of *A. niger*, *Trichoderma* sp., etc. The straw was well retted after 1 and 2 weeks and badly over-retted after 22 days; the fibre was of a dark colour, as at 10°C. and 24°C. The stained slides showed after 5 and 7 days enormous numbers of small, Gram-negative, non-spore-forming rod-shaped bacteria, and also of big, plump, Gram-positive rods, some of these having distinct capsules; after 10 and 14 days the second type had largely disappeared, but many free endospores were seen. A single slide showed a quite extensive growth of *Actinomyces* hyphae after 7 days. Agar-plates showed predominantly small, slimy, yellow colonies of an organism resembling *Bacterium herbicola*, and also many colonies of spore-forming bacteria largely conforming to *Bacillus mesentericus*. The following were isolated: *Alternaria* sp., *Macrosporium* sp., *Helminthosporium* sp., *Rhizopus nigricans*, *Aspergillus glaucus*, *A. niger*, *Trichoderma* sp. (*koningi*?), five strains of non-spore-forming and three of spore-forming bacteria.

At 37°C. the microflora was of a much simpler composition: abundant growth of green and yellow *Aspergilli*, with some admixture of *Aspergillus niger* and *Rhizopus nigricans*. The straw was fairly well retted after 4 and perfectly retted after 7 days; the fibre was yellowish and quite free from the dark colour that was produced at the lower temperatures. The slides showed mainly small Gram-negative bacteria, besides a few big rods with subterminal spores. An *Aspergillus* with yellowish-brown spores (*A. ochraceus?*) was isolated.

The types of organisms that appear under natural conditions were studied on samples of flax straw in different stages of dew-retting in the field. Such samples were collected at two localities in Victoria.\* As soon as practicable after collecting the samples, the straw was cut into pieces 10–12 cm. long, and 30–40 such pieces from each sample were placed on moist sterile cotton-wool in big Petri dishes, which were kept at a temperature of 19–24°C. The growth of organisms that appeared during the next few days was examined microscopically, and platings were made on malt-extract agar and ordinary nutrient agar.

From Koo-wee-rup Flax Mill, seven samples, all of the variety "J.W.S.", were obtained: 1. Unretted; 2. Spread on retting paddock day before sampling; 3. Spread 3 days before sampling; 4. Retted 14 days; 5. Retted 3 weeks; 6. Retted 5 weeks (finished); 7. Decayed straw, spread day before sampling; fibre destroyed, straw black with delicate white bloom.

All specimens of straw, except the abnormal No. 7, showed dark grey to brownish spots of fungal growth, which in samples 5 and 6 had coalesced into the uniform dark grey colour typical of dew-retted flax. The macroscopic picture of samples 1–6 during incubation was fairly uniform: a low, velvety, olive-grey to nearly black fungal growth developed, most conspicuously in the younger samples 1–3; specimens 4–6 showed more evidence of a slimy black layer on the straw. Microscopic examination before and during incubation showed, both on the surface and in the cortex of the straw, large numbers of fungal hyphae, mostly dark-coloured, some consisting of long slender cells, others of thick, short, almost coccoid elements—further an abundance of conidia resembling those of *Cladosporium* and *Alternaria*, yeast-like cells, and small non-spore-forming bacteria. Plate-cultures showed predominantly *Cladosporium* sp., *Alternaria* spp. (two types) and *Macrosporium* sp., very few other filamentous fungi, but very large numbers of *Dematium pullulans* and pink and white yeasts. The bacteria were mainly represented by *Bacterium herbicola* and *Pseudomonas fluorescens*. The decayed straw, No. 7, showed a more varied picture. The white growth became quite dense and pinkish during incubation, and revealed itself as *Cephalothecium roseum*; white and rust-red mycelia as well as *Alternaria* spp. were also common. *Dematium*, yeasts and bacteria were less abundant than on normal straw. The plate-cultures showed numerous colonies of a slowly-growing *Cephalosporium*. The samples 4–6 were largely over-retted after 10–12 days, and showed some growth of *Cephalothecium roseum*, together with scanty white aerial mycelium of an *Actinomyces*; otherwise the actinomycetes appeared largely to be absent from dew-retted straw, as also reported by Ruschmann and Bartram (1940), but contrary to earlier statements by Haumann (1902).

Another batch of samples was collected from Ballarat Flax Mill: 1. "Liral Crown", unretted; 2. "Liral Crown", retted 3 weeks; 3. "Concurrent", retted 5 weeks (finished); 4. "Liral Crown", unretted, grown in South Australia; 5. Same as 4, retted at Ballarat 5 weeks, then stacked; 6. "Concurrent", retted 5 weeks; straw white, fibre destroyed.

Samples 4 and 5 represented an exceptionally good, and the others mediocre to poor crops of flax straw. The microflora on the various samples was much the same as on the previous ones, except that No. 4 showed during incubation a scant growth of *Rhizopus nigricans*. The flora on the decayed straw, No. 6, was dominated by *Cephalothecium roseum*.

The flora of natural dew-retted straw thus differs mainly from the laboratory-flora at middle temperatures, by the almost total absence of *Mucor* and *Rhizopus*, and by the richer growth of *Dematium pullulans* and yeasts. A more varied flora, often dominated by *Cephalothecium roseum*, seems to arise only when the straw is over-retted. In the

\* This part of the work was done in the Forest Products Laboratory (C.S.I.R.), Melbourne.

field as well as in the laboratory, *Cladosporium* and *Alternaria* are prominent among the fungi, and *Bacterium herbicola* among the bacteria. The common occurrence of the last organism is not surprising in view of its very wide distribution on all kinds of plant material (Mack, 1936; Ruschmann and Bartram, 1940).

#### *Retting Experiments with Pure Cultures.*

All the organisms isolated in the previous experiments were tested for their ability to ret sterile flax straw. Two cultural methods were used. The first was designed to imitate dew-retting conditions as closely as possible: 10 to 12 sections of flax straw, about 8 cm. long, were placed in a test-tube which at its bottom had a firm plug of absorbent cotton-wool about 1.5 cm. deep. The tubes with cotton and straw were sterilized by autoclaving at 20 lb. pressure; after cooling, sufficient sterile water was added to saturate the cotton-wool, and the tubes were left at room temperature for 3-4 days in order to check the sterility and to give the straw time to saturate itself with water by imbibition. If necessary, sufficient extra water was added to cover the cotton-wool with a very shallow layer. Disintegration of the tissues by autoclaving in a wet condition was avoided by this procedure, and the tubes proved regularly sterile and without any spontaneous retting. Incubation of sterile straw caused a certain loosening of the tissues which, however, could always be distinguished from real retting: when the loose-core test was applied, the fibre-bundles showed a marked adherence to the core and came off in a coherent ribbon, which on drying assumed an appearance similar to that of the decorticated flax obtained by mechanical treatment. Several such control tubes were included in each batch of inoculated tubes. The inoculum (bacteria or fungal conidia, except in the few cases of sterile mycelia) was added to the small amount of water above the cotton-plug, and distributed by holding the tube almost horizontally and rotating it slowly under vigorous tapping. After different periods of incubation the straw was tested for degree of retting and character of fibre. The organisms that failed to provoke retting within 2-3 weeks were re-tested by a second method that provided for a higher degree of moisture: pieces of flax straw were placed in a layer on the bottom of 250 c.c. Erlenmeyer flasks, autoclaved, and moistened with 20 c.c. of sterile water, which immersed the straw in a very shallow layer of liquid. Most cultures were incubated at 24°C. and 30°C., some also at 10°C. and 37°C. The following results were noted:

1. *The bacteria* (altogether thirteen isolates, including varieties of *Bacillus mesentericus*) were all unable to ret by both methods, although they mostly grew well in the liquid in flask cultures. It appears, in agreement with the findings of Behrens (1902-03), Beijerinck and van Delden (1904), Tanner (1922) and Trevethick (1928), that only a few aerobic bacteria have retting properties, and these, if occurring at all, are not prominent in the dew-retting flora under Australian conditions.

2. *Yeasts* previously have been found unable to ret (Behrens, 1902; Beijerinck and van Delden, 1904; Tanner, 1922). Two yeast-like organisms ("*Torula*"), isolated from straw-samples Koo-wee-rup No. 6 and Ballarat No. 3, proved effective when tested in flask cultures. The first strain, which produced a red pigment, gave partial retting after 1 week and very good retting after 2-3 weeks at 30°C.; the fibre was light-coloured and strong, but felt somewhat "harsh". The other strain, without pigment, had a similar but weaker effect. When tried in test-tubes, both yeasts caused only a slight loosening of the fibres at the lower end of the straw that was in direct contact with the wet cotton-wool. A third yeast produced no retting at all. Since the yeasts evidently demand a quite high degree of moisture, they are unlikely to be active in dew-retting (cf. Ruschmann, 1923), but may perhaps be of some direct significance in water-retting.

3. *The fungi* were all capable of retting, but the rate of this process and the character of the resulting fibre varied considerably. A survey of the results is shown in Table 1.

The flax straw is retted promptly by all those fungi that predominate in the retting-flora, and all the common Dematiaceae (*Dematium*, *Cladosporium*, *Alternaria*, etc.) yield a fibre of the same dark colour as natural dew-retted flax, while the fungi with light-coloured mycelium (the Mucoraceae, Aspergilli, etc.) give a fibre almost as light as water-retted flax (Plate x, figs. 1-6). The tendency to "over-retting", resulting in a

TABLE I.  
Retting Ability of Fungi in Pure Culture.

Organism, and Conditions of Incubation.			Degree of Retting, and Condition of Fibre.
1*	24° C.,	20 d.	} Good retting, fibre light and strong. Fair retting, fibre light greyish-yellow. Also retting at 10° C. but not at 37° C.
	„	50 d.	
	30° C.,	9 d.	
1	30° C.,	5 d.	} Fair retting, fibre light greyish-yellow. Excellent retting, fibre light and strong. Similar at 37° C.
	„	12 d.	
	„	20 d.	
1	24° C.,	7 d.	} Good retting, fibre yellowish-grey. Excellent retting, fibre yellowish-grey. Slight over-retting, fibre somewhat weak.
	„	14 d.	
	30° C.,	6 d.	
	„	12 d.	
1	„	21 d.	} Fair retting, fibre dark, feels "harsh".
	24° C.,	7 d.	
	„	14 d.	
	30° C.,	8 d.	
1	„	14 d.	} Fair retting, fibre dark, feels "harsh".
	„	14 d.	
1	30° C.,	6 d.	} Fair retting, fibre light greyish-yellow. Good retting, fibre slightly weakened. Similar at 37° C.
	„	14 d.	
1	30° C.,	7 d.	} Good retting, fibre brownish-yellow. Similar at 37° C.
	„	14 d.	
1	30° C.,	7 d.	} Good retting, fibre yellow. Over-retting; fibre yellowish-brown, very weak. Fibre almost completely disintegrated.
	„	14 d.	
	„	20 d.	
1	24° C.,	7 d.	} Good retting; fibre soft but strong, dark grey. Good retting, fibre very dark olive-grey. Unchanged; fibre remains strong. Also retting at 10° C.
	„	14 d.	
	„	28 d.	
1	24° C.,	7 d.	} Fair retting, fibre dark grey, somewhat "harsh". Good retting, fibre very dark grey. Slight over-retting; fibre dark, somewhat weak.
	„	14 d.	
	„	21 d.	
1	24° C.,	7 d.	} Fair retting, fibre light grey. Good retting fibre grey, slightly weakened. Over-retting; fibre light grey, soft and weak.
	„	14 d.	
	„	21 d.	
2	24° C.,	10 d.	} Fair retting, fibre light greyish-yellow.
	„	14 d.	
2	30° C.,	7 d.	} Good retting, fibre light yellow. Slight over-retting; fibre somewhat weak.
	„	14 d.	
	„	21 d.	
2	30° C.,	7 d.	} Good retting, fibre light yellow. Slight over-retting. Similar at 37° C.
	„	14 d.	
2	30° C.,	7 d.	} Good retting, fibre dark grey. Over-retting, fibre grey, soft and weak. Strong over-retting; fibre disintegrated.
	„	14 d.	
	„	21 d.	
2	24° C.,	7 d.	} Good retting; fibre soft, light grey. Slight over-retting, fibre somewhat weak. Good retting; fibre soft, light brownish. Over-retting; fibre weak but not much discoloured.
	„	14 d.	
	30° C.,	7 d.	
2	„	14 d.	} Over-retting; fibre weak but not much discoloured.
	„	14 d.	

TABLE 1.—Continued.  
Retting Ability of Fungi in Pure Culture.—Continued.

Organism, and Conditions of Incubation.			Degree of Retting, and Condition of Fibre.
3			
<i>Cephalosporium</i>	24° C.	10 d.	Retting only beginning.
sp.	„	20 d.	Fair retting, fibre yellowish.
3			
<i>Cephalothecium</i>	30° C.,	7 d.	Fair retting, fibre greyish-yellow.
<i>roseum</i>	„	14 d.	Good retting, fibre light yellowish-brown.
3			
<i>Monosporium</i> sp.?	30° C.,	14 d.	Good retting ; fibre light yellowish-brown.
3			
<i>Nigrosporium</i> ?	30° C.,	12 d.	Good retting, fibre light, somewhat weak.
3			
Black sterile	30° C.,	7 d.	Good retting, fibre greyish-brown.
mycelium	„	14 d.	Slight over-retting ; fibre pure grey.
3			
White sterile	24° C.,	15 d.	Excellent retting, fibre pure white.
mycelium	30° C.,	7 d.	Good retting, fibre light, slightly weak.

\* Species marked "1" are those of prominent appearance on the straw, those marked "2" represent the fungi of more occasional occurrence, and "3" the fungi isolated from over-retted straw.

† Another strain showed identical behaviour.

‡ Another strain of this type showed almost identical behaviour ; growth and action of both types at 30°C. similar to 24°C.

fibre that easily breaks when attempts are made to separate it from the woody tissue, also varies strongly. *Mucor*, *Rhizopus*, *Dematium* and *Cladosporium* do not produce this effect to a serious extent, while others, especially *Strachybotrys* sp., show it at an early date and to a marked degree. The fungi found on decayed straw do not appear particularly active in this respect; their occurrence would thus seem to be the result rather than the cause of over-retting. A noteworthy phenomenon is a very definite, but hitherto unrecognized retting power of *Dematium pullulans*, of which two different cultural types were found. One of them showed predominantly mycelial growth in agar culture, had a comparatively weak retting ability, and stained the fibre badly; the other, of a more yeast-like appearance, produced quicker retting and less discoloured fibre. On sterile flax straw, *Dematium* developed as a thin, velvety, dark grey, moist layer, microscopically containing the same chains of dark, almost spherical cells, which were seen so frequently in the natural dew-retted straw. The very commonly-occurring *Alternaria* also comprised two types, one of them (*a*) producing a very voluminous mycelium with sparse conidia formation, and the other (*b*) a restricted vegetative growth but abundant sporulation; *b* gave a quicker retting and a less discoloured fibre than *a*, but it also damaged the fibre more rapidly (cf. Ruschmann and Bartram, 1940). Cultural tests on filter-paper in various nutrient solutions showed that a really strong cellulose-decomposing power was possessed only by *Trichoderma*, which is not a typical retting fungus. There was no obvious correlation between cellulose-decomposition and fibre-destruction, which thus does not seem due to actual breakdown of fibre-cellulose. It must be admitted, however, that the fibre-cellulose is not identical with filter-paper (Norman, 1937). A thorough investigation into the losses of the different flax straw constituents under dew-retting, on lines similar to the work of Kalnins (1937) and Couchman (1939) on water-retted flax, would no doubt prove highly valuable.

An interesting behaviour was shown by the white sterile mycelium isolated from flax straw that had been over-retted in the laboratory. When inoculated upon sterile straw together with *Cladosporium* or *Alternaria*, the white mycelium was at first not

visible, but after a few weeks its growth became conspicuous, repressed the other fungi, and seemed to decompose their dark pigments, so that the straw appeared quite pale after 4-5 weeks, at which time the fibre was completely destroyed (Plate x, A-B). A similar effect was seen on the straw from which the fungus was isolated. Organisms like this may be responsible for the peculiar bleached appearance of decayed flax straw which is sometimes seen in the retting paddocks. (Sample 6, Ballarat.)

*The Influence of Light on the Fungi.*

The paucity of *Mucor* and *Rhizopus* on flax straw retted in the field contrasts strikingly with the abundant growth of these fungi in laboratory experiments, and an experiment was carried out in order to ascertain whether this difference might be due to the influence of light. *Mucor*, *Rhizopus* and *Alternaria*, type *b*, were grown on glucose-peptone agar in Petri dishes which were inoculated at the centre and incubated in a greenhouse where the temperature varied between 13°C. and 22°C. Some of the dishes were placed on a bench where they were exposed to diffused daylight, and for some hours daily also to direct sunlight; others were placed alongside them but enclosed in a tin and thus shielded from the light. At intervals of 24 (later 48) hours the area of the colonies was measured planimetrically. The results are shown in Fig. 1, and prove clearly that *Rhizopus* is strongly inhibited in daylight, *Mucor* much less so, and *Alternaria* not to any significant degree. Considering that the experiment was performed at a season when solar intensity is low (June 3-13), and in a greenhouse where the ultra-violet fraction of the sunlight was largely removed by the glass, it seems probable that the difference would be even more accentuated in the open field and in the proper retting-season (March to May).

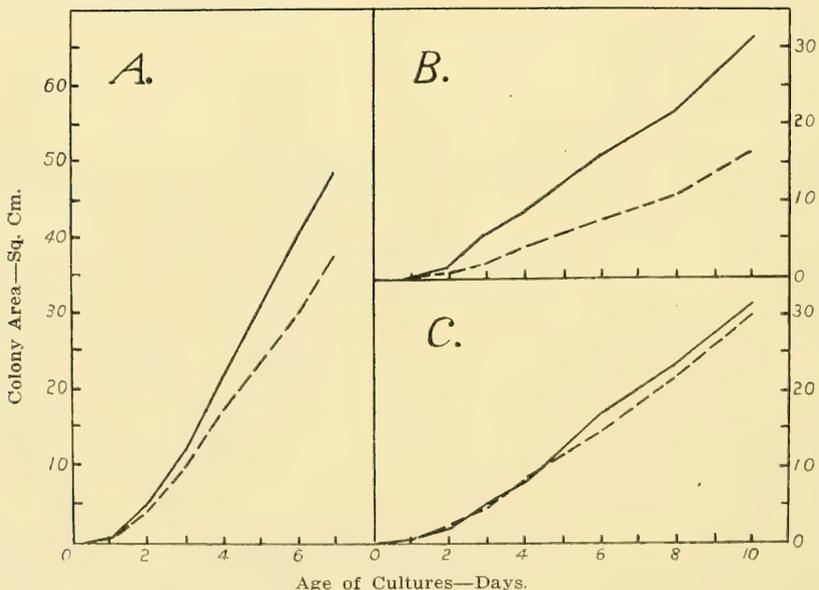


Fig. 1.—Growth of fungi in darkness (continuous line) and daylight (broken line).  
A, *Mucor racemosus*; B, *Rhizopus nigricans*; C, *Alternaria* sp.

At the same time a retting-experiment was carried out in the greenhouse, with *Rhizopus*, *Mucor* and *Cladosporium* on sterile flax straw in test-tubes, alone and in combined culture, exposed to light or enclosed in a tin. The macroscopically-visible growth of the two Mucoraceae, especially *Rhizopus*, was considerably retarded in light, and after 8 and 15 days the retting was definitely better in darkness; the action of *Rhizopus* was, upon the whole, rather weak at this temperature (cf. Ruschmann, 1923). Together with *Cladosporium* the Mucoraceae grew well in darkness, but both, and particularly *Rhizopus*, were suppressed by *Cladosporium* in light. The growth of this

fungus was not visibly affected by the light, and the retting was fair after 8, and good after 15 days. *Dematium pullulans* and *Alternaria* behaved likewise; to judge by the pigment formation, the former seemed even to be stimulated by the light. Everything thus suggests that the inhibitory effect of sunlight is at least partly responsible for the inactivity of *Mucor* and *Rhizopus* in natural dew-retting.

*Changes in the Reaction of Flax Straw under Dew-retting.*

During tank-retting the acidity of the retting liquor increases in a characteristic way, from which the end-point of the retting process may be determined (Eyre and Nodder, cit. after Thaysen and Bunker, 1927; Kalnins, 1937; Munro and Couchman, 1939). Some pH-determinations were made in order to see if any such characteristic changes take place during dew-retting. Natural dew-retted straw was first examined; 5-gm. portions of air-dry material were cut into very small pieces with scissors, and soaked for 2 hours at room temperature in 40 c.c. of distilled water; the reaction of the liquid was then measured by means of the glass electrode. Result:

<i>Samples from Koo-wee-rup.</i>		<i>Samples from Ballarat.</i>	
	pH		pH
1. J.W.S., unretted .. .. .	5.70	1. Liral Crown, unretted .. .. .	5.67
4. Do., retted 2 weeks .. .. .	6.32	2. Do., retted 3 weeks .. .. .	6.51
6. Do., retted 5 weeks .. .. .	6.61	5. Do., retted 5 weeks .. .. .	6.88
7. Do., decayed straw .. .. .	7.14		

The results suggest that the reaction of the straw changes from acid to approximately neutral, and that the change is already very pronounced when the straw is only half retted. Further observations were made on straw retted in the laboratory. Four-gm. portions of straw (Liral Crown), cut into lengths of about 12 cm., were placed in a thin layer upon a raft of glass rods resting on a layer of sand in a big Petri dish; the glass rods served to prevent the flax from direct contact with the sand. Sufficient water was added to saturate the sand, and an extra 10 c.c. of water were sprinkled on the straw. After different periods of incubation at 24°C. the straw was tested for retting, cut finely, soaked for 2 hours in 4 times its quantity of distilled water, and pH was measured. A copious growth of fungi, chiefly *Rhizopus* and *Cladosporium*, appeared after 3-4 days. The straw was partially retted after 7 days, well retted after 11-14 days, and slightly over-retted after 18-22 days. The results of the pH-determinations are seen in Fig. 2.

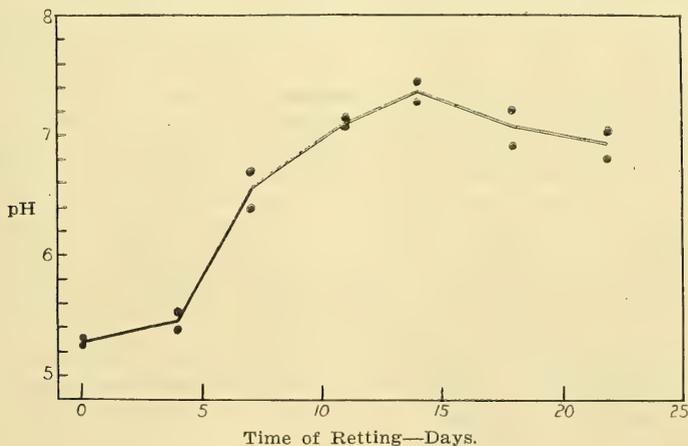


Fig. 2.—Change of pH in straw retted in the laboratory. Black dots indicate duplicate measurements.

This experiment corroborates the result of the first observations, in showing that the originally acid reaction of the straw changes to nearly neutral or faintly alkaline when fully retted, and that the main change takes place in the early stages before the retting is complete. No ammonia could be detected in the liquid; the increase in pH

is thus probably due to consumption of organic acids. It remains uncertain whether the slight drop in pH after 14 days is significant. As a further test, a number of organisms were grown in a 10% decoction of flax straw for 7 days at 24°C. The sterile solution had pH 5.48-5.50. Among the thirty isolates tested, only four (*Aspergillus niger*, *Stachybotrys* sp., two bacteria) showed strong acid production, changing the reaction of the solution to pH 4.18-4.96; ten others (*Dematium*, *Penicillium*, the yeasts, *Bacillus mesentericus*, *Bacterium herbicola*) caused minor changes (pH 5.18-5.63). The rest, including typical retting fungi like *Rhizopus*, *Cladosporium* and *Alternaria*, caused significant decreases in acidity (pH 5.88-6.86). Generally it seems clear that an approximately neutral reaction is characteristic of dew-retted flax straw, but the variation is considerable and the difference in pH of half and fully retted straw is comparatively small; a definite end-point, such as in tank-retting, can therefore hardly be determined on this basis.

#### General Conclusions.

There seems to be quite clear evidence that the dew-retting of flax in Australia is brought about by fungi, of which the most important under natural conditions appear to be *Cladosporium herbarum*, *Dematium pullulans*, and *Alternaria* spp. Except for the prevalence of the second species, this agrees well with the findings of Ruschmann (1923, 1940). It is very noteworthy that the predominant forms are the same as the prevalent *Fungi imperfecti* among the "sooty moulds" (Fraser, 1933).\* Apparently these fungi are nearly ubiquitous on plants and are able to suppress the many other potential retting organisms which, by virtue of their common occurrence in nature (*Mucor*, *Trichoderma*, *Penicillium* and *Aspergillus* are among the very commonest soil fungi) would have excellent opportunities of infecting the flax straw. *Alternaria* spp. are not only common in the soil and among the sooty moulds (Fraser, 1933), but also as seed-borne contaminants of flax. Dr. E. T. Edwards (personal communication) found this genus present in 7 to 62% of imported and 23 to 78% of Australian-grown flax seed; two isolates, which Dr. Edwards kindly supplied, retted flax straw promptly. The fact that such a well-defined flora of relatively few species gains ascendancy among the many other fungi potentially capable of retting, suggests that little benefit could be expected from attempts at artificial inoculation of the straw with cultures of organisms that give a particularly desirable product. One might here think of organisms like *Mucor*, *Rhizopus* and the Aspergilli, but the two first are suppressed by other fungi in sunlight, and the last group becomes predominant only at high temperatures. Thus the course of dew-retting under natural conditions must be left to the controlling influence of climatic factors; among these, moisture seems more important than temperature, since in the greenhouse experiment, straw was retted at the rather low temperature of 13-22°C. within 1-2 weeks, against an average retting-time of 5 weeks in the field. Measures for obtaining a good product would therefore mainly be confined to selecting localities with plentiful dew-formation for retting-sites, and general care to keep the straw free from moisture before and after the actual retting-period. The only alternative to such simple practical measures would seem to be the adoption of a retting-method that permits full control of the environmental factors. A step in this direction seems to be represented by the so-called "Hindley process",† which, so far as can be surmised from the scanty information available, consists in a kind of indoor "dew-retting" at fairly high temperature. To judge from the present results on retting at 37°C., the claim that high-quality fibre can be produced very rapidly by this method does not appear exaggerated. It must be left to future experiments to decide whether such systems of artificial dew-retting are practicable on a large scale, and whether the consumption of water is low enough to justify their use in localities where the water supply is insufficient for tank-retting.

\* The two types of *Dematium pullulans* met with in the present work were recognized by Dr. Lillian Fraser as being perfectly similar to the types encountered by her among the sooty moulds.

† Briefly mentioned in *The Irish Textile Journal*, May, 1940.

## SUMMARY.

Dew-retting of flax appears under Australian conditions to be due entirely to the action of fungi. Laboratory experiments showed that the most important retting organisms were at low temperatures (10–12°C.) *Mucor racemosus* (?) and *Cladosporium herbarum*, at middle temperatures (24–30°C.) *Rhizopus nigricans*, *C. herbarum*, *Alternaria* spp., and *Stachybotrys* sp., and at high temperatures (37°C.) *Rhizopus nigricans* and *Aspergillus* spp. The predominant forms under field conditions were *Cladosporium herbarum*, *Dematium pullulans*, and *Alternaria* spp. A more varied flora arose on over-retted straw. The absence of Mucoraceae, especially *Rhizopus nigricans*, seemed at least partly due to inhibition by the sunlight.

Pure-culture studies showed that bacteria found on dew-retted flax (*Bacterium herbicola*, *Bacillus mesentericus*, etc.) were unable to produce retting. A few yeasts were able to ret, but seemed unlikely to be active under field conditions. All the fungi tested could ret flax straw more or less quickly, and some of them, especially *Stachybotrys* sp., caused rapid destruction of the fibre; this effect was least pronounced in *Mucor*, *Rhizopus*, and *Cladosporium*, and was not particularly strong in the species found on over-retted flax straw; their occurrence therefore seems to be the result rather than the cause of over-retting. Fibres of the same dark colour as naturally dew-retted flax were produced by *Cladosporium*, *Dematium*, *Alternaria*, and other fungi that formed dark pigments. The finest fibre seemed to be produced by *Mucor*, *Rhizopus*, and the *Aspergilli*.

Dew-retting is accompanied by a loss of acidity, the reaction changing from acid (pH 5.3–5.7) in unretted to approximately neutral (pH 6.8–7.4) in fully retted straw.

## Acknowledgements.

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## EXPLANATION OF PLATE X.

A-B.—Flax-straw cultures, 4 weeks 24°C. A, *Cladosporium herbarum* + sterile white mycelium; B, *Cladosporium herbarum*.

1-6.—Samples of light- and dark-coloured flax fibre produced by different retting organisms. 1, *Rhizopus nigricans*; 2, Pink yeast ("Torula"); 3, *Aspergillus glaucus*; 4, *Cladosporium herbarum*; 5, *Dematium pullulans*; 6, *Alternaria* sp.

THE OVIPOSITION RESPONSES OF THREE SPECIES OF MOSQUITOES  
(*AEDES (STEGOMYIA) AEGYPTI* LINNAEUS, *CULEX (CULEX) FATIGANS*  
WIEDEMANN, *AEDES (PSEUDOSKUSEA) CONCOLOR* TAYLOR), IN  
RELATION TO THE SALINITY OF THE WATER.

By A. R. WOODHILL, Department of Zoology, University of Sydney.

(Two Text-figures.)

[Read 24th September, 1941.]

*Introduction.*

One of the major problems of mosquito ecology is the determination of the factors which limit certain species of larvae to certain types of breeding water. One of the many possible factors is the oviposition response of the female to the chemical composition of the water. In the following paper an account is given of experiments designed to test the oviposition responses of three different species, in relation to the salinity of the water.

*Material and Methods.*

Of the three species used, *A. aegypti* and *C. fatigans* are freshwater species which will not develop in water with a salinity greater than 10 gm. of salts per litre (Wigglesworth, 1933; Woodhill, 1938). They differ, however, in that *A. aegypti* is rarely found in very foul water or in ground water, while *C. fatigans* occurs in all kinds of clean and foul water in artificial receptacles and in ground water. *A. concolor* on the other hand is a salt-water species which normally breeds in water having a salinity up to 74 gm. of salts per litre, and which can even complete its development in water gradually raised to a salinity of 180 gm. per litre (Woodhill, 1936).

The mosquitoes used in the experiments were bred from eggs of *A. aegypti* and *C. fatigans* and from field collected pupae of *A. concolor*. Several hundred adults were placed in cages 16" × 7½" × 8½" and given blood feeds and raisins. At one end of the cage was placed an oviposition dish containing distilled water, and at the other end a dish containing saline water, and the positions of these two dishes were reversed each night. The females therefore had the choice of ovipositing on either distilled water or saline water. In addition, in order to check the experimental error, an experiment was carried out with *A. aegypti*, in which two dishes of distilled water were used, and a separate record kept of each dish, all other conditions being similar to the remaining experiments. The various salinities were made up by diluting clean filtered sea-water of known composition with distilled water, or when necessary, by adding salts to sea-water according to the formula given by Dakin and Edmonds (1931). The symbol S‰ represents grams of salts per 1,000 gm. of water. The room in which the cages were kept was completely darkened every night, while the temperature was kept constant at 80°F. ± 1°F., and the humidity maintained between 70% and 75%. The eggs were counted and removed each morning, and the water changed.

RESULTS.

The following tables give the results obtained:

TABLE 1.  
Culex (*Culex*) *fatigans* Wiedemann.

Observation No.	S. %	Per cent. eggs deposited on saline water.	Total eggs deposited.	Observation No.	S. %	Per cent. eggs deposited on saline water.	Total eggs deposited.
1	17.5	0	294	1	5.0	37.4	811
2	"	0	76	2	"	24.8	222
3	"	0	92	3	"	0	65
4	"	0	728	4	"	23.5	213
5	"	0	354	5	"	39.6	556
6	"	0	76	6	"	38.3	459
7	"	0	199	7	"	0	207
8	"	0	348	8	"	60.9	192
		Mean % 0	Total 2,167	9	"	39.6	260
				10	"	51.4	140
				11	"	35.9	993
				12	"	0	105
1	10.0	0	1,676	13	"	45.3	159
2	"	0	185	14	"	0	374
3	"	0	495	15	"	43.4	546
4	"	0	160	16	"	26.4	178
5	"	0	439	17	"	17.6	256
		Mean % 0	Total 2,955			Mean % 28.5	Total 5,736

TABLE 2.  
*Aedes* (*Stegomyia*) *aegypti* *Linnaeus*.

Observation No.	S. %	Per cent. eggs deposited on saline water.	Total eggs deposited.	Observation No.	S. %	Per cent. eggs deposited on saline water.	Total eggs deposited.
1	35.0	0	317	1	5.0	31.9	411
2	"	0	207	2	"	47.1	561
3	"	0	398	3	"	23.7	1,452
4	"	0	462	4	"	40.7	1,541
5	"	0	285	5	"	23.5	1,222
6	"	0	533			Mean % 33.4	Total 5,187
		Mean % 0	Total 2,202	1	0	57.1	478
				2	"	37.2	43
				3	"	0	62
1	17.5	15.2	408	4	"	78.6	112
2	"	0	192	5	"	0	66
3	"	2.4	832	6	"	100.0	77
4	"	0.6	490	7	"	45.5	270
5	"	0	352	8	"	44.1	186
6	"	1.2	416	9	"	45.6	272
		Mean % 3.2	Total 2,690	10	"	0	77
				11	"	0	53
				12	"	38.2	489
				13	"	50.9	163
				14	"	54.1	303
				15	"	40.4	280
1	10.0	19.0	342	16	"	91.3	23
2	"	17.9	697	17	"	25.7	222
3	"	20.0	379	18	"	62.3	239
4	"	14.8	594	19	"	90.5	95
5	"	15.4	273	20	"	43.6	101
6	"	22.2	464	21	"	0	58
		Mean % 18.2	Total 2,749			Mean % 43.1	Total 3,669

TABLE 3.  
Aedes (Pseudoskusea) concolor Taylor.

Observation No.	S. %	Per cent. eggs deposited on saline water.	Total eggs deposited.	Observation No.	S. %	Per cent. eggs deposited on saline water.	Total eggs deposited.
1	35.0	0	103	1	10.0	31.6	275
2	"	0	30	2	"	53.7	1,376
3	"	0	67	3	"	10.0	359
4	"	18.2	33	4	"	35.1	222
5	"	1.4	144	5	"	19.9	536
6	"	5.2	829	6	"	58.7	320
7	"	1.2	160	7	"	35.0	306
8	"	1.3	937	8	"	37.4	505
9	"	7.5	2,228	9	"	67.0	102
10	"	7.9	783	10	"	12.0	174
		Mean % 4.3	Total 5,314			Mean % 36.0	Total 4,175
1	17.5	26.6	425	1	5	29.1	1,262
2	"	21.6	1,362	2	"	61.3	2,057
3	"	16.9	362	3	"	47.6	1,052
4	"	2.6	307	4	"	63.0	1,364
5	"	47.1	346	5	"	42.9	1,168
6	"	14.6	308	6	"	56.1	1,555
7	"	59.7	211			Mean % 50.0	Total 8,458
8	"	35.8	358				
9	"	19.4	165				
10	"	31.1	167				
		Mean % 27.5	Total 4,011				

In Table 4 the previous three tables are summarized, and in Fig. 1 the results are expressed in the form of a graph.

TABLE 4.

Species.	S. %				
	35.0	17.5	10.0	5.0	0
<i>C. fatigans</i>	%	%	%	%	%
<i>A. aegypti</i>	—	0	0	28.5	—
<i>A. concolor</i>	0	3.2	18.2	33.4	43.1
	4.3	27.5	36.0	50.0	—

Statistical Analysis.\*

In Table 2 the figures are given for a check series of *A. aegypti*, in which two dishes of distilled water were used, and a separate record kept of each dish, their positions being changed each night. The result should have shown a random variation from 50% in each dish, but instead the percentages were 43 and 57, giving a significant difference by the usual  $\sqrt{npq}$  test. It is extremely likely, however, that where less than 100 eggs were deposited in a single night only one female was concerned, and that it would be justifiable to exclude figures of 100 eggs or less. This was therefore done in all the tables for purposes of analysis. In Table 2 the percentages then became 48.8 and 51.2. Nevertheless it was considered that the variance could not be assumed to be the same

\* Contributed by Miss H. Newton Turner, McMaster Animal Health Laboratory, C.S.I.R., Sydney.

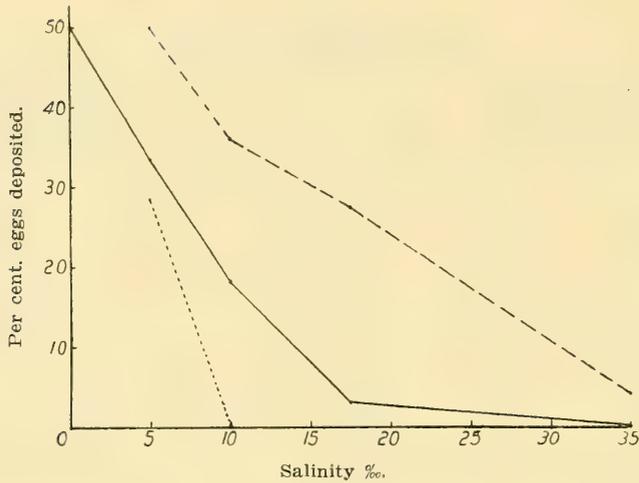


Fig. 1.—*C. fatigans* -----, *A. aegypti* ———, *A. concolor* ..... .

as that obtained in a binomial distribution. With a percentage calculated in this way the variance is likely to be dependent on the mean, and the actual percentages cannot be used in an analysis of variance, because in groups with different means the variances are not homogeneous. Fisher and Yates (1938) give tables for transforming the percentages into angles, the variance then being independent of the mean and therefore stable. Table A gives the actual mean percentages obtained in the various groups (omitting 100 eggs or less) and Table B the means of the same figures transformed.

TABLE A.  
Actual Percentages of Eggs Deposited. Omitting 100 eggs or less.

Species.	S. %				
	35.0	17.5	10.0	5.0	0
<i>C. fatigans</i> .. .. .	—	0	0	30.3	—
<i>A. aegypti</i> .. .. .	0	3.2	18.2	33.4	48.8
<i>A. concolor</i> .. .. .	3.5	27.5	36.0	50.0	—

TABLE B.  
Transformed Percentages of Eggs Deposited.

Species.	S. %				
	35.0	17.5	10.0	5.0	0
<i>C. fatigans</i> .. .. .	—	0	0	30.4	—
<i>A. aegypti</i> .. .. .	0	7.3	25.2	35.2	44.4
<i>A. concolor</i> .. .. .	9.2	30.5	36.2	45.0	—

Various points were investigated, as follows:

1. Differences between *A. aegypti* and *A. concolor*.

The difference was significant at every degree of salinity at which both were tested.

2. Differences between *C. fatigans* and other species at S‰5.

*C. fatigans* was not significantly different from either of the other species, owing to its large variability.

3. Differences between various salinities for each species. Fig. 2.

Lines were fitted to the transformed percentages, plotted against salinities.

For *A. concolor* a straight line fitted well, the formula being:

$$Y = -1.16x + 49.76$$

where  $x = \text{‰ salinity}$  and  $Y$  transformed percentages of eggs deposited. This line means that as the salinity increased the percentage of eggs decreased. Differences in the percentage of eggs between successive points were all significant.

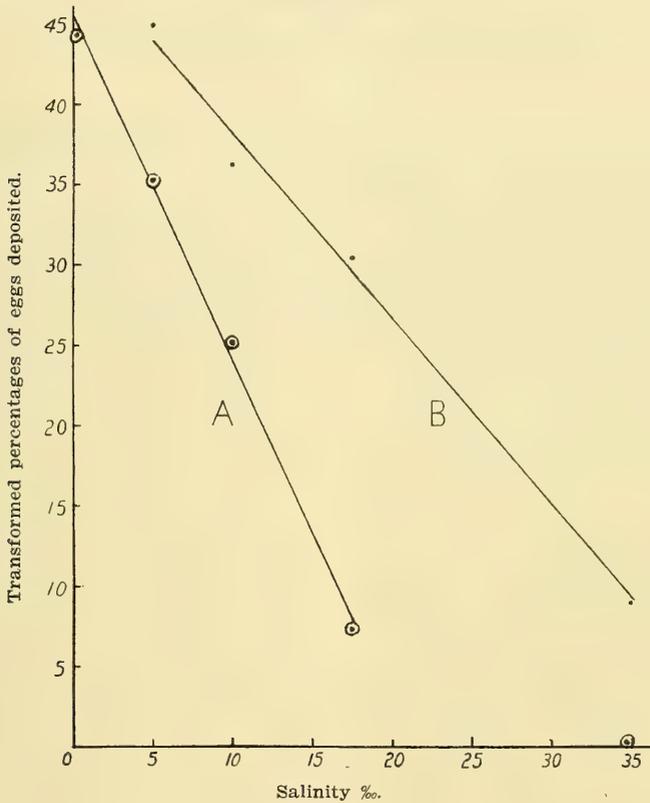


Fig. 2.—A, *A. aegypti*. B, *A. concolor*.

For *A. aegypti* a curved line could have been fitted to the data as they stand. The zero which occurs at S‰35, however, might have occurred first at a lower point (between 17.5 and 35) had one been tried. Omitting the zero, a straight line fits the data. The successive egg percentages at the salinities observed are significantly different. The equation of the line is  $Y = -2.14x + 45.3$ .

4. Difference between S‰5 values for *C. fatigans* and *A. concolor* and S‰0 for *A. aegypti*.

There is no difference between the figures for *A. concolor* and *A. aegypti*; but the *C. fatigans* figure is significantly lower than that for *A. aegypti*.

Conclusions.

1. *C. fatigans* is able to distinguish S‰5 and S‰10 from S‰0, and will not deposit any eggs on S‰10 or higher, if water of S‰0 is available. It is repelled to a significant extent by S‰5 as compared with S‰0.
2. *A. aegypti* is able to distinguish S‰5, S‰10, S‰17.5 and S‰35 from S‰0, and the percentage of eggs deposited increases significantly as the salinity decreases

from S‰17.5 to S‰0. It will not deposit any eggs on S‰35 if water of S‰0 is available.

3. *A. concolor* is able to distinguish S‰35, S‰17.5 and S‰10 from S‰0, but does not discriminate between S‰5 and S‰0. A small percentage of eggs is deposited by this species on water of S‰35 when water of S‰0 is available, and this percentage increases significantly as the salinity decreases to S‰5.
4. There is a significant difference between the oviposition responses of the three species. *A. concolor* is repelled by saline water to a much less extent than *A. aegypti*, and *A. aegypti* less than *C. fatigans*.

*Acknowledgement.*

The author is greatly indebted to Miss H. Newton Turner for the section of this paper dealing with the statistical analysis of the experimental figures.

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## ON CERTAIN DEBATABLE QUESTIONS IN CRANIOSKELETAL HOMOLOGIES.

By H. LEIGHTON KESTEVEN, D.Sc., M.D.

(Forty-four Text-figures.)

[Read 29th October, 1941.]

I. *Introduction.*

Work which I have carried out during the last twenty odd years, on the comparative osteology, myology and embryology of the vertebrate head, has led me to conclusions and interpretations which are at variance with those generally accepted. In his book "The Development of the Vertebrate Skull", de Beer has recently stated the accepted views very clearly, and has marshalled the evidence in their support. In compiling this book de Beer has presented those of us who are interested in this field of morphology and embryology, with a book of reference for which we must continue to be grateful for many years. His task was herculean, and that must explain the absence of any examination of the conflicting evidence relative to quite a number of interpretations which are presented as facts. Whilst it is quite clear that it would have been impossible to review the whole of the conflicting views, and very difficult to make a selection for such a review, it is still to be regretted that, in such a book, working hypotheses should have been presented as facts.

Thanks to the kindly co-operation of colleagues in many parts of the world, I have, during the last twenty years, been enabled to study the adult anatomy and development of the cephalic musculature of the Vertebrata in a very wide range of species representative of every group. At the same time the opportunity has been taken to study the embryonic cranial features.

The detailed accounts of that work will appear elsewhere. General statements of the observations made and the conclusions based thereon, have been introduced into the following discussion.

The present paper is offered as a contribution to the discussion and elucidation of the following problems:

1. The nature of the basiptyergoid process.
2. The homology of the alisphenoid bone throughout the Vertebrata, including, of necessity, a discussion of the "cavum epiptericum" and of the homology of the processus ascendens quadrati, the processus alaris and the ala temporalis.
3. The homology of the parasphenoid of the Anamniota and the pterygoid bone of the Amniota.

## II. THE BASIPTERYGOID PROCESS.

This process is really developed in quite a few reptiles only, and in fewer birds. In the lacertilians, where the process reaches a maximum of development, equalled only in some dinornithid birds, the process is a striking feature of the adult basis cranii and is no less striking in the chondrocranium. Unfortunately, under the leadership of Gaupp, the lacertilian cranial conditions have been accepted as a standard for the Reptilia generally, whereas these conditions are in many respects those of specialization along peculiar lines.

One result of this attitude toward the lacertilian cranium has been to accept the basiptyergoid process as a fundamentally important structure, and to seek it in all other crania.

As a matter of fact the basiptyergoid process is probably a special process developed under mechanical stress, as a result of the loss of the medial palatal portions of the two halves of the parasphenoid bone (the pterygoids of authors).

Although a processus basiptyergoideus has been identified in the chondrocranium of some chelonians, it is purely a courtesy title for a short length of the lateral edge of the basal plate in the appropriate situation; there is no real process developed in any chelonian. In the Ophidia there is no trace of the process, although Brock (1929) has given the title to the appropriate edge of the basal plate in *Leptodeira*.\*

In the birds a basiptyergoid process has been described in all the members of the Dromaeognathi and the Impennes whose development has been studied. De Beer and Barrington describe the process in *Hirundo*, and I have found the same process in *Podiceps*. It is probable that it will be found in other avian embryos as they are studied in the future. In the adult cranium the process is found only in the dromaeognathus birds.

It will be pointed out (Kesteven, 1942) that the basiptyergoid process of the birds is not definitely the same process as that of the Lacertilia. The latter has always been regarded as a trabecular process, whilst that of the birds is very definitely a polar derivative and, therefore, parachordal. Again, the ramus palatinus facialis passes dorsally to the process in *Struthio*, *Dromaeus*, *Apteryx* and *Podiceps*, and dorsally to the situation of the root of the process, in the absence of the process itself, in every other bird embryo studied, and those other birds constituted a fair representation of the whole of the Aves. It is, therefore, probably correct to say that the relation of the ramus palatinus facialis to the process, is quite different to the relation of that nerve to the process in the Lacertilia.

However, whatever be the decision as to the homology of the avian process, it is a fact that it is present in only a few birds in embryonic stages, and in fewer adults.

My own specimens of the chondrocrania of *Chelonia* and *Chelodina*, *Python*, *Pseudechis* and *Dendrophis* present no prominence of the edge of the basal plate in this region.

In the Lacertilia the length of the process is determined absolutely by the degree of severance of the pterygoid bone from the cranial base; it is completely absent from the adult amphisbenian and also in all probability from its chondrocranium.

In *Crocodylus* also, there is no basiptyergoid process.

In the birds a true basiptyergoid process is developed in the Dinornithidae and some few others. The so-called basiptyergoid process of the generality of birds, e.g., *Anas*, *Gallus*, is not the same structure as that of the dinorniths or the reptiles, as judged by all our standards of comparison. It is really an articular facet, developed late in embryonic life, on the ventro-lateral aspect of the trabecula communis.

In the adult cranium it is a process of the presphenoid. It is in advance of the pituitary fossa, and in front of the point of entry of the cerebral artery, and is not related to the orbital artery and/or ramus palatinus facialis as is the basiptyergoid process of the reptiles. Furthermore, even this misnamed basiptyergoid process is not developed at all in many birds, e.g., hawks, eagles, cockatoos, parrots and kingfishers.

Amongst extinct reptiles the basiptyergoid process is present in almost every species in which the pterygoid bone is separated from the mid-line, and in no others.

There is no basiptyergoid process in any recent amphibian adult, or embryonic chondrocranium. In these skulls the muscles, which in other tetrapods are attached

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\* De Beer (1937, p. 251), commenting on Brock's interpretation of the origin of the alisphenoid in *Leptodeira*, writes: "If Brock's interpretation, here adopted, is correct, the processus ascendens must be regarded as having lost connection with the remainder of the pterygoquadrate, become attached to the basitrabecular process, and then suppressed so that the ossification, the epiptyergoid, appears to arise intramembranously." A whole series of pure assumptions, about a non-existent pellicle of cartilage.

to the pterygoid bone, are attached to the parasphenoid. In them there is no pterygoid bone.\*

A "basitrabecular process" has been identified in the chondrocranium of some crocodiles. It has, however, been found to fuse with either the fore end of the auditory capsule or with the basal process of the quadrate.

Clearly then, this is not a basitrabecular process in the reptilian sense, for it lies behind both the second and third branches of the fifth nerve, whereas the basiptyergoid process lies in front of those nerves; moreover the process is but a projection from the side of the basal plate with its dorsal surface in continuity with that of the basis cranii. The basiptyergoid process is a projection from the ventral side of the trabecular plate. Disregarding this last feature, however—in the absence of evidence in support of the identification—it is quite impossible to disregard the relation to the branches of the fifth nerve.

A review of the varying extent of the development of the basiptyergoid process, when present, shows that its development at all is correlated with the presence of paired elongate pterygoid bones and that the size of the process is definitely adapted to, if not determined by, the degree of severance of the medial edge of the pterygoid bones from the lateral edge of the cranium.

A search for one instance in which a basiptyergoid process stops short of the pterygoid bone, or one in which it extends beyond, has met with complete failure.

These then are the facts relative to the size of the basiptyergoid process; there is no doubt as to the reality of the correlation and for the latter it is possible to offer a partial mechanical explanation.

Quite apart from the question as to whether the elongate pterygoids replace the parasphenoid phylogenetically or not, it is undeniable that they have replaced that bone functionally. They supply the fixed area of origin for more or fewer of the muscles which arise from the parasphenoid of the lower vertebrates. It also appears to be clear that the pterygoid bones in their most primitive, earliest, form covered the basis cranii, at least as far back as the basisphenoid, and were articulated to the ventral surface of that bone.

If this be so, then it is demonstrable that in a number of recent and fossil reptiles these bones have moved away from one another and from the basisphenoid.

However, whatever be the explanation, the facts are that the elongate pterygoid bone gives origin to powerful muscles of mastication, and has been strengthened by the development of a strut from the basisphenoid, by which it is firmly attached thereto.

This view of the process regards it as developed in response to mechanical stresses and therefore not phylogenetically important, not only its size but its actual existence at all being dependent upon and conditioned by other factors; it is even suppressed in the only recent lacertilian with wide pterygoid bones articulating directly with the basisphenoid bone.

This view is supported by consideration of the mechanical specialization of the cranio-visceral skeleton. The ophidians possess thin, relatively flexible pterygoid bones which would appear to need a strengthening strut even more than many lacertilians. At first sight it would appear that the mechanistic theory of the control of the development of the basiptyergoid process breaks down here altogether. Another, and more dominant mechanical factor has, however, supervened. The whole of the cranio-visceral skeleton has been, as it were, cast loose to permit extreme separation of the jaws. The basiptyergoid process is one of the stabilizing struts whose presence would have limited that extreme mobility; it has aborted. There is no fixation of the pterygoid to the neuro-cranium anywhere.

In the birds we find that the basiptyergoid process is retained, in the adults, in one group only, and in this group the upper jaw is quite rigid. In the rest of the birds

\* In certain fossil amphibians, more particularly the Embolomeri, in which the parasphenoid is almost, if not entirely, aborted, and in which the large paired pterygoids which take its place are separated by a gap, a small basiptyergoid process strengthens this muscle-carrying bone just as in the lacertilians.

the process is absent altogether, and amongst these, rigidity of the upper jaw, when present, has been attained in a variety of ways. In all these other birds, whether the upper jaw be mobile or not, the pterygoid bone is an abbreviated structure which does not extend back to the basisphenoid, and the *variety* of the modes of rendering the upper jaw rigid, justifies the view that all are secondary adaptations, each being peculiar to the groups wherein it appears.

In view of the fact that the processus basiptyergoideus, as an actual projection from the basi-trabecular cartilage and not merely a segment of the edge of that cartilage itself, is never developed at all in many sauropsids, and is only developed in correlation with separated elongate pterygoid bones in any sauropsid, it is, after all, to be expected that the process should fail to develop in the complete absence of the, apparently, controlling factors in other Vertebrata. This appears the more natural when it is remembered that the basiptyergoid process is most extensively and most commonly developed among sauropsids. If it may fail to develop in sauropsids, why insist that it must be present in other vertebrates?

It would be interesting to know whether the basiptyergoid process ever appears in the development of the chondrocranium of *Amphisbena*, a lacertilian which has the wide pterygoid bones of the chelonians and, in the adult, neither basiptyergoid process nor epiptyergoid bone.

The identification of the processus alaris of the mammals as the processus basiptyergoideus of the lacertilians depends very largely upon the correctness of the identification of the mammalian alisphenoid\* as the reptilian epiptyergoid and the mammalian ala-temporalis as the reptilian processus ascendens quadrati.

Apart from those questions the evidence in favour of the homology of the processus alaris and basi-trabecular process appears to be the single fact that the nervus palatinus facialis, vidian nerve, lies in the vidian canal between the pterygoid and the processus alaris. If de Beer (1929) be correct, the "pterygoid" of the mammals in this part is really the parasphenoid of lower tetrapods. In the lower Vertebrata the parasphenoid never covers a basiptyergoid process ventrally, the so-called parasphenoid lies behind the basiptyergoid process in the reptilian embryonic skull.

Whilst the situation of the vidian nerve dorsal to the pterygoid bone, between it and the basisphenoid, may be evidence as to the homology of the former bone, the fact that it lies beneath the processus alaris is not of value as determining the homology of the process. Since the nerve runs forward ventral to the neurocranium, it must be ventral to every process thereof.

The fact that the processus alaris lies beneath structures which lie above the basiptyergoid process, cannot be regarded as a reason for regarding the space above the processus alaris as having been gained for the cavum cranii by the inclusion of the epipteric space, unless it be previously demonstrated satisfactorily that the processus alaris and basiptyergoid process are homologous structures. In fact, until this inclusion of an extra-cranial space be proven, the fact that the dorsum of the processus alaris is intracranial is definitely a strong reason for deeming it not homologous with the processus basiptyergoideus, and this evidence far outweighs that of the situation of the vidian nerve.

The processus basiptyergoideus is a projection from the ventro-lateral surface of the basi-trabecular plate. The edge of the plate always extends laterally beyond the root of the process. The processus alaris is always a lateral expansion of the basi-trabecular edge, their dorsal surfaces being in uninterrupted continuity.

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\* If, independently of any consideration of its relation to the structure on which it rests, or with which it makes contact ventrally, it were demonstrated that the mammalian alisphenoid is homologous with the epiptyergoid, this would have to be accepted as evidence that the structure on which it rests is the basiptyergoid process. The converse, however, would not hold. If it be shown that the processus alaris is homologous with the processus basiptyergoideus, this would not, necessarily, be evidence that the mammalian alisphenoid is the homologue of the epiptyergoid, because the alisphenoid bone of the lower tetrapods rests, inferiorly on the root of the processus basiptyergoideus, or on the edge of the basis cranii in the location of the root of that process, in its absence.

*Conclusion.*—Having in mind the facts: (1) that the basiptyergoid process is essentially a sauropsid structure, (2) that in the Sauropsida it is only developed to act as a strut for the pterygoid bone when that does not make contact directly with basisphenoid bone, and (3) that it is not developed at all in the absence of the need of support for the pterygoid bone, it is concluded that it is highly improbable that the very different processus alaris of the mammalian chondrocranium is derived from, and homologous with, the processus basiptyergoideus.

It must be remembered that not one of the reptiles which have been regarded as ancestral to the mammals has a basiptyergoid process; if they were ancestral to the mammals they did not have the process to hand on.

### III. THE CAVUM EPIPTERICUM AND THE ALISPHENOID BONE.

#### (1). THE PRESENT INTERPRETATION OF THE CAVUM EPIPTERICUM.

G. R. de Beer (1937, p. 439) expresses the accepted views relative to the homology of the alisphenoid bone in the following words: "It was for long assumed that the hindmost bone of the orbital region of the skull, behind the orbitosphenoid and in front of the auditory capsule, was homologous in all vertebrates from fish to mammals, and it was called the alisphenoid. This view is still held by Kesteven. But since the recognition by Gaupp and Allis of the fact that the cavum epiptericum in mammals (enclosed by the alisphenoid) is extracranial in reptiles, and the identification by Broom, Fuchs, Gregory and Noble of the reptilian epipterygoid with the mammalian alisphenoid, it is clear that the bone previously called "alisphenoid" in non-mammals has no right to that title; for in these forms it is an ossification of the true cranial wall (pila antotica), whereas the mammalian is an ossification in a visceral arch structure, the ala temporalis which corresponds to the processus ascendens of the lower forms."

Goodrich (1930, p. 267) says of the cavum epiptericum: "originally an extracranial space; it is derived from the posterior region of the orbit. Through it pass the internal jugular vein, the orbital and facial arteries,\* and the profundus, trigeminal and facial nerves, whose ganglia lie typically in it."

He further says: "The disposition of these various structures entering and leaving the cavum epiptericum remains fundamentally unchanged throughout the Dipnoi and Tetrapoda, though considerably modified in many forms."

"The cavum epiptericum remains well defined in those Reptiles which have a well developed upstanding epipterygoid, such as the Rhynchocephalia and Lacertilia, but tends to merge again with the orbit in those where the processus ascendens is reduced, such as Aves, the Chelonia and Crocodilia among Reptilia, and the Amphibia, and lower forms."

Briefly, this might have been put thus: "The extracranial cavum epiptericum as above defined is to be found only in the Amphibia, Lacertilia, and Rhynchocephalia and some fewer extinct reptiles." Its presence in other tetrapods is entirely hypothetical, and conditions have been interpreted to fit the hypothesis.

Goodrich (l.c., p. 270) further says: "The validity of this explanation of the fate of the cavum epiptericum in the mammalian skull, its incorporation into the cavum cranii, depends to a great extent on our interpretation of the homology of the ala temporalis."

Before proceeding further it were as well to obtain a clear mental picture of this cavum epiptericum in the lacertilians and rhynchocephalians.

It is an undefined space located laterally to the cranial cavity. Ventrally it may extend slightly below the level of the cranial floor, but is without limiting structure except the processus basiptyergoideus. Posteriorly its boundary is an imaginary plane somewhere near the anterior limit of the auditory capsule. Anteriorly it is bounded by a similar imaginary plane located just in front of the epipterygoid bone. Superiorly the

\* This statement is rather misleading, the orbital (stapedial) artery turns laterad before it reaches the epipterygoid, but is regarded as typically passing over the basal and medial to the otic process of the quadrate. Actually it does not pass through the space.

cavum is equally undefined, but apparently is not regarded as reaching much more than half-way up the side of the cranium. Laterally the cavum is bounded by the epipterygoid bone and an imaginary plane which continues back and forth to meet the hypothetical front and rear boundaries. The medial boundary is complete and is formed by the membranous side wall of the skull.

This description may give the impression that it was deliberately designed to discredit, but even if that be granted, it is none the less the fact that it is a perfectly correct description of the cavum, and in no way distorted.

Now as to the contents of the space. Some three or four of the muscles innervated by the fifth nerve take their origin in part from the meagre solid boundaries of the cavum and encroach to some extent on the space as above described.

In addition the ganglion of the trigeminal nerve protrudes through the medial wall; the first branch of the nerve runs forward between the epipterygoid bone and the wall of the skull, the second and third branches pass laterad through the cavum behind the epipterygoid bone and then turn rostrad and ventrad laterally thereto. The vena capitis lateralis runs through the cavity along its floor, which has the palatine branch of the facial nerve below it. A branch of the mandibular of the Vth nerve trunk runs forward medially to the epipterygoid bone in some, if not all, lacertilians. This is the motor twig to the levator-bulbi muscle, but also carries sensory (?) fibres which leave the main nerve a short distance distal to the ganglion and join the ramus palatinus facialis just after that reaches the anterior boundary of the basiptyergoid process.

This last nerve turns ventrad in its forward course, so as to pass below the basitrabecular process, and is commonly accompanied by a large vein in this situation. At the fore end of the cavum, anterior to the epipterygoid, ophthalmic and facial or anterior-cerebral branches of the internal carotid artery pass laterad and rostrad. Nerves II, III, IV, and VI emerge from the cranium much further forward. Toward the posterior hypothetical boundary, the hyomandibular branch of the VII nerve passes dorsad and caudad and then rostrad and ventrad, whilst a small facial branch of the carotid artery accompanies the palatine branch of the nerve in its forward course.

It follows from the above description that the cavum epiptericum is present only in the amphibians, lacertilians and *Sphenodon*, and that in the amphibians it has no floor. The cavum is also present in those fossil reptiles which possess a true epipterygoid bone.

Beyond these groups the cavum is really non-existent as a defined space; therefore, when it is stated that the cavum epiptericum, extracranial in non-mammals, is intracranial in mammals, the real implication is that certain structures which are extracranial in non-mammals are intracranial in mammals.

It will be demonstrated in the following sections that not one of the structures which has been deemed to be typically situated in the extracranial cavum epiptericum is constantly extracranial throughout the saurians, and that only one of them is even commonly extracranial. It will, in fact, be demonstrated that all of them are, in the majority of the saurians intracranial, enclosed by the alisphenoid bone; excepting only the stapedia artery, and that is not enclosed by the alisphenoid bone in the mammals either.

It has been necessary to review the hypothetical cavum epiptericum and its contents because, contrary to the facts, it has been asserted that certain of those contents are enclosed by the alisphenoid bone in the mammals only, and that, therefore, this alisphenoid cannot be homologous with that of the non-mammals.

As a matter of fact, the whole case against the complete homology of the alisphenoid bones throughout the Craniata boils down to the observation that in amphibians, chelonians, lacertilians and *Sphenodon* (but not in bony fishes) the first branch of the fifth nerve lies lateral to the cranial wall and medial to the processus ascendens quadrati; whilst in mammals it lies within the cranial cavity, medial to the alisphenoid bone.

This question of the homology of the alisphenoid bones may be discussed from three angles:

1. A general survey of the topographical relations of the bone in the adults of the recent Craniata, with special reference to the relative situation of the structures deemed to lie typically in the cavum epiptericum.

2. A survey of the topographical relations of the bones in fossil reptiles and amphibians, and a comparison of these with those of recent forms.

3. A review of the development of the bones, again with special reference to the relation of the precursory cartilages to those structures, nerves and vessels, deemed to lie typically in the cavum epiptericum.

(2). THE MORPHOLOGY OF THE ALISPHENOID BONE IN RECENT ADULT VERTEBRATES.\*

The essential similarity of the topographic relations of the alisphenoid to the surrounding bones in all the Craniata has never been denied or seriously questioned. The facts are self-evident. Their homology has been denied, mainly on the evidence of the relative position of the branches of the fifth nerve.

The intent of this section, then, will be briefly to review the osteological relations, and in more detail those of the nerves and blood-vessels.

It will be shown that the relation of these to the bone in the snakes and birds is the same as in the mammals, whilst the crocodiles occupy a place, in this respect, intermediate between these and the rest of the reptiles.

(a). *Reptiles.*

(i). *Chelonians.*—In *Chelodina longicollis* the bony side wall of the cranium in front of the otocrane is constituted by descending sphenoidal laminae of the parietal and frontal bones, which meet a less extensive ascending sphenoidal lamina of the pterygoid bone. There is a slightly out-turned antero-inferior spur of the prootic bone meeting the basisphenoid and pterygoid bones beside the pituitary fossa. Immediately in front of this is the incisura prootica. A short distance behind the anterior margin of the prootic, which thus bounds the incisura prootica, the prootic bone is perforated by a fair sized foramen for the facial nerve.

The side wall of the cranial cavity, in front of the auditory capsule, is constituted by a strong membrane which posteriorly has the medial periosteum of the pseudo-mural cranial flanges on its lateral surface, but which is separated from these bones by an appreciable space anteriorly.

The ganglion of the Vth nerve is quite distant from that of the VIIth. It lies *inside* the cranial wall against the concave medial surface of the anterior inferior prootic process. The second and third trunks of the Vth nerve pass out of the cranial cavity through the incisura prootica. The first trunk passes forward *outside* the membranous side wall to the posterior limit of the orbit; here it enters the orbit behind and below the optic nerve, closely accompanied by the IIIrd and IVth nerves.

The ganglion as it lies in the cranial cavity is enclosed in a closely fitting glove-like diverticulum of the dura mater, but this "glove" has only three short "fingers": one for the first, the second for the second and third branches, the third finger runs back along the roots of the nerve, which are thus gathered into one rounded stem. Distantly the finger fitting the second and third trunks becomes merged with the membranous cranial wall, as it is attached to the margins of the incisura prootica, but that around the first trunk rapidly thins out, and following the nerve forward one cannot separate the dura on the inside from the cranial membranous wall laterally.

The ganglion of the VIIth nerve lies *against the prootic bone* and all its branches leave the cranium together along the facial canal, whose internal foramen has already been noted.

For the purpose of a later section, it is noted here that a short distance within the canal, the palatine branch of the nerve leaves the main trunk by turning abruptly ventrad through the bone to meet the parabasal canal. That canal carries the carotid artery; at the point of junction with the facial-palatine the canal and artery divide, the internal carotid artery runs diagonally rostrad and mediad to reach the pituitary

\* The morphology of the bone in the fishes and amphibians will be conveniently discussed when describing its development in those forms.

fossa, whilst the orbital artery continues directly forward along with the palatine branch of the facial. This limb of the parabasal canal lies in the basisphenoid, but is floored by the pterygoid bone. Once it crosses the pterygoid-basisphenoid suture, the artery continues forward on the dorsal surface of the pterygoid.

*Chelone viridis*. Here the conditions are so similar to those of *Chelodina longicollis* that detailed description is uncalled for.

(ii). *Crocodylus johnsoni* (Figs. 1 and 2).\*—In this form the extensive alisphenoid bone supplies most of the side wall of the brain-case in front of the prootic bone. The incisura prootica is closed above and may be referred to as the fenestra prootica. It is bounded by the prootic behind, as seen from within, and by the alisphenoid above, in front and below. The gasserian ganglion *lies in a fossa* in front of, not lateral to, the prootic. This fossa forms a much expanded inner segment of the prootic fenestra, but itself has a somewhat constricted median aperture. The second and third branches of the nerve pass out together through the external aperture, the fenestra prootica. The first branch runs forward through the substance of the alisphenoid bone, nearer the external than the internal surface.

(iii). In the Ophidia the alisphenoid bone is said to be indistinguishably fused with the surrounding bones in some forms but, in all the young skulls examined, its limits and contacts both internally and externally are clearly defined by readily discernible sutures.

In *Pseudechis* and *Notechis*, which are perfectly typical ophidians, it is a fair sized bone (Figs. 3A and 3B) in the side wall of the skull, located between the parietal above and in front of it, the epiotic above it behind, the prootic behind it and the basisphenoid below it. The parietal bone has developed a particularly extensive descending orbito-sphenoidal lamina, so that the cavum cranii in front of the alisphenoid is enclosed by this bone on both sides as well as above.

Sutures with the bones mentioned above may be seen as clearly internally as externally, but whereas the outer surface is smooth and nearly flat, the inner surface is deeply excavated to form a "gasserian" fossa.

The prootic fenestra is a large oval foramen bounded behind by the prootic bone, above, in front and partly below by the alisphenoid. The posterior wall of this foramen is much longer than the anterior (see Fig. 3), and it is perforated towards its outer end by a small foramen for the palatine branch of the VIIth nerve. The only branch of the Vth nerve which issues from the foramen prooticum is the third. The foramen prooticum interrupts the suture between the alisphenoid and prootic behind it. In like manner a veritable "foramen rotundum", for the second branch of the Vth nerve, interrupts the suture in front, between the alisphenoid and the parietal. This is smaller than the foramen prooticum. The first branch of the Vth nerve runs forward along the floor of the cranial cavity medially, to the lower margin of the orbitosphenoid lamina of the parietal and turns outward round the anterior margin thereof. This "foramen sphenopticum" permits the egress also of nerves II, III, IV and VI. The gasserian ganglion and first and second branches of the nerve are *medial* to the alisphenoid bone.

The ganglion of the VIIth nerve lies close to the floor of the cranial cavity, just posterior to the roots of the Vth nerve, *medial* to the anterior end of the otic capsule. The whole nerve leaves the cranial cavity through a single foramen which is the entry to a canal which, turning caudad, carries the nerve into the tympanic cavity. A short distance inside this facial canal, there is the opening of a finer canal which permits the palatine branch of the nerve to reach the outer end of the foramen prooticum.

(b). *Aves*.

Throughout the birds the cranium presents a remarkable uniformity, which must assuredly indicate a very dominant factor in the inherited potential which has directed its moulding.

\* The lettering of drawings such as these has become so standardized as to be, for the most part, self-explanatory, therefore only the exceptional letterings will be explained.



of the temporal fossa, usually partly embedded in a well-marked groove. Close to the anterior margin of the alisphenoid, there is a foramen which permits the nerve to leave the cranium. This foramen is commonly so close to the edge of the bone that there is only a spicule between it and the foramen lacerum anterius in some forms, and in others it appears to interrupt the suture between the alisphenoid and either the orbitosphenoid or the orbitosphenoid lamina of the frontal, depending on the relative development of the two.

The alisphenoid bone presents its only variation of note among the bones in the topographic relations of its anterior margin. This sutures with the parietal, frontal, orbitosphenoid and basisphenoid, in that order, beginning above and passing forward and ventrad. In various birds poor development may lead to the excluding of either the frontal or orbitosphenoid. The suture is always interrupted by the sphenoptic fissure (foramen lacerum anterius and foramen opticum) and usually appears to be interrupted by the foramen for nerve VI.

The ganglion geniculatum lies *against the medial wall* of the otocrane in close contact with the ganglion of nerve VIII, partly in a fossula which is a veritable internal auditory meatus, for its depth is perforated, like that of the chelonians among the saurians, for the VIIIth nerve as well as the VIIth. The facial canal passes dorsad and caudad leading the nerve to the tympanic cavity, but before that is reached a tiny branch of the canal carries the palatine branch ventrad rostrad and slightly laterad to the parabasal canal.

(c). *Theria.*

*Echidna* may be described as representing the morphology of the bone in the Prototheria. Much of the side wall of the cranium which, in eutherian skulls, is supplied by the alisphenoid, is here constituted by an extension in membrane from the auditory capsule; and the alisphenoid is correspondingly reduced. On the floor of the cranial cavity the alisphenoid appears as an oval area of bone beside the broad basisphenoid, lateral to the sella, between it and the antero-medial edge of the auditory capsule (Fig. 6). As viewed from below (Fig. 7) it is an oval bone placed diagonally against the posterior edge of the palatine. The antero-lateral corner of the bone makes suture with the alisphenoidal lamina of the periotic. Behind this the lateral margin appears to be free and has the tympanic attached to it by fibrous tissue. Medial to this edge the bone is excavated to form a small tympanic bulla. The suture, with the periotic bone in the roof of this bulla, runs right back to the basi-occipital, a short distance behind the suture of that bone with the basisphenoid. The posterior half of this suture is not visible within the cranial cavity because the alisphenoid is plastered onto the ventral surface of the periotic. Medial to the little tympanic bulla the bone is relatively thick, inner and outer tables being separated by loose cancellous tissue. On removal of the outer table and the cancellous tissue, the bone is found to make a suture with the edge of the basisphenoid above the palatine bone, with the posterior end of the pterygoid bone articulating with both for a short distance.

The foregoing description is based upon skulls in my own possession, one of which is younger than that which served me for my description of the bone in 1918 and, by the clarity of its sutures permits some amplification of that description.

The bone lies ventral to all three branches of the fifth nerve. These, together forming a broad ribbon, run forward and laterad to emerge from the cranial cavity in front of it. The vena capitis lateralis receives its main cerebral tributary at a point posterior and lateral to the bone, and the orbital tributaries lie dorsally and laterally to it. The internal carotid artery enters the cranium through a foramen which is situated immediately behind the posterior corner of the alisphenoid bone. This foramen gives entry to a canal which lies between the alisphenoid below and laterally, the basioccipital above and pterygoid medially (for a short distance) and then burrows through the basisphenoid bone forward and mediad and finally opens into the sella turcica under cover of the posterior end of ossified processus clino-orbitalis.

This alisphenoid bone presents as its major portion that which is homologous with the quadrate wing of the alisphenoid of the cynodonts. De Beer questions this identification of the bone. He and Fell believed that they had found an alisphenoid bone in

*Ornithorhynchus* developing ectochondrally at the lateral edge of the processus alaris. In association with Furst (1929, p. 451) I stated that the basisphenoid develops from three centres of ossification, one median and two lateral, these latter situated in the processes alares medial to the canal for the (orbital) artery. A re-examination of the question (Kesteven, 1940a) confirms the interpretation of 1929; de Beer and Fell's 'alisphenoids' are the lateral centres of ossification of the basisphenoid bone. The three centres of ossification rapidly fuse, and in the process of fusion present no semblance of even an evanescent suture. In this respect the basisphenoid of the *Platypus* resembles the ossification of that of several therians.

The skull of *Thylacinus* (Figs. 8 and 9) is an essentially typical marsupial skull, but presents points of resemblance to that of *Echidna* which are not so marked in *Dasyurus* (Fig. 10) and *Macropus*, the usual standards for comparison with marsupials.

The alisphenoid is an extensive bone, which in my specimen is fused with the basisphenoid medially, to the complete obliteration of the sutures; but its sutures with

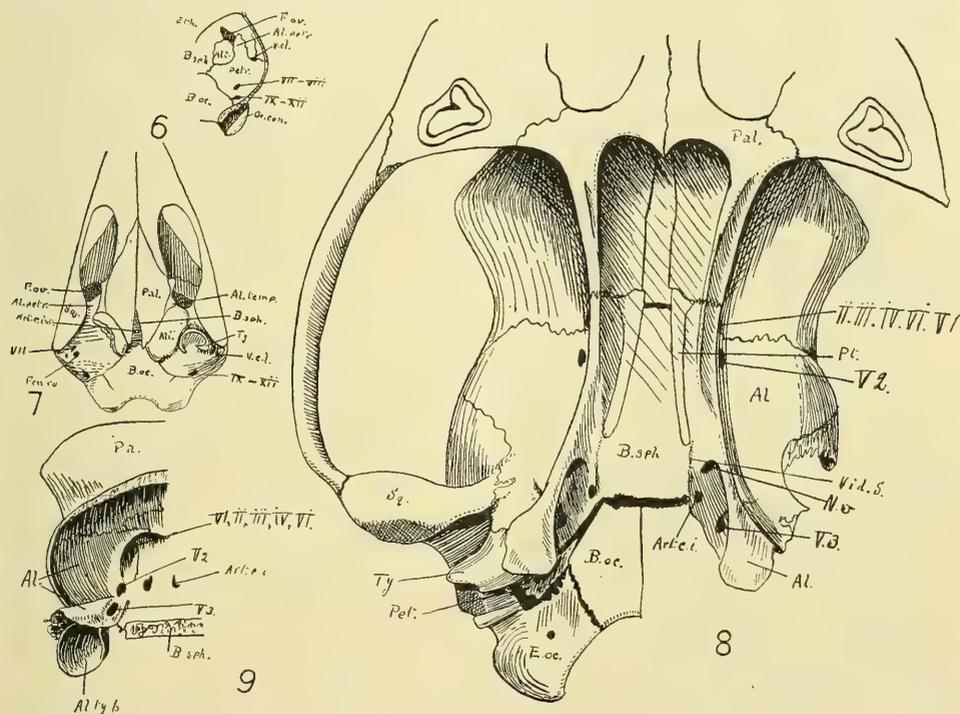


Fig. 6.—Internal view of one-half of the floor of the cranium of *Echidna* (from Kesteven).  
 Fig. 7.—Ventral view of the skull of *Echidna* (from Kesteven). *Al. petr.*, alisphenoidal lamina of the petrosal.  
 Fig. 8.—*Thylacinus*, ventral view of the cranium with the right side partly disarticulated to emphasize the boundaries of the alisphenoid bone.  
 Fig. 9.—*Thylacinus*, the right half of the same skull seen from behind.

all the other bones are very clear, so much so that it has been possible to disarticulate the bones behind, above and medial to it on one side without breaking any but a peculiar little flange of the squamosal, which will be described in its place.

The bone may most usefully be described as consisting of three parts, anterior, posterior and pterygoid lamina, the junction between the two former being an imaginary line at right angles to the long axis of the skull, through the foramen for nerve V2. The pars anterior is a concavoconvex lamina of bone which is fused to the basisphenoid between the sphenoptic foramen and that for the second branch of the fifth nerve. It forms the side wall of the sphenoptic, and the side wall and roof of the other foramen. In front of the sphenoptic fissure the alisphenoid makes suture with the posterior and

inferior edges of the orbitosphenoidal lamina of the fused fronto-orbitosphenoid bones, extending onto the floor of the cranial cavity and forming part of the side wall. The portion of the bone contributing to the side wall, visible on the inside, is very largely covered by the lamina of the squamosal externally, whilst the portion of the bone visible, externally, in front of this is largely covered internally by the orbitosphenoidal lamina. Actually this portion of the bone is nearly twice as extensive as it appears on viewing it either internally or externally.

The pars posterior\* consists of a neuro-cranial and a tympanic portion. The neuro-cranial component lies in the floor of the cranium behind and lateral to the foramen for nerve V2. It bears internally a wide, shallow groove for the maxillary nerve along its inner margin, and at the posterior end of this groove is perforated by the large foramen for nerve V3. This foramen is at the postero-median edge of the bone and is completed by a bar of bone. Immediately to the medial side of this bar, and parallel with it, is a thin spicule of bone. The deep notch between the two is occupied by the vidian nerve in the flesh. The lamina contributing to the cranial floor, lateral to the maxillary groove and mandibular foramen is concave in front and convex behind, as viewed from above, the curves being at right angles to the long axis of the lamina.

The pars tympanica forms a roughly cubical tympanic bulla suspended below the neurocranial lamina, lateral to the mandibularis foramen. This bulla is widely open posteriorly, but with all the bones in place, is closed by the petrosal and tympanic. As viewed from below, the bulla is quadrilateral, with the anterior angle continued forward by a flying buttress which joins the pterygoid lamina just in front of a large foramen for nutrient vessels. To the outer side of the bulla there is a thin irregularly shaped tongue of the squamosal bone insinuated between the pars tympanica and the neuro-cranial lamina, which in this situation is relatively thick. This tongue of the squamosal, however, does not extend deeply so that it is covered by the lamina; it was broken off in disarticulating.

The pterygoid lamina is a thick ridge which stands down and out from the junction of the pars anterior with the basisphenoid.

The form of the pterygoid bone is of interest (Fig. 8); it is an elongated narrow squame of bone plastered to the medial side of the line of fusion of the alisphenoid and basisphenoid and extending forward just beyond it, to make suture with the outer edge of the presphenoid and the palatine bone. This bone is relatively more reduced than that of *Echidna*, and occupies a precisely similar situation.

The relation of two of the three branches of the Vth nerve to the alisphenoid bone will have been gathered from the situation of the two foramina. The first branch emerges from the cranium along with nerves II, III, IV and VI through the foramen sphenoticum. The internal carotid artery enters the carotid canal close to the end of the side of the basisphenoid bone, and runs forward and medially to emerge at the posterior end of the sella. The orbital artery runs forward under the flying buttress of the alisphenoid, and then to the outer side of the posterior end of the pterygoid lamina. The vena capitis lateralis receives one of its two main cerebral sinusoidal tributaries between the petrosal and squamosal bones almost directly above the middle of the anterior border of the tympanic bone, behind and above the inner end of the glenoid surface on the jugal process. Within the cranium the sagittal sinus penetrates the sagittal suture. Towards the posterior end of the suture the sinus divides into right and left branches which, enclosed in the tentorial ridge along the hinder margin of each parietal, curve backwards, laterally and down to emerge from the bone close to the parieto-squamosal suture. After a very short course in the open, each branch passes between the squamosal and petrosal to reach the external foramen. The ventral cerebral sinus, the second main tributary to the jugular vein, running back from the sphenotic fissure medially to the branches of the Vth nerve, emerges from the brain cavity by burrowing through the basioccipital bone. Just where this last bone makes contact with the anterior corner of the exoccipital another sinus joins the last. This has tunnelled the basioccipital in the opposite direction. The conjoint vessel turns

\* This portion corresponds very closely with the whole of the bone in *Echidna*.

ventrad around the outer edge of the exoccipital just medially to the root of the short paroccipital process.

The vidian nerve, after issuing from the foramen on the lateral surface of the petrosal bone, finds itself almost at once in the notch already described, at the posterior end of the pars posterior of the alisphenoid bone. It runs forward medially to the ramus mandibularis trigemini, passing under the orbital artery just after the latter branches from the internal carotid. Continuing forward alongside the basisphenoid, it reaches the vidian canal under cover of the pterygoid bone. At the anterior end of that canal it passes out between the fore end of the pterygoid lamina and the hinder end of the vertical lamina of the palatine bone and reaches the outer surface of this last, but a little further forward turns mediad again through a foramen which interrupts the palatino-orbitosphenoid suture.

The form of the mammalian alisphenoid bone is so well known that there is no need to describe it here (see Fig. 11). It is, however, quite important that we remind ourselves that the branches of the fifth nerve may emerge from the cranium through three foramina, as in *Thylacinus* and marsupials generally, but that in many, if not most, mammals both first and second branches emerge through the foramen lacerum along with nerves III, IV and VI, whilst the third branch is commonly surrounded by the alisphenoid bone at its point of emergence, the foramen ovale. This relation of the bone to the nerves was regarded by Gaupp (1900, 1902) as of prime importance, and he was of the opinion that the mammalian alisphenoid bone must be a new structure. Believing the mammalian alisphenoid bone to be homologous with the epipterygoid, Goodrich (1930, p. 271) explains the situation of the second branch of the nerve as follows: "It may be supposed that the mammalian processus ascendens spread backwards so as to pass on both sides of the maxillary nerve, and that then the anterior limb disappeared while the posterior persisted." De Beer (1937, p. 439) states that the epipterygoid "in the mammals expanded in a posterior direction, and the maxillary branch of the trigeminal nerve is enclosed in a foramen rotundum".

Thus, under the accepted interpretation of the relative cranial structures, it has to be assumed that the processus ascendens, or the bone developed from it, has grown backwards to surround two branches of the nerve, the second and the third.

It is just as reasonable to assume that the process, or the bone developed from it, has grown back to surround all three branches. If it be admitted that it may have grown round two, why deny that it could also have grown round the first? And if this be granted, then, it is easier to believe that it was the original cranio-mural components, chondrocranial and osteocranial, which came to surround the nerves, than it is to believe that the original wall has gone, and has been replaced by one developed from a visceral arch structure in front of two of the nerves, and then this has grown backwards to enclose those two nerves.

Edgeworth (1935, p. 69) writes: "The theory that the ala temporalis, an upgrowth of a lateral process of the chondrocranium, is homologous with an upgrowth of the palatoquadrate, which is an entirely different structure, may be acceptable to some but for me is too difficult an exercise in belief."

### (3). THE INTERPRETATION OF THE FOSSIL BONES.

It has been argued (1) that a bone in certain fossil skulls, which has been identified as an epipterygoid, and which presents all the osteological topographical relations of the mammalian alisphenoid bone and presumably (and probably correctly so), the same relations to nerves and blood-vessels, is homologous with the mammalian bone. The soundness of this argument is self-evident.

It has been argued further (2) that this is evidence that the mammalian alisphenoid has been derived from an epipterygoid similar to that of lacertilians and that, therefore, the saurian alisphenoid cannot be homologous with that of the mammals.

The whole of this latter argument is unsound. It depends on the assumption that the "epipterygoid" bone of the particular fossils is homologous with that of the lacertilians.

The truth of this assumption has never been established.



are postero-external to the pterygoids and laterally embrace the basisphenoid; they are also chiefly external to the foramina for the internal carotids." (Figs. 8, 9, 10 and 11.)

"In Cynodonts (Figs. 12, 13A, 13B and 14) there are a pair of elements showing strong resemblance with the mammalian alisphenoids and so named by Broom. In the internal view of the Cynodont skull (Fig. 13A) as figured by Broom (1911), it is seen that these alisphenoids are anterior to the prootics, lateral to the basisphenoid and pituitary fossa, and inferior to the parietals. They also lie in front of the foramen prooticum (for nerves V2, V3); to judge from the relations of the small process running from the prootic upward, inward and forward, it seems probable that the supposed alisphenoids also lay outside the gasserian ganglion; their anterior border looks much like the posterior boundary of the sphenoidal fissure (foramen lacerum anterius), hence they were probably posterior to the exits of nerves II, III, IV, V1 and VI, like the alisphenoids of mammals. On the lower surface of the skull the bones called alisphenoid were postero-external to the pterygoids and embraced the basisphenoid laterally, just in front of the two openings which Broom identifies as 'probably for the carotids.' Thus the evidence for homology with the mammalian alisphenoids is very strong."

"Likewise in *Crocodylus* (Figs. 1 and 2) and Dinosaurs (Figs. 15, 16, 17, 18, 19 and 20), the bones usually called alisphenoids . . . are anterior to the prootics, lateral to the basisphenoid and pituitary fossa, inferior to the parietals and notched or pierced posteriorly by the foramen for nerve V3; they are also chiefly posterior to the exits for nerves II, III, IV and VI. In the inferior view of the skull the alisphenoids embrace the basisphenoid, are external to the carotid canals, and posterior to the pterygoids."

"These comparisons, summarized in the following table, offer strong evidence for the view that the bones usually called alisphenoids in the Dinosaurs and Crocodiles are rightly so named."

"*Topographic Resemblances between the Alisphenoids of Crocodiles, Dinosaurs, Cynodonts and Mammals.*"

Topographic feature of 'Alisphenoids' of:	Mammals.	Cynodonts.	Crocodiles.	Dinosaurs.
Lateral to basisphenoid and pituitary fossa ..	+	+	+	+
Anterior to the prootics .. .. .	+	+	+	+
Inferior chiefly to parietals .. .. .	+	+	+	+
Posterior to presphenoids and orbitosphenoids ..	+	?+	+	?+
Anterior to foramen prooticum for nerve V3 ..	+	+	+	+
External to gasserian ganglion or to separate trigeminal roots .. .. .	+	?+	-	?
Chiefly posterior to exits for nerves II, III, IV and VI	+	?+	+	+
Postero-dorsal to pterygoids .. .. .	+	+	+	+
Inferior wings laterally embracing basisphenoid ..	+	+	+	+
Inferior wings external to canals for carotids ..	+	+	+	+

"There can be little doubt, then, that the mammalian alisphenoids have been derived from 'alisphenoids' of the type represented in the Cynodonts and that these in turn are homologous with the alisphenoids of Crocodiles and Dinosaurs."

Gregory no longer agrees with the latter half of the conclusions stated in the last sentence of the above quotation, but this changed opinion does not affect the truth of the statements on which the conclusion was based. They are, undeniably, statements of fact, or probability.

He then proceeded to equate all the 'alisphenoid' bones with the epipterygoid of *Sphenodon* and the lacertilian skulls. In this portion of the work one fundamental error vitiated the whole argument; he was unaware that the alisphenoid of *Crocodylus* is developed directly from the pila prootica, and was therefore not homologous with the epipterygoid. This fact was subsequently demonstrated independently by Shino (1914) and by Kesteven (1918).

It is a curious fact that the discovery of the fundamental error in equating the crocodylian alisphenoid with the reptilian epipterygoid, appears subsequently to have been interpreted to mean that the homology of the crocodylian bone with those of the fossils was disproven. This, in effect, is the attitude adopted by Gregory in his contribution to the elucidation of these homologies in collaboration with G. K. Noble (1924).



diversity of opinion. The topographical relations of the bones in the cynodonts are such as should convince all of us that Broom was correct.

Unfortunately Gregory and Noble deviated to demonstrate also that the 'alisphenoid' (epipterygoid) of cynodonts is homologous as well with the epipterygoid of *Sphenodon* and the Lacertilia and the embryonic ascending process of the quadrate of the lower vertebrates.

It is proposed to analyse the evidence they advance in support of this latter contention.

They open with the statement that: "In embryonic amphibians the otic ramus of the palato-quadrate bar has a similar position to the embryonic epipterygoid of *Sphenodon* and lizards." This is so obviously wrong that it is either a case of confusion of terms or a *lapsus calami*.

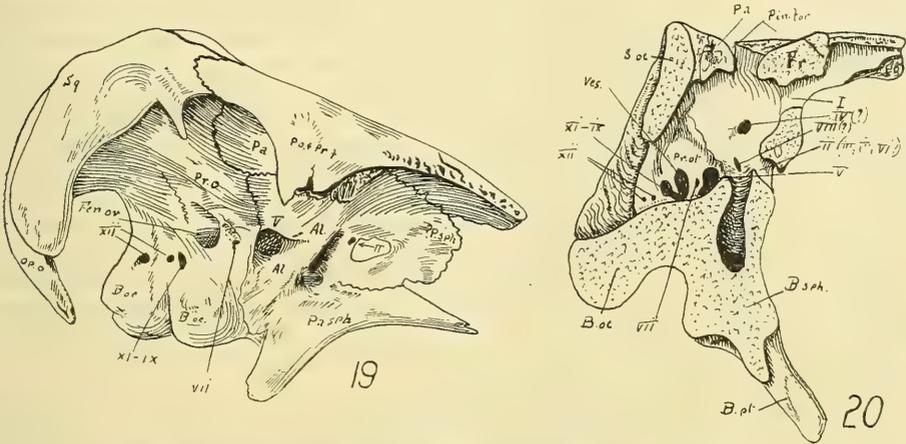


Fig. 19.—Side view of the skull of *Trachodon* (after Osborn).  
 Fig. 20.—Internal view of the skull of *Diplodochus* (from Osborn).

In the next paragraph we meet the following: "In fishes, amphibians and modernized reptiles the so-called alisphenoid, if ossified at all, forms part of the lateral wall of the neurocranium." Along with the context, this implies that in all other forms but these, the alisphenoid is not part of the primitive neurocranium. They make no serious attempt to prove this generality. The facts are that throughout the whole of the recent Craniata, the alisphenoid is developed in membrane in the side wall of the neurocranium or from a pellicle of cartilage which is continuous, *ab initio*, with the chondrocranium or very early fuses with it. Notwithstanding this the embryological evidence has been interpreted as indicating that the bone is not a primitive neurocranial element. In the case of the fossils there is, of course, no such evidence and we have only the adult relations to guide us. There is, however, an unfortunate tendency to adopt the view that because the bones have been equated with the epipterygoid of the Lacertilia, they could not have been developed in the primitive side wall of the neurocranium.

If it be conclusively proven that the 'alisphenoid' of the cynodonts and the epipterygoid of the lacertilians are homologous bones, then, of course, it will be agreed that they developed in similar manner. Until this be proven it is distinctly unsound argument to assert—the 'alisphenoid' of the cynodont skull is probably homologous with the epipterygoid of *Sphenodon*, it is certainly homologous with the alisphenoid of the mammalian skull and, therefore, *the mammalian alisphenoid cannot be regarded as having developed in the side wall of the neurocranium.*

Gregory and Noble, in effect, adopt the attitude that the homology of the cynodont alisphenoid and lacertilian epipterygoid has been sufficiently established by the work of Gaupp and Broom and Watson, and, for the most part, devote themselves to the demonstration of the homology of the cynodont and mammalian alisphenoids.

A much more extended statement of the topographic resemblances than that of Gregory alone is given.

This extended statement is given in the seven paragraphs which follow. It should, however, be kept constantly in mind that all those statements relative to the relations of the fossil bones to soft structures are *interpretations* of the bony features and not statements of fact. This is not to say that they are not correct; it is believed that, in the main, they are correct, but always it should be remembered that our conclusions are arrived at *on the assumption* that those interpretations are correct.

The topographic relations, as given by Gregory and Noble, of the alisphenoid bone in the cynodonts are as follows:

(I). It articulates above with the parietals and frontals; posteriorly it connects with the prootic, inferiorly with the pterygoid and basiptyergoid.

(II). Part of it borders the pituitary fossa laterally as well as the tunnel for the internal carotid.

(III). Its postero-inferior process, running out to meet the quadrate (= incus) and the squamosal, corresponds in position to the tympanic wing of the alisphenoid of marsupials and with the *Echidna*-pterygoid of the monotremes.

(IV). It is pierced or notched by two main openings: (a) in front, corresponding to the position of the foramen lacerum anterius, and, apparently, transmitting nerves II, III, IV, V1 and VI: (b) one in the rear, corresponding in a general way to the foramen ovale of mammals, except that, according to Watson, it transmits V2 as well as V3.

(V). It is grooved near its dorsal border by a horizontal canal corresponding (?) to the sinus canal in the mammals.

(VI). It apparently afforded origin on its lateral face to the deepest part of the temporal muscle mass, and on its lower border it probably contributed to the area of origin of the pterygoid muscles.

(VII). It is closely appressed to the basisphenoid in the position of the ala temporalis of the mammalian chondrocranium.

The agreement or disagreement of the preceding topographic features (indicated in the first column by the Roman numerals) with the bone in the mammals, crocodiles, ophidians, Aves, *Capitosaurus* and *Sphenodon* is indicated in the table below. The table is followed by critical comments on some of its recordings; their relevance is indicated by the numbers within the table:

Cynodont Feature.	Mammals.	Crocodiles.	Ophidians.	Aves.	<i>Capitosaurus</i> .	<i>Sphenodon</i> .*
I .. ..	+	+	+	+	+	-
II .. ..	-(1)	-	-	-	+?	-
III .. ..	+(2)	+	-	-	+	-
IV .. ..	+(3)	+	+	+	+	-
V .. ..	+(4)	+	-	+	?	-
VI .. ..	+(5)	+	+	+	+	-
VII .. ..	+	+	+	+	+	-

(1). Had this description been worded—It lies lateral and close to the pituitary fossa and also close to the canal for the internal carotid artery where that turns mediad towards the pituitary fossa—then unqualified agreement could have been recorded throughout the series, except, of course, for *Sphenodon*. It is probable that the above would actually have been a more correct description of the feature in the cynodonts.

(2). This agreement is found only in those mammals which, like the marsupials, have a tympanic wing. In the case of the reptiles and birds the complete agreement depends more upon the form of the quadrate. The postero-inferior and lateral angle of the bone in ophidian and avian skulls extends back to the position where, in other skulls, the otic ramus of the quadrate articulates with the skull, but in these skulls there is no such attachment or process.

(3). The course of the branches of nerve V in the cynodonts is largely a matter of speculation; experience teaches us that in the recent skulls, osseous grooves can be very

\* The reference here is, of course, to the epiptyergoid bone of *Sphenodon*, or of the *Rhynchocephalia* and *Lacertilia* generally.

misleading, and if the matter be one of importance, we all endeavour to confirm our interpretations, or correct them, by actual dissection. In *Crocodylus* V2 and V3 emerge behind the alisphenoid, V1 runs forward through it (Figs. 1 and 2). In birds, nerves V2 and V3 emerge behind the bone as in *Crocodylus*, but V1 runs forward medial to the bone, within the cranial cavity, and issues through a foramen close to its anterior margin (Figs. 4, 5 and 21B). In the ophidians, nerve V2 may issue from the cranial cavity behind the bone along with V3, but in the great majority of instances it emerges through a notch on its anterior border, separately from both branches, whilst V1 runs forward medially to the bone and issues from an opening comparable to the foramen lacerum anterior (Fig. 3).

(4). The interpretation of this groove in the fossil is largely speculative, and depends entirely upon the fact that the bone in the mammalian skull commonly bears a groove in this situation, which is occupied in the flesh by a sinus. In *Crocodylus johnsoni* a large vein impresses its course on the inner surface of the bone in some skulls, but the impression is very variable. A similarly formed groove is present along the dorsal part of the bone in most birds.

(5). There is no question as to the origin of the temporo-masseteric muscles from the alisphenoid bone in most mammals, the crocodiles, ophidians and birds, and the suggestion that the muscles in the cynodonts have a similar origin, rests entirely upon the observation of those facts; it is probably correct.

On the grounds that things which are equal to the same thing are equal to one another, the above tabulation and analysis of the evidence which constitutes the, admittedly convincing, case in favour of the homology of the alisphenoid bones of the mammals and cynodonts, constitutes an equally convincing case in favour of the homology of those two alisphenoids and those of the Ophidia, Aves and crocodiles.

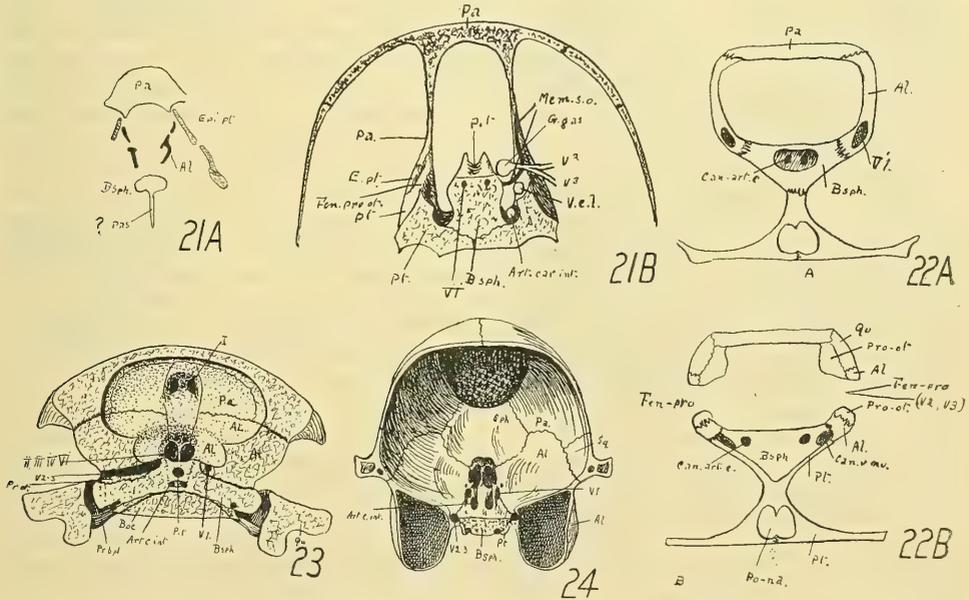


Fig. 21A.—Transverse section of the skull of *Bauria* through the alisphenoid and epipterygoid bones (from Broom).  
 Fig. 21B.—Transverse section through the skull of *Chelone* just behind the epipterygoid bone.  
 Figs. 22A-B.—Transverse sections through the skull of *Crocodylus johnsoni*. 22A. Section just in front of the fenestra prootica. 22B. Section through the fenestra prootica. Can. v. nu., canal for a nutrient vein. Po-na., posterior portion of narial passage.  
 Fig. 23.—The internal view of the anterior half of the cranial cavity of *Dromaeus*, cut transversely at the level of the fenestra prootica on the left, and a little further forward on the right.  
 Fig. 24.—Anterior portion of the cranial cavity of *Bettongia*, cut transversely at the level of the foramen for nerves V2 and V3.

Inasmuch as the latter are all developed in the side wall of the skull, this evidence constitutes, at the same time, an equally strong case against the homology of the epipterygoid bone with the alisphenoid bone of any of these forms.

Further than that, if the congruence between the first six columns, or any two of them, be evidence in favour of homologies, then surely the incongruence between those six and the last must be deemed to be evidence against homologies.

It may be observed here, that the alisphenoidal lamina of the *Apteryx* chondrocranium (Fig. 41) presents every one of the topographic relations tabulated above.

The following series of illustrations of cross sections of various skulls in the region of the alisphenoid and/or epipterygoid bones are offered without comment; they speak for themselves (Figs. 21A, 21B, 22, 23 and 24).

So far, in this section, attention has been given almost entirely to the fossil reptiles; the evidence provided by the morphology of the fossil amphibians next calls for examination.

The comparison with the stegocephalian skull, which is included in the last table, is based upon Watson's description (1919) and illustration of *Capitosaurus* (Figs. 25 and 26) and is in conformity with that writer's views, as far as may be judged by the fact that he designates the bone 'epipterygoid'. He, Gregory and Noble and Sushkin (1928) equate the alisphenoid region of the side wall of the skull of certain stegocephalians with the epipterygoid of the lacertilians.

There is an almost convincing mass of evidence that the lacertilian epipterygoid bone is derived from the processus ascendens of the amphibian palatoquadrate, so much so that the belief stands unchallenged.

Watson (l.c., p. 28) writes: "the otic process" (of the epipterygoid of *Capitosaurus*) "gives origin to the main mass of the bone, which runs forward inwards and upwards as a *processus ascendens*". There is here a regrettable misuse of terms which have a well-established meaning. If the generally accepted interpretation of the origin of the epipterygoid is correct, then that bone *is* the processus ascendens, and the 'otic process' is another process of the palatoquadrate, which has never been regarded as having been incorporated into the epipterygoid bone. It is possible that the confusion arises from his identification of both portions as constituents of an epipterygoid. The 'otic process' rising behind the incisura prootica is, of course, not in a position in which any portion of a true epipterygoid bone could be found—i.e., behind all the branches of the 5th nerve. On the other hand, if this be the otic process of a completely ossified quadrate, similar to that of the Dipnoi and Urodela, then the otic process is at once recognizable in its typical situation; whilst his processus ascendens also at once assumes its correct rôle, is correctly named, and in its typical position. But if so, there is here no epipterygoid bone in the reptilian sense, but a typical primitive, massive quadrate, differing from that of the Dipnoi and *Urodeles* only in that it is ossified. The chelonian quadrate almost approaches this condition in some of the marine species.

The epipterygoid bone figured and described by Sève-Söderbergh (1936) in *Lyrocephalus* is, he says: "usually an ossification in the ascending process of palatoquadrate, but in the most completely ossified specimens, it includes the basal, otic and ascending process and the neighbouring parts of the palatoquadrate".

The whole of this statement is peculiar and displays the same disregard for established nomenclature as does Watson's statement quoted above. The three processes said to be present are those of the quadrate, and if he be correct in his identification of them, then the whole bone can be none other than the upper portion of the quadrate.

This is not a statement of my own interpretation or opinion, but the statement of the inescapable conclusion his identifications lead to, if the terms otic, basal and ascending process are used with their well-established meaning. The fact that he tells us that "neighbouring parts of the palatoquadrate" are included, makes it fairly certain that their accepted interpretation is attached to the terms by him.

Though without close parallel amongst recent forms, it is not impossible that the parts are all correctly identified, but if so, the bone is the upper portion of the quadrate itself and cannot be only the processus ascendens as implied, perhaps unknowingly, by the designation epipterygoid.

The confusion arising from the nomenclature of the palaeontologists does not end here. Säve-Söderbergh (l.c., p. 141) points out: "That the entopterygoid and adjoined palatoquadrate ossification reach dorsally to close below the dermal cranial roof, thus forming the dorso-lateral wall of a typical cavum epiptericum"; and in a footnote: "The floor of the cavum epiptericum is formed by the shelf of the endocranium." Since the "adjoined palatoquadrate ossification" is the hyomandibula, this implies that he deems that ossification and the entopterygoid to be collectively (or separately?) homologous with the processus ascendens quadrati and the ala temporalis. Further, he identifies as the basiptyergoid process a structure situated a long way further forward, on the ethmo-sphenoid ossification. Does this mean that the palaeontologists completely reject Gaupp's theory of the cavum epiptericum and have, without due definition, evolved one for themselves? For of course the whole theory from the point of view of Gaupp and his followers hinges upon the homology of the processus alaris and the processus basiptyergoideus. In fact the only two bounding structures were the basiptyergoid process ventrally and the epipterygoid laterally.

The confusion does not end here. He says (p. 141): "The development of the cavum epiptericum is also exactly similar in the Rhipidistia and the Labyrinthodontia. In both groups it has a floor formed by a shelf of the neural endocranium, and is closed off dorso-laterally by the epipterygoid part of the palatoquadrate."

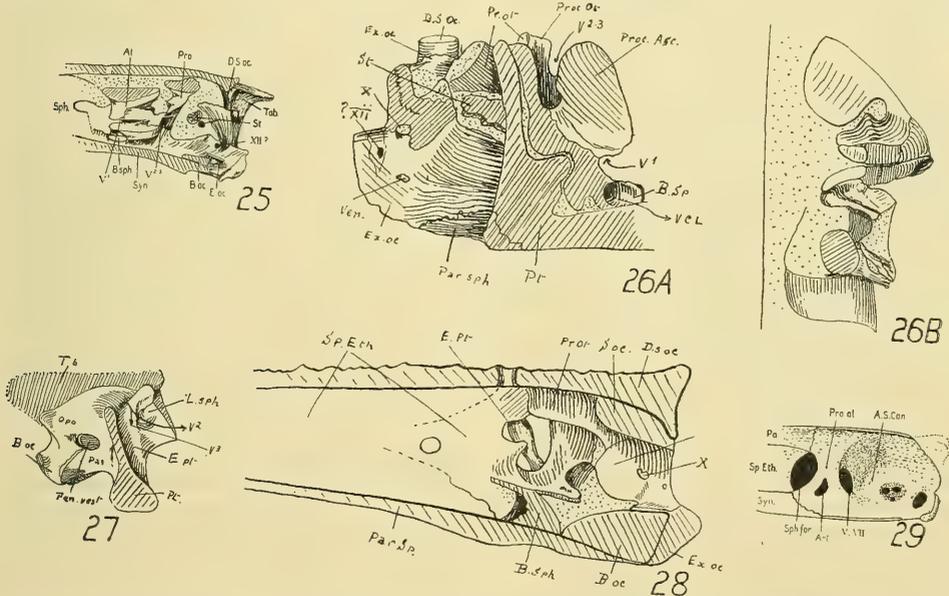


Fig. 25.—Interior view of the side wall of the skull of *Capitosaurus* (from Watson).  
 Fig. 26A-B.—*Capitosaurus*. 26A. Right side of the brain case from without. 26B. The same from above (from Watson).  
 Fig. 27.—*Eryops*, side wall of brain case from without (from Gregory and Noble).  
 Fig. 28.—*Eryops*, side wall of the brain case from within (from Watson).  
 Fig. 29.—*Hyla*, the side wall of the brain case from within (from Kesteven).

Apart from the bold use of the word "development", perhaps "formation" was intended; the statement is surprising. He says "exactly" similar; then neither had a floor formed by the processus basiptyergoideus.

Further, if the situation of the nerves is either as indicated by his own interpretation of the *Rhizodopsis* neurocranium (Fig. 58, p. 137) or in the normal situation as determined by comparison with the modern fish crania,\* it is self-evident that the all-

\* The jugular canal of Säve-Söderbergh's illustration bears such a striking resemblance to the trigeminal and facial openings of the trigemino-facialis chamber, that it is difficult for the student of living fishes to believe them other than these.

important mandibular and maxillary rami of the fifth nerve issued from the cranium in front of, and medial to his epipterygoid in the Rhipidistia, and in the normal relation in the labyrinthodonts.

As a matter of fact, since all the statements and implications relative to the development of the bones in the fossils are pure speculations, weight of evidence is that the lateral wall of the cavum cranii in front of the otocrane in the labyrinthodonts was developed just as in the modern amphibian neurocranium. If this be not so, from what ancestor have all the modern amphibians inherited this mode of development?

In *Eryops*, Gregory and Noble identify both a laterosphenoid and an epipterygoid. The former is equated with the alisphenoid of *Crocodylus*. According to these writers, as judged by their illustration, the epipterygoid makes contact on its outer surface with a process which rises up from the pterygoid, and medially it meets the parasphenoid below and the laterosphenoid above. There is no foramen indicated between any of these contacting margins, and nerves V2 and V3 are inferred by them to issue from the cranium behind the "laterosphenoid" and then to course forward over the dorsal edge of, and therefore laterally to, the "epipterygoid". There is no foramen between "epipterygoid" and laterosphenoid through which nerve V1 might issue, medially to the epipterygoid (Fig. 27).

For comparison with *Capitosaurus*, Watson illustrated, but did not describe, "a median section of the brain case of *Eryops*" (Fig. 28). In this illustration no laterosphenoid is recognized. The bony boundaries of a widely open prootic fenestra are depicted as prootic behind, and sphenethmoid in front.

Watson and Gregory and Noble worked upon material in the American Museum of Natural History, presumably the same material, and we observe that their interpretations are so different that the text alone enables us to know that both illustrate *Eryops*. Clearly one of them is wrong; possibly all three are. This much, at least, is clear: the structure of these fossils is far from satisfactorily understood, and homologies based upon such imperfect understanding should be used with the utmost caution, as evidence in the elucidation of homologies in other forms.

In the present state of our knowledge the side walls of the fossil amphibians may be equated, with fair probability of correctness, with those of recent amphibians (*vide* Kesteven, 1926) (Fig. 29).

The essential similarity of the form and mode of attachment of the quadrate in the Stegocephalia, Cotylosauria, recent Amphibia and Chelonia, renders it highly probable that the recent forms reflect in the ontogeny of their quadrato-ptyerygoid structures that of the fossil forms.

If already the carboniferous, earliest known, tetrapods had so far departed from the broad plan, as we see it in the embryology of all the recent Tetrapoda below the range of the monotremes, as to have evolved a separate and expanded epipterygoid from the processus ascendens, whence comes the remarkable similarity in the ontogeny of the recent forms, and also why do none of them show us any trace of the expanding processus ascendens?

It is finally concluded that the imperfect information we have, relative to the morphology of the skulls of the extinct amphibians,\* sheds no light upon the questions under discussion, and that the evidence of the fossil reptiles is definitely opposed to the idea that the processus ascendens of the amphibians, which appears in the reptiles as the epipterygoid bone, gave rise to the alisphenoid bone of any of the Craniata.

#### (4). THE ONTOGENY OF THE ALISPHEOID BONES.

Since Gaupp made the original error of believing that *Lacerta* might be accepted as presenting the chondro- and osteocranial development typical for the reptiles, and

\* There is, at times, the temptation to accept as valid descriptions, the reconstructions of fossil skulls offered us by various workers. A moment's hesitation, however, permits one to remember that these are not descriptions of complete skulls, but interpretations of fragmentary remains, and that in almost every instance in which more than one palaeontologist has offered reconstructions, the two or more interpretations differ in important details. Before we may use these reconstructions as evidence, we are forced to *assume* that the particular interpretation is correct, and our whole case is weakened because it is based upon an assumption.

building thereon his theory of the cavum epiptericum, practically every worker has accepted his conclusions.

In the result, the whole of the observations on cranial development and the relation of the chondral bars, processes and fenestrae, have been interpreted in terms of those conclusions.

To what flights of imagination some workers have been forced by these beliefs will appear in the following pages, which are devoted to a review of the facts.

It is submitted that the whole of the recorded variations are explicable on the single, simple assumption that the soft structures varied in their courses relative to the primordial cranial wall, and that this simple explanation is more likely to be correct than the complex series of changes called for under Gaupp's hypotheses.

It should be remembered that the side wall of the chondrocranium does not suddenly spring into being fully-formed, but that it grows upward from the edge of the basis cranii. In both the birds and the mammals the side wall of the brain case has been thrust outwards by the expanded brain, and the floor of the cavum is wider. It is, therefore, at least not unreasonable to assume that at some stage in this process of widening, the first branch of the fifth nerve grew forward directly, above the cranial floor, instead of proceeding laterally around the outer side of the wall.

It has been maintained that the alisphenoid of the lower Vertebrata cannot be homologous with that of the Theria because the former is developed from the pila antotica or another cartilaginous bar in the side wall of the primordial chondrocranium. It, therefore, becomes necessary to examine the relation of the cartilaginous process to the bones and soft structures in the several forms.

At the outset it may be stated that the development of the alisphenoid throughout the Craniata, from fish to man, in the same situation in the side wall of the cranium, is here regarded as *prima facie* evidence that the bones in this particular situation are homologous, irrespective of whether their development commences in membrane, in or on cartilage, or partly in one and partly in the other. It is also believed that those bones which commence in cartilage and extend in membrane, indicate the manner whereby the bone which develops entirely in membrane originated, namely, by the gradual reduction of the cartilage and its final suppression, the condition which is almost or actually attained to throughout the Theria.

This attitude towards the question was adopted by the writer in an earlier contribution, and is really in nowise novel. We have equated the supraoccipital bone throughout the Craniata, wholly and solely on the evidence of its situation. It may ossify on or in cartilage, the tectum synoticum, or partly so and partly by extension in membrane or entirely in membrane. Because they are the first two bones in the gape and apparently present similar topographical relations to contiguous bones, maxilla and premaxilla have been equated throughout the Craniata by all workers except myself, and this, although it is well known that their manner of development, in cartilage, on cartilage and/or in membrane is very varied. The alisphenoid of the fishes and saurians is indifferently developed in cartilage or membrane, yet, under the name of laterosphenoid or pleurosphenoid, the bones have been regarded as homologous within these groups, although it is also known that within the fishes the bone develops from different cartilaginous bars. Again, the situation alone has justified the equation.

The absence of any ossification in the elasmobranchian skull, except the chondrostea, prevents their being of much assistance in the present discussion. It is, however, not without significance that the nerve VI emerges from the cranium separately from the other two branches, through a foramen further forward, in both *Acipenser* and *Polyodon*. It is of interest to observe that, even amongst the cartilaginous fishes, there are examples in which the gasserian ganglion lies at least partly within the cavum cranii, and in which the first branch runs an intracranial course rostrad for a short distance before being given egress through a foramen of its own.

Amongst the bony fishes both the ganglia of nerves V and VII lie largely outside the cranium, the proximal portions lying in the prootic foramen against that cartilaginous rod which has recently been designated the lateral commissure, and behind that which has been termed pila lateralis.

There is a fairly wide range of variation in the fenestration of the side wall of the chondrocranium of the bony fishes, with, of course, a corresponding variation in the position of the cartilaginous bridges between them. The recent interpretation of these variations has, designedly, been such as to bring them into line with the belief that the cavum cranii of the Theria includes the 'cavum epiptericum'. The identification and designation of the various pila has, therefore, been determined entirely by their relation to the contiguous nerves and vessels.

Thus de Beer (1937, p. 391): "In *Teleostomes* a duplication of the side wall is formed, laterally to the prefacial commissure, by the lateral commissure. This structure, which lies laterally to the head vein and orbital artery (the prefacial commissure, as part of the primitive wall, of course lies medially to the vessels), is formed by the junction of the prootic process developed from the auditory capsule, and the basi-trabecular and postpalatine process, developed from the edge of the trabecular and basal plate. In *Teleostei*, where the lateral commissure forms the side wall of the trigeminofacialis chamber, the prefacial commissure is lost."

Thus, the acceptance of the cavum epiptericum theory brings in its train the necessity of regarding as new, and not part of the primitive wall, any craniomural element in the lower Vertebrata which lies medial to any of the vessels and/or nerves, which lie in the epipteric space in the saurians. This applies not only to the bones but also to the struts of the fenestrated primordial cranium.

Although it has never been stated, perhaps because it was never realized, the assumption underlying these interpretations is that the situation and course of the nerves and vessels remained constant and the skull varied in relation thereto. The alternative assumption that the solid cranoskeletal structures were constant and that the soft structures varied in their relation thereto, would surely have been easier to accept.

(a). *The Fishes.*

The pila antotica appears to be constantly developed in a typical manner in every elasmobranchian skull of which the development has been studied. In *Scyllium* (Fig. 30), which is a fairly representative example, as in a number of other elasmobranchs, there is no separation of the foramen for the VIIth nerve, so that there is no prefacial commissure defined, but in *Heterodontus*, *Torpedo* (Fig. 31) and *Squalus* the separation of these foramina permits the identification of the prefacial commissure.

This simply means that our designation 'prefacial' is at fault; had we termed the structure 'anterior otico-basal commissure' we should recognize it without difficulty and at the same time record the fact that in some elasmobranchs the facial nerve emerged in front of it.

Turning next to the Osteichthyes, the prevailing interpretation of the constitution of the side wall of the chondrocranium is as follows (de Beer, 1937, p. 390): "The formation of the posterior myodome in teleostome fishes involves the disappearance of the pila antotica and pila metoptica. In those forms which have lost the myodome, the cartilaginous side wall may be reformed, but it shows atypical features. . . . In *Amia* the orbital cartilage becomes supported posteriorly by a pila lateralis."

Of this region of the chondrocranium in *Polypterus* (Fig. 32) de Beer writes: "The cartilage which forms the anterior boundary of the trigeminal foramen does not answer the requirements of a pila antotica, for the profundus, which should emerge behind the pila antotica, emerges through the same foramen as the oculomotor (which always emerges in front of the pila antotica in other forms). The conclusion which must be drawn is that there is no pila antotica in *Polypterus*, and that the cartilage which forms the side wall of the skull in this region is perhaps a secondary structure."

Surely this is making 'confusion more confounded'. The obvious fact is that the point of emergence of the nerve is different. If the pila antotica is a structure at all, and not merely a name, then it can be recognized in its usual place in front of the prootic fenestra.

In *Lepidosteus* also this need to interpret the structures in terms of the cavum epiptericum theory gives rise to difficulty. De Beer writes (l.c., p. 112): "The cartilage which forms the posterior border of the pituitary vein foramen and the anterior border



commissure and the pila antotica, respectively, but undeniably those two structures are there, plainly to be seen; only the position of the soft structures is different.

In *Salmo* a large foramen, which at first is an open prootic notch essentially similar to that of the sauropsids, permits the egress of the facial nerve (except the ramus palatinus) and head vein and the entrance of the orbital artery, whilst the trigeminal nerve branches leave the cranium further forward, with the 'lateral commissure' between them (Figs. 34 and 35). Again, there is neither prefacial commissure nor pila antotica according to the prevailing view, although both the cartilaginous bars are there to be plainly seen.

Just at this point we would do well to remind ourselves that the prefacial commissure and the pila antotica are generally regarded as being primitive structures. Therefore, in all these instances in which, under the prevailing interpretation, they are absent, there is, inescapably, an assumption that they have been *replaced* by the so-called secondary structures. That is to say the primitive side wall components have gone entirely, and their place has been taken by these newer bars.

Referring back to *Amia*, it will be remembered that the orbital artery enters the cranium medial to the parachordal cartilage. Now, if the orbital artery lie medial to a bar which otherwise might be regarded as a pila prootica or prefacial commissure, that bar cannot, in the prevailing view, be so regarded. Here then is an inconsistency. If the orbital artery may so vary its relation to the parachordal cartilage as to enter now medial and now lateral thereto, without altering the nature of that bar, why may it not present the same variation to the prefacial commissure and/or the pila antotica?

A comparison of these chondrocrania of the Osteichthyes with those of the Chondrichthyes, will reveal that all these cartilaginous bars are portions of the primordial chondrocrania and develop in essentially similar manner, and that variations in the relations of the vessels and nerves are only deemed to be of significance, when their interpretation on the simple assumption that they have varied in relation to the cranium, would run counter to the view that the epipteric space and its contents have been incorporated into the cavum cranii of the Theria. The inconsistency in connection with the orbital artery has just been mentioned, and to a lesser degree the same position arises in connection with the internal carotid; and the ramus hyomandibularis facialis may issue either through the prootic fissure or may penetrate the otic capsule, without involving the related cartilaginous structures in any change of name or character.

Further than this, a critical survey will reveal that the so-called pila lateralis and the so-called lateral commissure, may present variations to the all-important nerves and vessels as great as those which disqualify the pila antotica and prefacial commissure, and yet have been permitted to retain their identity.

Unless these varying relations may be regarded as *merely* differences in the manner and degree of fenestration of the side wall of the chondrocranium, *devoid* of fundamental significance, it becomes necessary to recognize a whole *series* of "secondary" side walls; and this, apparently, is the intent of the terms—pila lateralis, lateral commissure, pila antotica secundaria and others which we shall meet later.

In some instances, owing to the manner in which the fenestration is brought about, the chondrocranium will present two or more secondary side walls as it develops, and one or more of these will belong to different categories at different stages of the development.

When, in our investigation of homologies, we base our comparisons on the relations to cranial nerves, we are on relatively safe ground, for there will be no doubt as to the identity of the nerve. This, however, is not the case when the comparisons are based upon relations to blood-vessels.

When we write about, e.g., the fifth nerve, we are absolutely confident that in each and every group of the Craniata it is the same nerve, more or less modified perhaps, but none the less certainly always the same nerve.

When we write about, e.g., the internal carotid artery or the vena capitis lateralis, there is not the same certainty.

The vascular system develops out of a maze of indeterminate capillary vessels and sinuses, more or fewer of which become permanently or temporarily dominant, and as

certain of them acquire permanence, others are aborted or reduced in size. During these changes the blood may flow one way along a given vessel at one stage, and in the opposite direction later.

From this it follows that when we find the vena capitis lateralis above or external to a given cartilaginous structure in one animal, and below or medial to the same structures in another animal, it may be *the* important vein of the region, but also it may well be that the blood stream has availed itself of, and rendered permanent, another channel. Physiologically it may be the vena capitis lateralis, but anatomically and embryologically it may not. The internal carotid artery enters the cranial cavity, in the great majority of the craniates, at the posterior margin of the sella, in some cases, most amphibians, a good deal further forward, and then turns back to reach the region of the pituitary gland. The segment of the vessel extending forward beneath the skull in front of the pituitary fossa and then turning back to reach it, is not, anatomically or embryologically, the same vessel. The early arterial anastomosis through the fenestra hypophyseos was occluded and that segment of the vessel aborted.

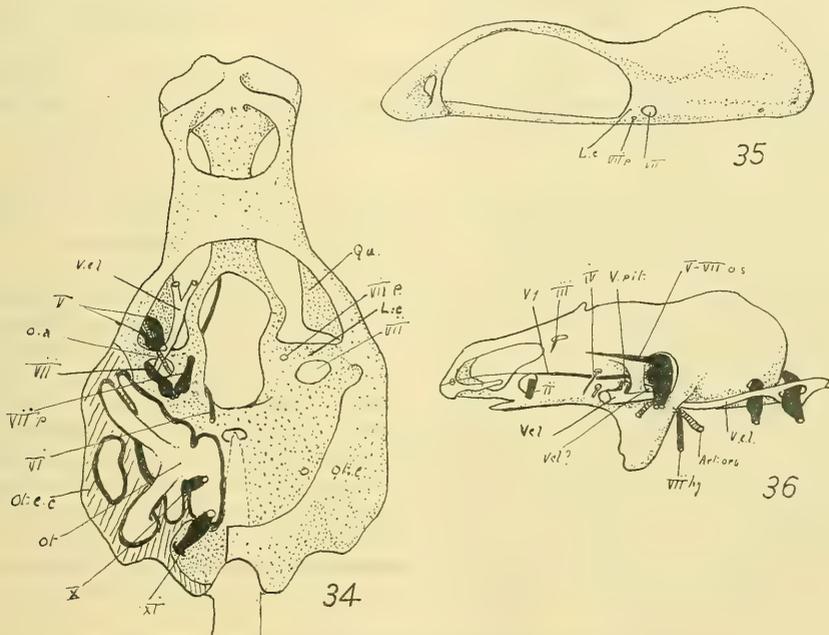


Fig. 34.—*Salmo*, the chondrocranium (from de Beer, modified).

Fig. 35.—*Salmo*, chondrocranium (from de Beer).

Fig. 36.—*Ceratodus*, chondrocranium and nerves (from de Beer).

From this, in turn, it follows that we should not attach great significance to the relation of the blood-vessels to the chondrocranial bars; the changed relations are more likely to have been due to a change in the course of the vessel than to a change in the cranial structure. When the changed relation of the vessel is to a structure whose identity is indisputable, it has always been tacitly admitted that the vessel has altered. The vena capitis lateralis passes in some forms above the columella auris, in others below it. No one has thought fit to suggest that one of these is a "columella auris secunda"; nor has the identity of the anterior margin of the sella been questioned when, as in the Anura, the internal carotid artery enters the cranium in front of it.

When, throughout the series of animals whose evolution we are studying, we find certain structures presenting the same relations to one another, we are justified in believing that these characters are derived from a common ancestor, either under the direction of a strong inherited potential or some constantly acting physical factor. The

structures are both analogous and homologous. On the other hand the occasional departure from the norm within the series cannot be regarded as of equal importance; they do not, necessarily, indicate anhomology.

There are certain relations of the vessels and nerves to the first antotic pila which are so constant as to justify the belief that they are of prime importance. At times the relations are not the same, but the change does not indicate that the antotic pila with the altered relations is not homologous with the antotic pila in the generality of instances. As an example let us take the lateral commissure. Before it can be asserted that this is not homologous with the pila antotica, it must be demonstrated that it originated differently. This can only be done by showing that its development is different, and that it presents fundamentally different relations to surrounding structures or functions in such a fundamentally different way as to preclude the possibility of its origin from the same primitive structure as the antotic pila.

Actually it develops in the same way; as a process of the trabecular rod; its function is essentially the same and its relations to surrounding structures are the same, except in regard to certain nerves and vessels. But what evidence have we that the vessels are really the same, or that the nerves have not taken a slightly different way out of the cranial cavity?

These considerations lead one to the conclusion that it will be best, at least for the present, to regard the observable differences in the fenestration of the cartilaginous side wall of the chondrocranium in this region, as minor variations of no fundamental significance.

The alternative is to follow de Beer and recognize a series of side walls instead of simply recognizing that the bar or bars in question are indisputably the alisphenoid portion of the chondrocranium, and to that extent completely homologous.

The alisphenoid bone in the fishes has, of recent years, been fairly generally designated pleurosphenoid or laterosphenoid on account of its supposed difference from the alisphenoid bone of the mammals. Although it presents variations, both in development and in morphological relations to the nerves and blood-vessels, greater than those presented by the cartilaginous structures it replaces, no one has, as yet, thought fit to bestow a series of names upon the various forms of the bone. In effect it has been agreed to regard the bone as always homologous within the fishes, an utterly inconsistent procedure for those who regard the precursory cartilages as anhomologous.

In *Acipenser*, the only bony fish which is credited with a true pila antotica by de Beer, there is, according to the same authority, a pleurosphenoid "developed in the postero-dorsal corner of the orbit", whilst the prootic "ossified in the anterior wall of the auditory capsule" surrounds the prootic foramen through which emerge all the branches of the fifth and seventh nerves. The prefacial commissure is missing in this, as in other elasmobranchian crania.\*

In *Amia* the alisphenoid develops in the pila lateralis and extends into the orbital cartilage above and in front of the pila; it forms the anterior boundary of the foramen trigeminum and is perforated for the exit of the nervi ophthalmici, and lies laterally to the head vein and orbital artery.

In *Polypterus* the auditory and nasal capsules are, to a large extent, unossified but the cranial side wall between them, in the adult fish, is constituted by a bony continuum which Allis (1922), following Traquair (1871), designates the sphenoid. The posterior portion of this bone is the alisphenoid, the anterior portion being the orbitosphenoid. It would appear that these two ossify from separate centres. The alisphenoid ossifies in the pila antotica secundaria and in the orbital cartilage above it.

In *Salmo*, according to de Beer (1937, p. 128): "The pleurosphenoid arises late, in the form of outer and inner perichondral lamellae in the hinder part of the taenia marginalis (now enveloped in the tectum cranii). Ossification spreads ventrally in membrane, and the pleurosphenoid thus comes to enclose the trochlea nerve and the ophthalmic branch of the trigeminal nerve in separate foramina."

\* I have elsewhere (1939) advanced reasons for regarding the Chondrostei as "bony elasmobranchs".

The manner of the development of the alisphenoid bone is known in a number of other fish, but further examples are not necessary; they would but serve to multiply the diversity of the modes of development, already sufficiently illustrated.

If the precursory cartilages are not homologous then, of course, the bones derived from them cannot be. My own view is the broad one, that these cartilaginous bars and the bones developed from them *are* the alisphenoid portion of the cranium, primordial and adult; they are homologous but present minor variations which have no phylogenetic significance, except that they may be used as parallels for other similar non-significant variations in other structures or animals.

It will be argued, later, that the mammalian condition may be derived directly from the fishes by the absorption of portion of the bone medial to certain structures, and its extension to surround others. It certainly seems more reasonable to assume these, comparatively slight, changes rather than to assume the complete disappearance of the bone and then its replacement by a remarkably modified visceral structure.

(b). *The Amphibia.*

Except in the Gymnophiona the pila antotica presents the typical relations throughout the amphibians.

The chondrocranium of *Ceratodus* (*Neoceratodus forsteri*) is essentially similar (Fig. 36) in all its features to those of the Urodeles, that is, in all the features relevant to the present discussion. Immediately in front of the massive auditory capsule, and close to the floor of the cranium, there is a large foramen prooticum, through which all the branches of the fifth and seventh nerves emerge. The anterior boundary of this foramen is the pila antotica. There is no prefacial commissure. Immediately behind the prootic foramen the otic process of the quadrate is fused with the outer wall of the capsule, so that the lower and inner edge of the fusion is only slightly lower than the upper margin of the foramen. In front of the foramen the ascending process of the quadrate is fused to the outer surface of the pila antotica, where it also is close to the upper margin of the foramen. Below the foramen the basal process is fused to the parachordal, just where this meets and fuses with the antero-ventral corner of the capsule.

The vena capitis lateralis runs backward, laterally to the ascending process and to the pila antotica. There is, however, a smaller branch lying medial to the ascending process, which communicates with the pituitary vein and with the main vein, both in front of and behind the process. Posterior to the ascending process the vein passes backwards below the emerging branches of nerves V and VII and then above the basal process, between the otic process and the outer wall of the capsule. In this part of its course the vein has the orbital artery below it; in front of the otic process the latter vessel turns laterad and passes forward laterally to the ascending process.

The three motor oculi nerves run forward medially to the pila antotica and emerge through separate foramina in the orbital cartilage. The profundus nerve runs forward medially to the ascending process, between it and the pila antotica and above the basal process. The ophthalmicus superficialis runs forward laterally to both ascending process and the pila antotica.

In the Urodela the embryonic chondrocranium (Fig. 37), and the relations of the vessels and nerves thereto, are essentially the same as in *Ceratodus*, and do not call for separate description. The palatal process of the quadrato-ptyergoid cartilage which is commonly present, is not a difference of any importance in the present connection.

In the Anura there is a somewhat different arrangement. The palato-ptyergoid cartilage is attached, posteriorly, to the parachordal cartilage at the level of the basis cranii. This is the processus ascendens and it is the only attachment of the palato-ptyergoid posteriorly until the inception of metamorphosis. At the inception of metamorphosis the processus ascendens is absorbed, and other attachments to the auditory capsule are developed; these are not comparable with the basal or otic processes of the Dipnoi and Urodela.

The following description is based upon the conditions presented by a late, premetamorphic stage, in the development of *Lymnodynastes peronii* (Fig. 38).

The ganglia of the fifth and seventh nerves are fused together and protrude through the foramen prooticum, so that all the trunks of both nerves emerge through it, and, therefore, behind the pila antotica. The ramus palatinus passes ventrad against the side of the parachordal cartilage and, turning, runs forward immediately below the trabecular rod. The ramus hyomandibularis also leaves the ventral surface of the fused ganglia, a little in front of and laterally to the point of departure of the palatine nerve. The second and third branches of the trigeminal nerve pass forward over the ascending process of the quadrate, whilst the profundus nerve leaves the anterior surface of the ganglion below these two and runs forward below and medially to the process.

The internal carotid artery runs forward below the ascending process. Its division into cerebral and orbital branches takes place anteriorly to the process. The cerebral inclines mediad and dorsad to penetrate the basis cranii laterally to the pituitary fontanelle. The orbital artery continues directly rostrad for a short distance and then turns laterad and dorsad. At no time is the vessel found lateral to the ascending process, as in *Ceratodus*, the Urodela and Lacertilia.

It has not been possible to identify the vena capitis lateralis with any confidence, amongst the numerous large, thin-walled veins and sinuses. A very definite sinus emerges from the cranial cavity through the foramen prooticum. Immediately within the cavity, and behind the pituitary, these sinuses of opposite sides communicate, and they are also joined by other intracranial sinuses both anteriorly and posteriorly. Outside the cranium this vessel runs backward close to the cranium, but is joined by sinuses from in front, which reach it both above and below the ascending process. There are also numerous cross communications with a much larger longitudinal sinus situated further out, away from the cranial wall.

Except for those of the orbital artery, these relations of nerves and vessels to the pila antotica and processus ascendens, though presenting peculiarities of their own, are essentially the same as those in the Dipnoi and Urodela. If the attachment of the processus ascendens were to be moved dorsad and the profundus nerve and the orbital artery were carried dorsad with it, the relations of all the nerves would be as in the rest of the Amphibia. The artery, of course, would lie medially, instead of laterally, to the processus.

In the Gymnophiona the chondrocranium is very incomplete, and the prootic fenestra is very large. The palatine nerve is enclosed in a separate foramen, that is to say there is a prefacial commissure present. The palato-pterygoid cartilage is attached to the cranium by a relatively slender ascending process only. This attachment is a temporary one and is to the taenia marginalis, a short distance in front of the auditory capsule.

The ramus maxillaris is, apparently, the only branch of the fifth nerve to emerge behind the ascending process; the profundus and mandibularis certainly emerge in front of it.

The pila antotica is placed far forward and forms the posterior boundary of the sphenoptic foramen, through which nerves II, III, IV and VI all emerge (Norris and Hughes, 1918).

I have been unable to find any description of the relation of the vessels to the pila antotica and ascending process, and unfortunately my youngest coecilian material has most of the cartilage of the skull replaced by bone. So far as may be judged from this material, the relations are as follows: The veins are most conveniently described proceeding against the blood stream. Just posterior to the cranio-quadrate articulation two veins are to be seen, one above the other. They lie below the outer edge of the basal bone. The dorsal aorta lies laterally to these vessels and at a slightly lower level. If the two veins be traced forward, the more dorsally placed one will be found to incline dorsad and slightly mediad and to penetrate through the basal bone just medial to the parachordal cartilage, in front of the auditory capsule, and below and medial to the posterior corner of the incisura prootica. The palatine nerve emerges from the cranium by the foramen through which the vein passes in. Immediately within the cranium the vein receives tributaries from large and small intracranial sinuses and itself inclines laterad, dorsad and rostrad, passing out of the cranium through the large

foramen prooticum and dorsal to the antero-internal end of the cranio-quadrate joint. The lower of the two veins will be found to run forward below the joint. In front thereof both veins communicate with the large ventral orbital sinus.

The dorsal aorta continues forward below the cranial floor, inclines laterad and sends the cerebral artery into the cranial cavity via the orbit and the sphenoptic fissure.

Whilst the course of the artery is similar to that in the Urodela the venous conditions are quite different. If we designate them vena capitis dorsalis and ventralis respectively, then the "dorsalis" enters the cranial cavity behind the articulation and certainly behind the position of a processus basalis quadrati, and does not emerge again until anterior to that situation. The "ventralis" is certainly situated below the location of a processus basalis throughout the whole of its length.

(c). *The Reptiles.*

We commence with the lacertilians; *Sphenodon* is so similar to the lizards that it will not be described.

The chondrocranium in front of the auditory capsule is reduced to a number of rods (Fig. 39). The prefacial commissure is a relatively wide flange of cartilage. It forms the posterior boundary of the incisura prootica, of which the pila antotica forms the anterior boundary. The basipterygoid process is situated below the junction of the pila antotica and the trabecular plate, and stands out and down just in front of the middle of the antero-posterior length of the pituitary fontanelle. The epipterygoid cartilage rests upon the basipterygoid process, with the meniscus pterygoideus between them, and stands vertically, with a slight inclination towards the mid-line. In some lizards there is a horizontal, forwardly-projecting, pterygoid process continuous with the base of the epipterygoid. There is no trace of this in *Physignathus*.

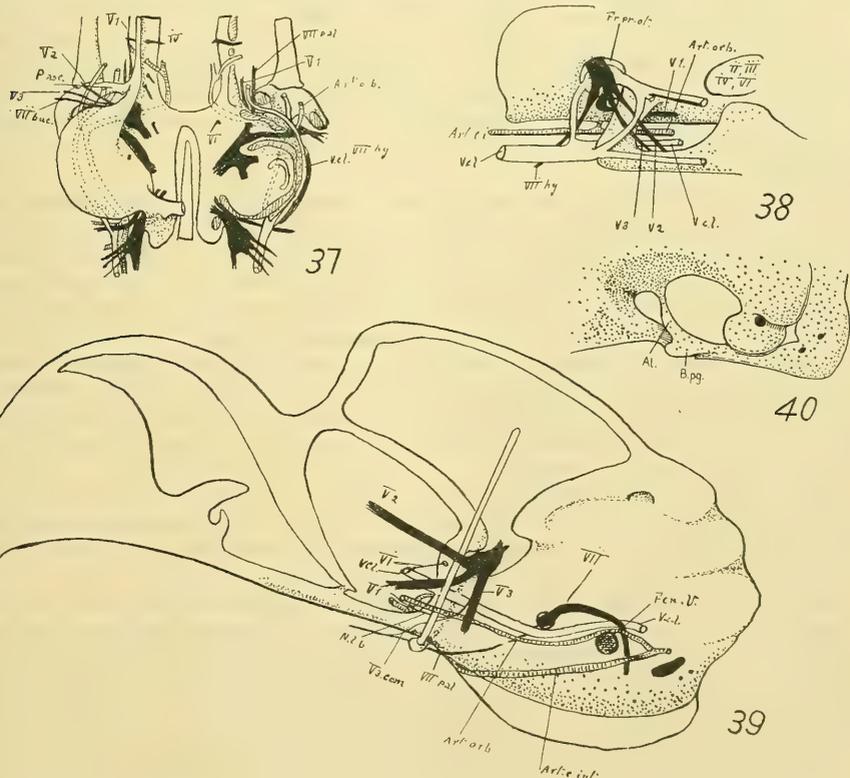


Fig. 37.—Salamander, chondrocranium and nerves and vessels (from de Beer).  
 Fig. 38.—*Lymnodynastes*, chondrocranium with nerves and vessels.  
 Fig. 39.—*Physignathus lesurii*, chondrocranium with nerves V and VII and vessels.  
 Fig. 40.—The chondrocranium of *Dasyurus* (from Broom, after Kesteven).

The ganglion of the facial nerve lies partly on the inner side of the cranial wall and partly outside. The palatine ramus runs down and forward, close to the outer surface of the prefacial commissure and the parachordal part of the basis cranii, below and medial to it, and gains the under side of the basiptyergoid process and then continues straight forward. The main trunk of the facial nerve runs backward over the fenestra vestibuli and the columella auris. The ganglion of the fifth nerve protrudes through the incisura prootica. The profundus nerve runs forward medial to the epiptyergoid, processus ascendens quadrati, with the vena capitis lateralis between it and the pila antotica. The mandibular branch of the nerve runs downward behind the epiptyergoid and basiptyergoid processes. A short distance beyond its emergence from the ganglion, the nerve gives off a fine branch which runs forward across the lateral wall of the vena capitis lateralis and medial to the epiptyergoid. This branch carries the motor fibres to the levator bulbi muscle, and communicating sensory fibres to or from the ramus palatinus, which it joins just after that nerve has emerged in front of the basiptyergoid process.\*

The internal carotid artery divides into cerebral and orbital branches behind the columella auris. The latter runs forward below the columella and turns under the basis cranii; after passing beneath the basiptyergoid process, medial to the palatine branch of the facial nerve, it inclines mediad and then turns dorsad and reaches the cranial cavity through the posterior lateral corners of the pituitary fontanelle. The orbital artery runs forward above the columella and reaches the orbit, passing laterally to the epiptyergoid.

The vena capitis lateralis also courses backward above the columella; anterior thereto it is close to the wall of the cranium and passes medially to the branches of the fifth nerve and the epiptyergoid, laterally to the pila antotica.

These are the conditions on which Gaupp's theory of the cavum epiptericum and the epiptyergoid homology of the mammalian alisphenoid bone was developed. As described above for *Physignathus*, the chondrocranial structures and the relations of the nerves and blood-vessels are as in *Lacerta*. It is assumed that the nerve to the levator bulbi and the N. communicans mandibularis ad palatino is the same in *Lacerta* as in the lizards examined. No account of these nerves appears to have been published previously.

In the crocodile chondrocranium the pila antotica is a fairly wide band of cartilage which joins the anterior edge of the auditory capsule below the centre of its height, with the result that the fenestra prootica is very much reduced in size as compared with that of the lacertilians. There is no basiptyergoid process. The pterygoid process of the quadrate is short and the processus ascendens is reduced to a mere spur. All the branches of the fifth nerve emerge through the foramen prooticum, the ramus mandibularis runs down behind the ascending process and the maxillaris and profundus nerves turn forward above and medial to it. The vena capitis lateralis runs backward medial to and above the ascending process, whilst the orbital artery runs forward a little further from the wall, dorsal to the process. The facial nerve issues through a separate foramen, as in sauropsids generally.

The alisphenoid bone ossifies endochondrally in the pila antotica and then extends forward in membrane. Its relations to the nerves and blood-vessels are the same as the pila, but in late embryonic stages a spicule of bone develops laterally to the profundus nerve, and, growing thicker and wider, encloses the nerve in a canal.

In chelonians the pila is not so wide as in the crocodiles. It may end freely dorsally or may meet and fuse with the taenia marginalis to enclose completely the fenestra prootica. Though better developed than in *Crocodilus*, both pterygoid and epiptyergoid processes are small and end freely. All three branches of the fifth nerve emerge through the fenestra prootica, the seventh nerve separately, further back. The profundus nerve runs forward medial to the ascending process, the other branches of the fifth pass around

\* The point of departure of these two sets of fibres varies somewhat; in the agamid lizards *Physignathus* and *Amphibolurus* conditions are as just described. In *Varanus varius* they come away from the main nerve separately, very close to the ganglion. In *Tiliqua* and scincoid lizards generally, they have independent origins, but leave the nerve further down. In every lizard examined they both run forward lateral to the vein and medial to the epiptyergoid.

it laterally. The vena capitis lateralis is medial to the process, the orbital artery lateral to it.

There is no alisphenoid bone developed. Shaner (1926) writes: "In the Turtle the pila (antotica) disappears and the gap in the brain case is filled by an epipterygoid ossification of the epipterygoid and pterygoid processes of the quadrate." In *Chelone midas* a process from the under surface of the parietal reaches down to an ascending process of the pterygoid bone, and at the back of the suture between them, a small epipterygoid bone sutures with both. This tiny ossification of the epipterygoid process is, however, outside the cranial cavity. In *Emydura* and in *Chelodina* there is no ossification of the pterygoid process, or of its ascending process.

In the ophidian chondrocranium the pila antotica is not developed, and neither is the processus pterygoideus nor ascendens quadrati. The alisphenoid bone is developed entirely in membrane, its adult form and relations to nerves and blood-vessels are described on p. 300.

In the birds a definite pila antotica is developed but it lies laterally to the profundus nerve, and on that account has been designated pila antotica spuria by de Beer and Barrington (1934). For these authors, only that part of the structure which lies medial to the profundus is to be regarded as the pila antotica. The greater part of the structure, that which lies laterally to the nerve, develops later than the rest in some birds and is regarded by them as a secondary structure. According to them a small peg of cartilage in front of the nerve, in *Anas*, is the pila antotica. The large, independently developed prootic pila, situated laterally to the nerve, is the pila antotica spuria.

The following description of the relevant portions of the chondrocranium of the Kiwi\* (*Apteryx*) is based upon the study of transverse sections, and the model reconstructed from them (Fig. 41), of a head which measured 5.5 cm. from tip of snout to occiput.

The gasserian ganglion protrudes partly through the foramen prooticum, and the second and third branches of the fifth nerve arise from the portion of the ganglion outside the foramen. The anterior and superior boundaries of the foramen are supplied by the posterior edge of a broad sheet of cartilage, which arises from the edge of the basis cranii, between the prootic foramen and the sphenoptic fissure. This sheet is attached to the antero-superior corner of the otocrane above the prootic foramen, and forms the side wall of the cranium, between that capsule and the sphenoptic fissure. A large part of the gasserian ganglion lies upon the inner surface of this cartilaginous cranial wall, just at and above its attachment to the cranial base, in front of the prootic foramen and extending forward a little more than two-thirds of the antero-posterior width of the wall. At the anterior end of the ganglion the first branch of the nerve leaves it, and penetrating the cartilage in a forward and lateral direction, appears on the outer surface very close to the sphenoptic fissure.

In this specimen the prootic fissure is at once recognizable. It seems equally obvious that the cartilaginous bar in front of it must be the antotic pila. De Beer and Barrington would, perhaps, argue that this is the pila antotica spuria and that the true pila antotica is the little flange of cartilage, which intervenes between the profundus nerve and the sphenoptic fissure. It is probable that this little piece of cartilage did not have an independent origin and is simply an extension of the main sheet around the nerve. Assuming, however, that it had an independent origin and is an upgrowth from the basis cranii, which has fused completely with the rest of the sheet, it is still difficult to recognize it as the pila antotica. Its situation, that of a pila metoptica, bounding the sphenoptic fissure posteriorly, is a long way too far forward for a pila antotica. Whether it arises independently from the basis cranii or not, there is little room for doubt that this little flange of cartilage is the same structure as that which was found medial to the profundus nerve in *Anas* by de Beer and Barrington, and designated pila antotica by them, and that the main sheet of cartilage, between the first and the other two branches

\* This specimen was presented to me by Professor W. Benham. After staining it was embedded in nitro-cellulose and cut in the saggital plane to the mid-line. It was then remounted and the remaining half cut transversely. I have, gratefully, to acknowledge the donor's kindness.

of the nerve is the same structure as that which they describe in *Anas* under the name of *pila antotica spuria*. The close approximation of the two structures in *Anas*, perhaps, excuses the peculiar identification of those two writers. Had they been as far apart there as they are in *Apteryx*, it is exceedingly doubtful whether they would have been recognized as other than *pila antotica* and *pila metoptica*.

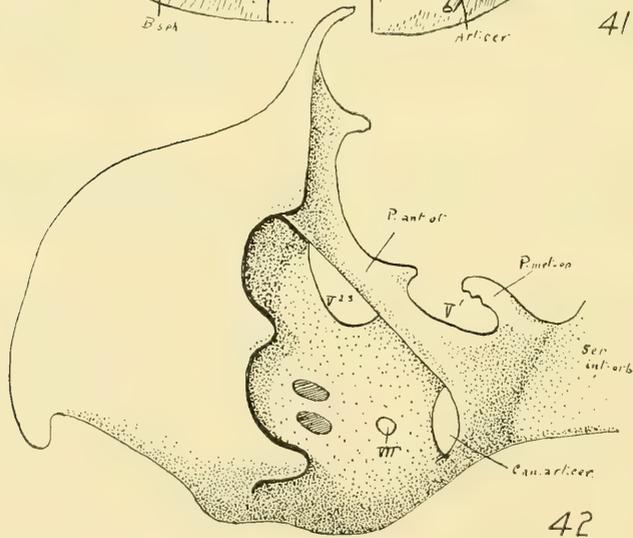
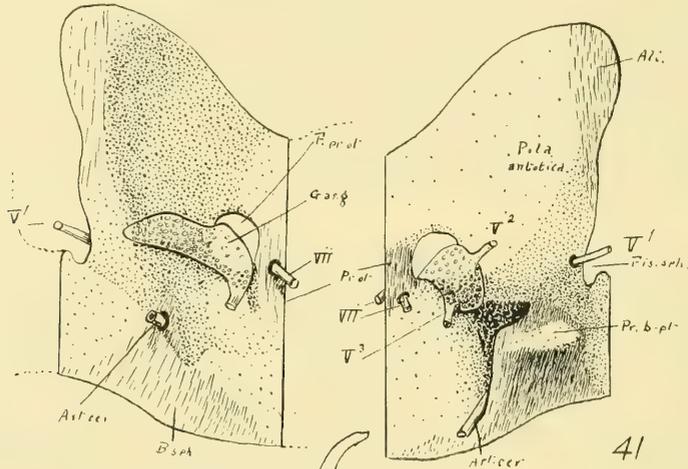


Fig. 41.—Internal and external views of a model of the ali- and basisphenoidal regions of the chondrocranium of *Apteryx*.

Fig. 42.—Lateral view of the chondrocranium of *Podargus*.

T. J. Parker's illustration of the chondrocranium of *Apteryx* represents the situation of the foramen for the profundus nerve too far back, and the representation of the optic foramen in the illustration reproduced by de Beer on Plate 103, fig. 1, is absolutely erroneous. The optic nerve issues from the cranial cavity rather high up in the sphenoptic fissure, actually just in front of the alisphenoidal lamina of my reconstruction about half-way between the slight sinuation of the front edge and the position of the profundus nerve. In the situation of the optic nerve of his drawing, there is a wide hiatus through which the orbital sinuses communicate with those of the front end of the cranium and the nasal capsule. This persists in the adult skull, and is probably characteristic of the Dinornithidae, for it is also present in the Emu skull. Actually the posterior end of the nasal cavity extends further back than his optic foramen; and the cranial cavity lies at a higher level than it in this location.

De Beer was, obviously, misled by Parker's description. Believing that the pila metoptica was present behind the so-called optic fissure, the identification of that in front of the profundus nerve is, perhaps, understandable. Had both the foramina been depicted in their correct positions, it is difficult to believe that the little piece in front of the profundus would have been identified as a pila antotica.

In *Podargus*, an owl (Fig. 42), the pila antotica is a much narrower bar resembling, herein, the generality of birds, and differing from the dinornithid condition. In front of the antotic pila, separated from it by a fairly wide bay, there is a short spur of cartilage, which forms the inferior portion of the posterior boundary of the sphenoptic fissure; this is the pila metoptica. This metoptic pila lies medial to the profundus nerve, which passes out between it and the pila antotica. The other two branches of the nerve emerge behind the pila antotica.

Here again, the situation of this pila metoptica is clearly too far forward to permit of its identification as a pila antotica. There is, however, little doubt that it is the same structure as that so identified by de Beer and Barrington in *Anas*.\*

Brock has described the chondrocranium of *Struthio*, and she apparently found no cartilage medial to the profundus nerve.

It would surely be foolish to conclude that the pila antotica has been replaced by a pila antotica spuria in *Struthio*. That, however, is the conclusion to which we would be forced, if we adopt the interpretation of de Beer and Barrington.

But even if this identification of de Beer's be accepted, changing the name of the pila does not change its character; and the "pila antotica spuria" still presents relations to the nerves identical with those of the ala temporalis of certain mammals, and also with those of the epipterygoid process of the reptiles. It is hardly necessary to stress the fact that its mode of development is utterly different to that of the epipterygoid, but essentially the same as that of the ala temporalis.

It is certainly not homologous with the epipterygoid, but there is no convincing evidence that it is not homologous with the ala temporalis.

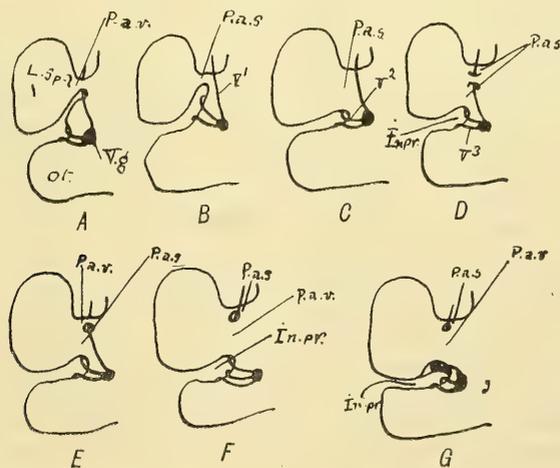


Fig. 43.—A diagrammatic presentation of the relations of the pila antotica vera and of the pila antotica spuria to the rami of the fifth nerve in avian embryos. A. Emu, all stages and *Podiceps* late stage. B. Fowl and Turkey, all stages, *Podargus*, head length 15.2 mm. and *Melopsittacus* 13th day and onwards. C. *Botaurus*, head length 22 mm. D. *Phalacrocorax*, head lengths 11.3 and 14.6 mm. E. *Apteryx*, head length 58.0 mm. and *Himantopus*, late stage. F. *Podiceps*, head length 11.9 mm. G. *Iridepara*, head lengths 4.5 and 9.7 mm. In. pr., incisura prootica; L. sp-l., alisphenoidal lamina; P.a.s., pila antotica spuria; P.a.v., pila antotica vera; V.g., gasserian ganglion. V'. V'. and V', the three rami of the fifth nerve.

\* Three specimens of *Podargus* were available for study, but all in the same early stage of development, so that it is not possible to say whether or not the pila metoptica increases in size in the later stages. The specimens were stained by the van Wijhe method and cleared in a Spalterholtz fluid.

I have recently studied the development of the pila antotica in a variety of avian embryos and found (Kesteven, 1942) that there were seven different arrangements of the relation of the pila to the branches of the fifth nerve. These are illustrated diagrammatically in Figure 43. From these it appears that, as determined by the relation of the processes to the first branch of the fifth nerve, the pila antotica spuria may be located either in front of, or behind, the pila antotica vera.

Whatever interpretation be placed upon the first antotic pila in the birds, there is here incontrovertible evidence that the relation of skeletal structures to nerves may not be accepted as conclusive evidence for or against homologies.

In view of the similarity in development, as a process rising from the edge of the chondrocranium, together with the place of that development, and the relation to the branches of the fifth nerve, one feels justified in asserting that the weight of evidence supports the conclusion that the first prototic pila in the birds is homologous with the ala temporalis of the mammals.

The fact that the ala temporalis appears first as a separate pellicle of cartilage in a number of mammals, is not evidence which may be quoted against this conclusion and in favour of the accepted interpretation. It is more probable that the side wall of the chondrocranium had become slightly fragmented in the mammalian embryos, than is the supposition that a fragment of an evanescent visceral arch has become incorporated into the cranial wall. The assumption of fragmentation has to be accepted under either hypothesis.

But if the pila antotica of the birds is homologous with the ala temporalis of the mammals, so also is the pila antotica of the crocodiles, and the bones which are developed from the three processes are homologous also.

(d). *Theria*.

The chondrocranium of the *Theria* calls for comparative examination of three grades, monotreme, marsupial and mammal. The best known chondrocranial history of the monotremes is that of *Echidna*, thanks particularly to the work of de Beer and Fell (1936). The development of the chondrocranium of *Dasyurus* has been described by Broom (1909) and by Fawcett (1918).

The first bar in front of the auditory capsule in the monotreme chondrocranium (Fig. 44) presents all the relations of the pila antotica to the branches of the fifth nerve, that is to say, it is anterior and medial to them all. It arises from the lateral end of the dorsum sellae and not from the true edge of the basal plate, which lies below, and later grows beyond it laterally. Posterior to the root of the bar, and posterior to the sella, the edge of the trabecular plate is produced to form a processus alaris. This is perforated by the orbital artery and bears dorsally a low projection, which has been identified as the ala temporalis. The internal carotid arteries enter the cranium at the depth of the sella, in front of the root of the so-called pila antotica.

The pila itself early develops a dorsal, backwardly projecting process, which is the first appearance of the orbital cartilage. This continues to grow backward and ultimately fuses with a forwardly projecting flange from the auditory capsule.

The pila in question is the taenia clino-orbitalis of earlier writers.

In a recent communication, already referred to (Kesteven, 1940a), it was pointed out that the relations of this process are more closely like those of the lacertilian pila metoptica than to the pila antotica.

In *Dasyurus* (Fig. 40) the first pila in front of the auditory capsule rises from the lateral edge of the processus alaris, and is attached above to the orbital cartilage. Its relations to the branches of the fifth nerve differ from those of the taenia clino-orbitalis in that the profundus and maxillary nerves lie medial to it. *Perameles* (Esdail, 1916) and *Caluromys* (Dennison and Terry, 1921) differ from *Dasyurus* in that the pila does not extend upward to meet the orbital cartilage, and that it is perforated by the maxillary branch of the fifth nerve. De Beer (1937, p. 303), describing the *Caluromys* chondrocranium, writes: "The maxillary branch of the trigeminal nerve passes through a cartilaginous foramen rotundum—i.e., both processus ascendens and ala temporalis are present, attached to the processus alaris."

This peculiar belief in the presence of two structures in this situation is also expressed in the following passage (p. 431): "In many mammals (e.g., *Trichosurus*, *Mus*, *Mustelus*) the cartilage is to be found not only between the profundus and maxillary, but also between the maxillary and mandibular branches of the trigeminal nerve. The maxillary branch is thus enclosed in a (cartilaginous) foramen rotundum. The cartilage in front of this foramen is the processus ascendens, that behind it is the ala temporalis of those forms in which the maxillary branch emerges freely in front of it." The same views are expressed again on page 301.

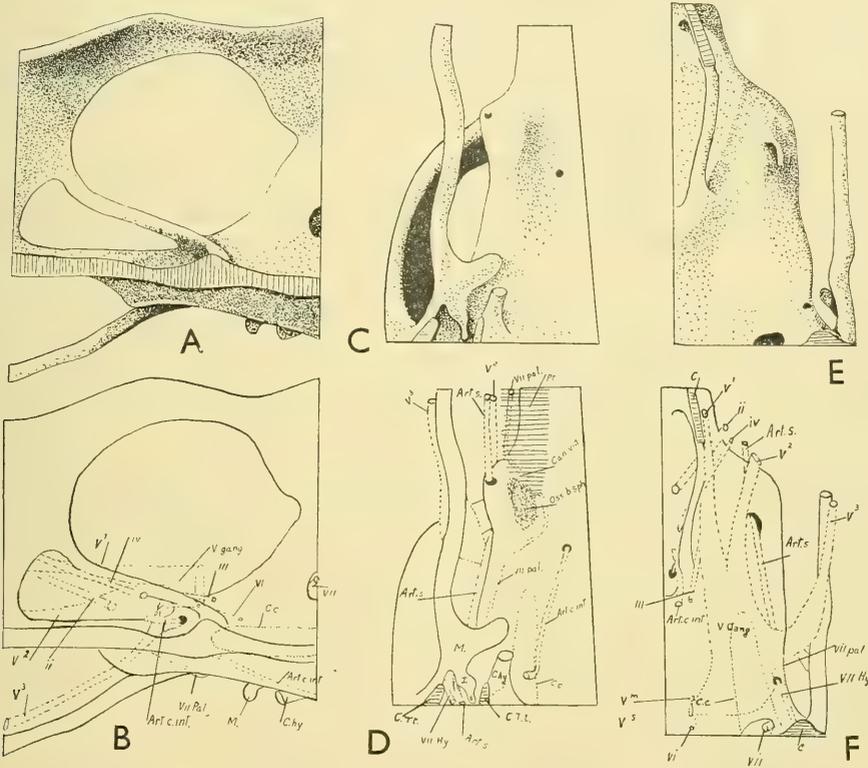


Fig. 44.—Reconstruction of portion of the chondrocranium of *Ornithorhynchus* (from Kesteven, 1940a).

This makes "confusion more confounded". Does this mean that in those latter forms—e.g., *Perameles* and *Sus*—the alisphenoid bone is developed from an ala temporalis and there was no processus ascendens? It certainly is quite clear, if we are to agree with de Beer, that we will no longer regard the ala temporalis as being homologous with the processus ascendens. This, of course, is what I have been, and still am contending, but on quite other grounds. If de Beer's interpretation be accepted, it will be necessary to coin still another term; ossis alisphenoidea spuria (!) will perhaps fit that alisphenoid bone in the mammalian cranium, which is not developed from a processus ascendens, and therefore not homologous with the lacertilian epipterygoid bone.

But the confusion does not end here. De Beer states that, according to Fuchs, the processus ascendens alone is present in *Didelphys*. If this be so, then the alisphenoid bone of that marsupial is the only true alisphenoid bone as yet known amongst the therians, under this peculiar interpretation of his. In every other skull as yet studied the evidence points, under his theory, to either a dual origin from both the cartilaginous bars or from the ala temporalis only.

Perhaps the difficulty might be met by coining another term. May I suggest 'ossis alisphenoidea dualis' ! !

Continuing, the therian alisphenoid bone is at times, but very rarely, developed entirely from membrane. Shall we call this variety of the bone 'ossis alisphenoidea membranogenica', to avoid confusion? Here, in the manner of Euclid, we write not Q.E.D., but "which is absurd".

Though we have arrived at an obvious *reductio ad absurdum*, it is none the less a fact that these satirically proposed designations have as much claim to recognition as some of those proposed for the cartilaginous bars, which have been found between the branches of the fifth nerve amongst the fish chondrocrania.

As a matter of fact, the therian alisphenoid bone develops, in the great majority of instances, first in cartilage, which may or may not be attached to the processus alaris. The frequency with which the initial centre of ossification appears in the little pellicle of cartilage, justifies the belief that the chondral origin is an inherited feature, and the rare intramembranous origin secondary.

The question then arises—what is the nature of the cartilaginous pellicle?

It has been demonstrated, that throughout the Craniata an alisphenoid bone may develop in the side wall of the embryonic chondrocranium. Whatever be its relations to the nerves and blood-vessels, it always presents the same relations to the surrounding bones.

It is probable that the complete cartilaginous cranium should be regarded as an elasmobranchian specialization, which has been handed on through the Dipnoi to the Amphibia. The evidence for this is the fenestrated nature of the early chondrocranium in all Craniata, and it would not be surprising that the phase of complete chondral encasement of the brain should have been subsequently eliminated from the life-history, just as the phase of complete gill-formation has been eliminated.

If this be granted, we still have ample evidence that there has been a reduction in chondrification in various directions, and in different ways in different groups. The outstanding "group" example of this is provided by the ophidian chondrocranium, whilst the outstanding example of structural reduction throughout the whole of the Craniata is provided by the reduction of the visceral arches.

When we attempt the determination of the nature of the cartilaginous pellicle in which the therian alisphenoid bone so constantly originates, we have, apparently, two fundamentally different alternatives. It may be studied under the assumption that it is a fragment of the first visceral arch or under the assumption that it is a fragment of the primordial cranium.

The second alternative is certainly the more reasonable; it envisages only a slight and gradual change in the relations of the cranial wall.

Both assumptions demand that we believe a cartilaginous structure may be fragmented, and only portion of it persist.

Both demand that we accept it as a possibility for the relation of the nerves and vessels to the cartilage, to have changed somewhat.

The first assumption, or epipterygoid theory, demands, in addition, that we believe the primordial cranial wall to have dissolved or become completely aborted in some way before the expanding brain in this one particular region, and its place to have been taken by a remnant of an evanescent visceral arch structure, which had then been incorporated completely into the cranial wall.

If we accept the epipterygoid theory, then we must be prepared to believe that the wall of the mammalian neurocranium gave way and retreated before the enlarging brain without any break in the continuity of inheritance of its component bones, except in the region of the alisphenoid. The auditory capsule was pushed out from the centre, the frontal and parietal bones expanded, the sphenoid bones in front of the alisphenoid have been enlarged and their internal concavity increased. Without any absorption and/or replacement, room has been made in every direction, except in the region of the alisphenoid. Why the exception?

Actually the strongest evidence that a new cranial wall has appeared in this region in the therian cranium, lateral to that of the lower Vertebrata, is the situation of the

so-called *pila antotica* of the Prototheria. Even were the relations of this to the nerves and vessels, and to the rest of the chondrocranium, precisely those of the *pila antotica* of the reptiles, it would not, in my mind, constitute as strong evidence in favour of the epipterygoid theory as that which opposes it. The *taenia clino-orbitalis* differs from the *pila antotica* in that it does not rise from the edge of the basal plate. Actually it is not a structure in the side wall of the cranium, but is situated within the cranial cavity. This, of course, is what should be found if the *cavum epiptericum* has been incorporated into the cranial cavity, but until that inclusion is proven on other grounds, the situation of the *taenia clino-orbitalis*, inside the cranial cavity, must continue to be regarded as definite evidence that it is not a true *pila antotica*, for that structure is definitely part of the primordial wall. Furthermore, its relation to two of the oculomotor nerves and to the *vena capitis lateralis* is not that of a *pila antotica*.

Without the evidence of a true *pila antotica* in the monotreme chondrocranium, the epipterygoid theory of the mammalian alisphenoid bone rests upon the single fact that the profundus nerve runs medial to it. When also the maxillary nerve runs medial to it, it must be regarded as having been developed from two primordia, the *processus ascendens* and the *ala temporalis*. What is the nature of the *ala*? Is it also a secondary structure like the *pila lateralis*, the lateral commissure, the *pila antotica secundaria* of the fishes and the *pila antotica spuria* of the birds, or is it part of the primordial cranium?

It seems absurd to maintain that it is not a secondary structure, if those others are to be so regarded, but then wherein does it differ from the so-called *pila antotica spuria* of the birds? Its relations to all the structures deemed to be important are precisely the same. They must surely be homologous structures, and the alisphenoid of the birds must be homologous with that of the mammals, and it seems impossible to deny that the alisphenoid of the bird is homologous with that of the crocodile and the ophidian.

If, however, we return to the more generally accepted belief—that the *ala temporalis* and *processus ascendens* are homologous structures—then, whichever way we look, we meet the same difficulty.

Whether we accept this view or my own contention—that the *pila antotica* and *ala temporalis* are homologous structures—we have to admit that the cartilage has grown back around, or otherwise come to lie medial to, in the one case all three nerves, and in the other two nerves, the maxillary and mandibular.

Rather than accept as possible, that the cartilage could grow around the three nerves, those who accept the epipterygoid theory, believe that it was destroyed altogether, that its place was taken by a structure, completely outside the brain case, which developed a bone having all the relations to the contiguous bones, which the primitive cranial bone had, and which had, in addition, to grow back around two of the nerves.

Rather than accept the simple gradual change, with its reasonable explanation, they have substituted a whole series of so-called secondary side walls, which come and go in a most bewildering and, if they be really secondary structures and not merely simple variations in the fenestration of the side wall, incomprehensible manner.

Why should they have been necessary? Can any one of those, who see the epipterygoid of the reptile in the alisphenoid of the mammal, offer any mechanical reason why the cranial wall could not have merely retreated before the expanding brain in this region, as in others? Can they offer any mechanical explanation of the complex changes they postulate in place of the simpler explanation?

#### IV. THE HOMOLOGY OF THE PARASPHENOID BONE OF THE ANAMNIOTA AND THE PTERYGOID BONES OF THE AMNIOTA.

The interpretation of these bones, which is adopted here, was first suggested by the author in 1916. It was, and is, believed that the evolution of the bones on the ventrum of the mammalian skull is most simply and understandably explained on the assumption that the paired pterygoids have been derived from the unpaired parasphenoid.

It is not intended to review again all the evidence in support of this thesis, which was advanced in previous contributions (Kesteven, 1916, 1919, 1925, 1931), but to

examine, mainly, the evidence on which the ossification on the under surface of the basisphenoid in the reptiles has been identified as the parasphenoid.

De Beer has accepted my interpretation, without acknowledgement, in so far as it applies to the mammals; but for him the lateral wings of the parasphenoid, which constitute the dorsal portion of the mammalian pterygoids, are those of the, so-called, tiny parasphenoid of *Lacerta* and of the reptiles generally. He believes the reptilian pterygoid to be represented by the ventral portion of the mammalian pterygoid, which, in some instances, ossifies separately.

In support of his identification of the "mammalian" pterygoid of *Ornithorhynchus* as the lateral wing of the reptilian parasphenoid, he points out that it forms the floor of the vidian canal, below the basisphenoid.

This line of argument appears to be quite sound, but it must apply with equal force in the chelonians and crocodiles, in both of which the vidian canal is supplied with a floor by the pterygoid bone.

Amongst the fishes the parabasal canal is enclosed between the parasphenoid and the cartilaginous basis cranii, or the bone developed from it.

In the Dipnoi, as represented by *Neoceratodus*, the parabasal canal is open ventrally in its posterior portion and enclosed entirely by cartilage, above the parasphenoid and pterygo-palatine bones, anteriorly.

There is no parabasal canal in any recent amphibian.

The parabasal canal is present, but is enclosed in different ways in different reptiles. In chelonians it lies either between the pterygoid and basisphenoid, or partly so, and partly in the substance of the basisphenoid. In the crocodile it lies between pterygoid and basisphenoid bones. In ophidians there is no parabasal canal. In *Lacertilia* and *Sphenodon* the canal lies entirely in the basisphenoid bone. At no stage in the development, does the tiny, so-called parasphenoid contribute to its formation. In birds the parabasal canal is enclosed by the basisphenoid bone throughout its length. The so-called basitemporal takes no part in its formation at any time during development.

In the Theria the vidian canal, anterior portion of the parabasal canal of the fishes and saurians, lies entirely in front of the sella and is closed below by the pterygoid bone.

I (Kesteven, 1940*b*) recently conducted a search for the parasphenoid in a saurian embryo. Although embryos of five lacertilians, two chelonians, four ophidians, and fifteen birds were studied, the parasphenoid bone was not found. In the majority of the forms studied, numerous stages of development were available for study, and in several, very complete series were studied.

Except in the ophidians it was found that in every saurian embryo the basisphenoid was ossified ectochondrally, and that in no single species was ossification observed to commence outside the perichondrium. In a number of species the ventral table of the basisphenoid presented the appearance of a membrane bone beneath the cartilage, but this ventral table was always situated between the perichondrium and the cartilage, or was in complete continuity with endochondral ossification from the first appearance of the bony spicules.

The so-called rostrum basisphenoidei, which has been regarded as the parasphenoidal precursor of the vomer, was demonstrated to be an ectochondral presphenoidal ossification, and not a membrane bone at all (Kesteven, 1941). This finding supports the conclusions of Parrington and Westoll (1940) that the mammalian vomer was not derived from the parasphenoid of the lower tetrapods.

The ossification of the basisphenoid of the Ophidia is endochondral. The cartilage ossifies throughout its whole thickness from two symmetrical centres of ossification, and thence spreads through the whole of the cartilage. No dorsal and ventral tables are formed first as in the rest of the saurians.

It has been generally agreed that the Ophidia have no parasphenoid bone.

If the ventral ossific centre of the basisphenoid in the generality of the saurians be really a parasphenoid bone, as contended by Gaupp and his followers, then its complete absence from the ophidian developmental history is strange, and difficult of explanation, but if it be merely a ventral centre of ossification, then we are presented with merely a

slight variation in the manner of ossification of the one bone, a comparatively insignificant phenomenon, paralleled in a number of other instances.

Throughout the bony fishes and in all the recent amphibians, certain of the muscles of mastication arise from the parasphenoid bone. In all the recent reptiles certain of these same muscles arise from the pterygoid bones. Reduced in size, some of these same muscles arise from the pterygoid bone in the mammals and marsupials.

If it be a fact that the dorsal portion of the mammalian pterygoid is derived from the parasphenoid bone, and the reptilian pterygoids are not, then the following changes call for explanation: The large and important parasphenoid bone of the Anamniota suffered almost complete extinction throughout the Sauria and the embolomorous amphibians, and its function as the bone of origin for certain muscles of mastication was taken over by the pterygoid bones. The tiny remnant, the so-called representative of the parasphenoid bone in the saurians and the Embolomeri lies, for the most part, behind the sella. In the therians the parasphenoid once more grows to some size and again functions to give origin to some of the same muscles of mastication, and it is found, for the most part, in front of the sella. In the fishes the lateral portion of the parasphenoid bone on each side, in front of the sella, forms the floor of the vidian canal. Throughout the amphibians, Embolomeri, reptiles and cynodonts, the parasphenoid takes no part in the formation of the vidian canal, but in the therians the bone once more takes on its old function of forming the floor of the canal.

This sequence of events presents a picture of discontinuity and reversal, culminating in a coincidental similitude of relations, for which there is no explanation whatsoever.

De Beer accepts Broom's explanation of the mammalian vomer—that it is derived from the parasphenoid (Broom, 1902). Therefore, under this theory of de Beer's, as under my own contention—that the anamniote parasphenoid is represented by the amniote pterygoids, it is necessary to recognize that the parasphenoid has been divided into three parts. If three bones may be accepted as representing the parasphenoid in the mammals, then also may that number be accepted as representing the bone in the Embolomeri, the Dipnoi and the reptiles.

It is generally agreed that the embolomorous amphibians had progressed along the main stream of evolution which produced the reptiles from the lower forms. So far had they progressed along this stream that it may be asserted, had we only the palatal structure of the skull to guide us, we should unhesitatingly have identified them as reptiles. Almost one might say that one is, even with all the evidence we have, called upon to decide whether they should be regarded as primitive reptiles or advanced amphibians.

In the dipnoans we may recognize a primitive parasphenoid which has been split up into three parts. I have previously shown, as conclusively as the nature of the problem permits (1931), that the palato-ptyergoids of the Dipnoi cannot be regarded as homologous with the pterygoids of the generality of the amphibians, but that they may be regarded as homologous with those of the Embolomeri.

There is no question that these bones, the palato-ptyergoids, have replaced the lateral wings and anterior portion of the parasphenoid of the fishes and the generality of the Amphibia. Though separated from it by a thin layer of cartilage, they lie beneath the vidian segment of the parabasal canal, and are applied to the base of the cranium.

That they may be accepted as the primitive form, the starting point, of the reptilian pterygoid bones, is beyond dispute. Whether they were or not, will probably never be conclusively proven.

They must be regarded either as new bones which appeared quite suddenly, without any relation to any other bones in the osteichthyid skull, as portions split from the parasphenoid.

This latter explanation appears the more reasonable, if we are prepared to believe that the parasphenoid may be so divided at all.

However, whatever be the true story of their origin, their enlargement as seen in the Embolomeri must be admitted as a possible, gradual and natural change.

No one doubts that the pterygoids of the Embolomeri are homologous with those of the reptiles.

Their position justifies the belief that they formed the floor of the vidian canal just as in recent reptiles, chelonians and crocodiles, in which the pterygoid bones meet one another in the mid-line and suture with the ventrum of the basisphenoid.

Thus, by way of the cynodonts and chelonians, with their large pterygoid bones, we pass to the Theria, and find the pterygoids meeting the basisphenoid and enclosing the vidian canal below, without any discontinuity or reversal in the process of the evolution.

The Lacertilia, Ophidia and Aves have clearly specialized away from the mammalian line. They present the pterygoid bones widely separated from the mid-line, and, therefore, not contributing to the parabasal canal. Recent Amphibia are members of a static branch which failed to progress. They retain the archaic parasphenoid of the fishes.\*

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\* The very complete lists of reference to literature relevant to the subject, which have appeared in recent publications, makes it unnecessary to provide a complete one here. Consultation of the lists in de Beer's book or in my own publications in the *Records of the Australian Museum* in 1931, will lead to the location of all the works referred to in this communication up to the date of those publications.

THE PHYSICAL EFFECTS OF HEAT ON THE TORBANITES OF  
NEW SOUTH WALES.

By J. A. DULHUNTY, B.Sc., Linnean Macleay Fellow of the Society in Geology.

(Seven Text-figures.)

[Read 29th October, 1941.]

*Introduction.*

As part of an investigation into the nature of New South Wales' torbanites, the effects of heat on physical properties have been studied; and the results obtained are recorded in the present paper. All the physical properties undergo certain changes, as the materials are unstable when heated; and some of the changes provide data which may be used in studying the relations between torbanites of different type and grade, and which may be applied in field problems for correlating outcrops, and characterizing deposits which occur on closely associated horizons. Other physical changes are important in connection with the commercial treatment of torbanite, as the processes involved depend on the thermal decomposition of the materials.

*Changes in Colour, Streak, Lustre, Texture, Flexibility and Surface Condition.*

The following description of changes which occur in the common physical properties of torbanite, as a result of heating at successively higher temperatures, is based on data obtained as follows:

Small slabs of torbanite, 10 mm. square and 5 mm. in thickness, were prepared from each of a number of specimens from different deposits. Eight of the slabs from each deposit were placed in an electric furnace with efficient temperature control and apparatus for recording the temperature accurately to within 2°C. The furnace was heated at the rate of 25°C. per minute to the first of the required temperatures, held constant for 5 minutes, then one slab was removed, and the temperature again raised at the same rate. This procedure was repeated commencing at 100°C., and slabs were removed at intervals of 100° up to 300°C., 50° up to 400°C., then 25° up to 475°C. Each set of slabs, together with an unheated member belonging to the same specimen of torbanite, was examined for changes in the physical properties.

*Colour.*—The normal colour of torbanite, as seen by sunlight reflected from a freshly fractured surface, varies from black to dark bluish-black, brown, greenish-brown and dark greenish-grey. In each deposit one colour predominates, independently of variations in quality or texture.

It was found that the colour of all torbanites becomes lighter on heating till a certain temperature is reached, then it changes quickly to black, as illustrated by the data given in Table 1 for torbanites from four deposits representing different types.

TABLE 1.

*Table showing colour change due to heating at different temperatures for torbanites from four different deposits.*

Temperature.	Baerami.	Barigan.	Glenn Davis.	Joadja.
Unheated	Dark greenish-brown.	Dark greenish-grey.	Dark bluish-black.	Dark greenish-black.
300°C.	Medium greenish-brown.	Dark greenish-brown.	Dark bluish-black.	Dark greenish-black.
350°C.	Light greenish-brown.	Medium greenish-brown.	Dark brownish-black.	Very dark green.
400°C.	Dark yellowish-green.	Medium brown.	Dark brown.	Dark green.
425°C.	Light yellowish-green.	Light brown.	Medium brown.	Greenish-brown.
450°C.	Dark greenish-brown.	Dark brown.	Dark brown.	Dark greenish-black.
475°C.	Black.	Black.	Black.	Black.

No colour change was noted in any of the torbanites below 300°C., while the Glen Davis and Joadja materials showed no change till the temperature reached 350°C. In all cases, after the change commenced, the colour became lighter with increasing temperature up to 425°C., then rapidly darkened to black over the remaining interval to 475°C. The sudden change, which occurs in the vicinity of 425°C., may be correlated with a strong evolution of vapour which occurs at about that temperature, and the darkening to black at 475°C. accompanies the coking process, which commences above 450°C., with the rate of heating adopted in these tests.

*Streak.*—The colour of the streak, or powder, of torbanite is much lighter than the colour of the fractured surface, and varies from light yellowish-white to dark brown. The heated slabs show very little change in the colour of the streak until 350°C. is reached, when it becomes slightly darker. The torbanites with light yellowish-white streaks, such as Baerami and Barigan, give a dark yellow or yellowish-brown streak after having been heated to 400°C.; and those with yellow or brown streaks such as Glen Davis, give darker browns. At 425°C. the streaks assume darker shades in all cases; and at 450°C. the Baerami and Barigan torbanites give dark brown streaks, while that of the Glen Davis material is almost black. The slabs heated at 475°C. are usually too soft and plastic to give a satisfactory test for streak; but those which can be scratched give black streaks.

It is of interest to note that the colour of the streak does not behave in the same manner as the colour of the fractured surface, which becomes progressively lighter between 300° and 425°C. The darkening of the streak above 425°C. is no doubt linked with the maximum evolution of vapour and rapid coking which occur above that temperature, and with which the sudden darkening of the fracture surface may be correlated.

*Lustre.*—The natural lustre of torbanite, observed on a freshly fractured surface at right angles to the bedding plane, varies greatly from a bright, silky sheen to a dull mat surface—all specimens from any one deposit having characteristic lustre which varies in degree only slightly. The torbanites with bright, silky lustre, such as Joadja and Coolaway Mountain, show very little change when heated at temperatures up to 350°C. At 400°C. the lustre is considerably reduced, and assumes a somewhat granular, or coarse-grained appearance. At 425°C. it is reduced to a dull, silky lustre, and, after heating to 450°C., it is quite dull. The torbanites with naturally-dull lustre, such as Glen Davis and Barigan, show no change up to 300°C.; but in the vicinity of 350°C. there is a tendency towards the development of a very dull, silky lustre. This secondary lustre disappears again when heated at 425°C.

The cause of bright, silky lustre in some torbanites, and its absence in others, has been explained by the writer (Dulhunty, 1939), and attributed to the fact that torbanites with bright lustre possess a particularly hard matrix, causing the particles of gelosite and retinosite to fracture, and exhibiting bright surfaces when the material is broken. The development of the secondary, bright lustre in naturally-dull torbanites at about 350°C., is explained by the fact that gelosite and retinosite become soft when heated, and the particles tend to fracture, although the matrix may be comparatively soft. The disappearance of this secondary lustre at 425°C. is due to the reduction of the naturally-bright lustre of gelosite and retinosite at that temperature. This also causes the torbanites normally possessing bright lustre to become dull at the same temperature.

*Texture.*—The natural texture of torbanite may be described as compact and homogeneous. The texture is not affected by heating until 350°C. is reached, at which temperature some torbanites develop small, short cracks parallel to the bedding plane. At higher temperatures, up to 475°C., these cracks become more numerous and slightly larger. Torbanites which do not develop cracks between 350° and 400°C. retain their compact texture at all temperatures up to 475°C.

It has been noted that the torbanites which develop cracks on heating, such as Glen Davis, Wollar, Tong Bong Mountain and Barigan, if heated until all volatiles have been driven off, will form porous cakes retaining the original shape of the pieces of torbanite, and exhibiting open cracks parallel to the bedding. Those which remain compact on heating to 400°C., such as Joadja, Coolaway Mountain, Baerami and Hartley, tend to

intumesce and undergo partial or complete fusion, if heated strongly, until all the volatiles have been removed, and the resulting cokes bear little or no evidence of the original shape of the pieces of torbanite, or the direction of their bedding.

*Surface Condition.*—The slabs of torbanite, heated in the manner already described, assumed a dark colour on the surface at 300°C. and became black at 400°C. Furthermore, it was found that powdered torbanite, light brown or yellow in colour, would change to dark brown at 350°C., and rapidly become black at 400°C. This surface colour change could not be connected with any of the changes in the other physical properties, most of which occur at considerably higher temperatures. For the purpose of investigating the cause of this colour change, powdered torbanite was placed in a glass tube, so arranged that it could be heated at different temperatures in a stream of gas or air. It was found that there was very little change in the colour of the powder at 375°C. when heated in a stream of coal gas or nitrogen; but it became dark brown at 350°C., and black at 400°C., when heated in air. Thus it was concluded that the surface colour change was due to a reaction between the torbanite and the oxygen of the air at comparatively low temperatures, indicating some form of oxidation. The small amount of air remaining in a closed furnace, or newly-charged retort, is sufficient to effect this surface oxidation. A thin transparent section was cut from a small slab of torbanite, which had been heated at 400°C. in a current of air for ten minutes. The section showed that the surface colour change, or oxidation effect, had penetrated to a depth of 0.75 mm. from the surfaces of the slab.

*Flexibility.*—The flexibility and toughness of torbanite are well-marked physical properties, particularly in the high-grade varieties. In investigating the effects of heat on these properties, the following procedure was adopted:

Five small rods of torbanite about 45 mm. in length and 5 mm. square, cut in a direction parallel to the bedding, were prepared from specimens from several different deposits. One unheated rod from each specimen was tested for breaking strength by supporting at two points, 40 mm. apart, and applying pressure at the centre, in a direction at right angles to the plane of bedding, by means of a vertical plunger forced down by a graduated lever carrying a sliding weight. The flexibility, or amount of bending of the rods at their breaking strain, was determined by means of a fixed vertical scale at the free end of the lever. Four additional rods from each specimen were then placed in an electric furnace, and the temperature raised at a rate of 10°C. per minute, and held constant for five minutes at 300°, 350°, 400° and 425°C. One rod from each specimen was withdrawn from the furnace after being heated at each of the foregoing temperatures. The rods were then cooled and tested for breaking strength and flexibility in the manner already described. The results obtained for three torbanites of different type and quality are recorded in Table 2.

TABLE 2.

Table showing the effect of heat on breaking strength and flexibility of three different torbanites.

Temperature.	Hartley.		Glen Davis.		Baerami.	
	Wt. lb.	Flex. mm.	Wt. lb.	Flex. mm.	Wt. lb.	Flex. mm.
Unheated.	13.2	1.4	13.75	1.6	14.5	0.96
300°C.	14.2	1.9	15.50	2.1	15.75	1.2
350°C.	12.5	1.9	16.50	2.5	16.25	1.4
400°C.	11.4	2.5	10.75	2.9	14.75	1.6
425°C.	8.5	5.7	9.00	3.5	2.95	3.2

It will be noted that there is not a great deal of difference in the breaking strength of the unheated rods, although the flexibility varies considerably. The breaking strength first increases as a result of heating, and then decreases. For the Glen Davis and Baerami torbanites it is maximum at 350°C., and the Hartley material at 300°C. In all cases there is a rapid decrease between 400° and 425°C. The increase in breaking strength at the lower temperatures is evidently due to greater toughness developed as a result of

softening of the gelosite, and the rapid decrease at temperatures above 400°C. appears to be caused by the breaking up of the matrosite structure.

The flexibility becomes greater between 300° and 400°C., and increases to a marked extent after heating at 425°C. This sudden increase is no doubt due to the breaking down of the matrosite structure, and the softening of the gelosite. The increase in flexibility of torbanite, after heating at 425°C., appears to be proportional to the amount of fusion which it undergoes during retorting. The Hartley torbanite fuses completely, Baerami undergoes partial fusion, and Glen Davis does not fuse at all. The increase in flexibility for these three torbanites is 4.30 mm., 2.24 mm., and 1.90 mm. respectively. The greater increase in the flexibility of torbanites, which fuse during retorting, can be connected with the nature of their matrosite, which causes the complete breakdown in structure during the more advanced stages of thermal decomposition.

#### *Changes in Micro-structure and Optical Properties.*

The general microscopical structure of New South Wales' torbanites has been described by the writer in a previous paper (Dulhunty, 1939). For the purpose of investigating the changes in micro-structure produced by heating at successively higher temperatures, sets of nine small slabs, 15 mm. square and 5 mm. in thickness, were cut from Baerami, Barigan, Glen Davis and Joadja torbanites. In each case the sets of slabs were cut from the same plane in the specimen, parallel to the bedding. Eight of the slabs from each deposit were heated in a manner similar to that adopted in the investigation of changes in common physical properties, as already described.

Thin transparent sections were prepared by grinding down an unheated slab from each torbanite, and those heated at the various temperatures up to 425°C. The two slabs heated at 450° and 475°C. were too soft and plastic to permit of grinding down in the usual manner; but it was found that very thin shavings could be cut from them by using a razor blade. These shavings, when mounted in Canada balsam, were suitable for microscopical examination. Sections could be prepared with a microtome; but the small grains of silica would damage the blade of the instrument.

The principal changes in micro-structure are illustrated in Fig. 1. Diagram B.1 represents a normal unheated section of Barigan torbanite; B.2, B.3 and B.4 are sections of the same material after having been heated at 400°, 450° and 475°C. respectively, and J.1 and J.2 are sections of Joadja torbanite heated at 450° and 475°C. It was found

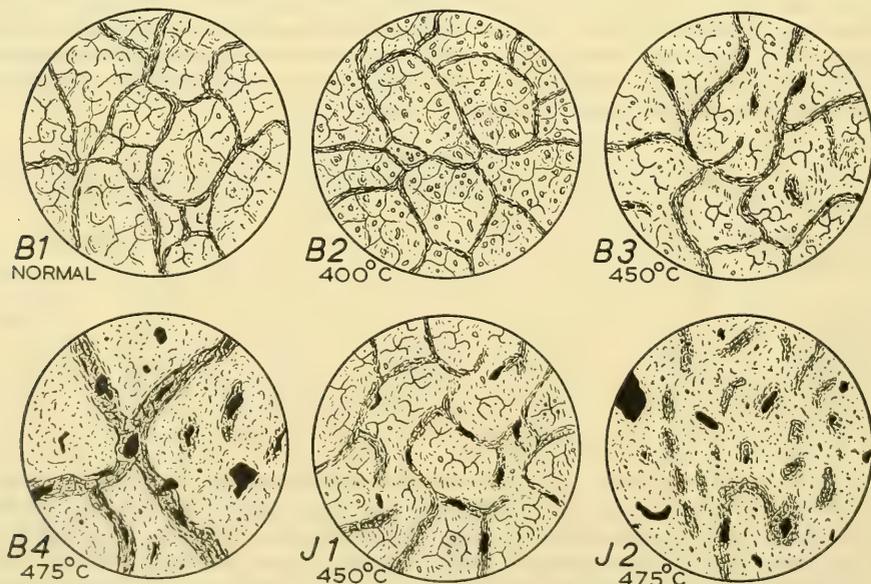


Fig. 1.—Thin sections of torbanite, showing changes in micro-structure after heating at different temperatures. B, Barigan; J, Joadja.  $\times 50$ .

that no change at all was produced in any of the torbanites by heating at temperatures up to 350°C. In the vicinity of 400°C. small spherical structures developed within the masses of gelosite and retinosite, and the cell structure became less evident (Fig. 1, B.2). The spherical structures have the appearance of minute bubbles, and it is possible that they may represent the first stages of thermal decomposition, or centres of incipient volatilization. After heating at 425°C., the bubble-like structures become less numerous, but considerably larger in size; and the cell structure commences to disappear, although each particle of gelosite retains its identity; and the enveloping films of matrosite remain intact. At 450°C. the spherical structures disappear almost completely, the particles of gelosite and retinosite commence to lose their original shape, and the films of matrosite become somewhat disorganized (Fig. 1, B.3 and J.1). Only traces of the original cell structure remain at this temperature, and the gelosite assumes a slightly clouded appearance. A temperature of 475°C., which causes rapid evolution of volatiles, completely destroys the original cell structure, and the particles of gelosite tend to coalesce. In certain torbanites, such as the Barigan material (Fig. 1, B.4), the films of matrosite lose their separate identity at this stage, and form a large open structure, which supports the mass of decomposing hydrocarbons. In other cases, such as the Joadja torbanite (Fig. 1, J.2), the matrosite breaks up and becomes distributed through the mass in the form of isolated fragments.

It is well known that certain torbanites, especially those of high quality, undergo partial or complete fusion during thermal decomposition, and flow as liquids before finally consolidating to form a coherent mass of coke. This property is common in material from Joadja, Hartley, Coolaway Mountain, Ulan and parts of the Baerami deposit, and causes difficulty in treatment by certain types of continuous retorts, the successful operation of which depends on the pieces of torbanite retaining their original shape, and producing non-coherent coke. The cause of this fusion in some types of torbanite is explained to a certain extent by the difference in the behaviour of the matrosite above 450°C. The fusion of the Joadja material illustrated in Fig. 1 is accompanied by the breaking up of the matrosite into small isolated fragments, which allows the decomposing gelosite and retinosite to flow as a liquid. In the case of the Barigan torbanite, which does not fuse during retorting, the structure of the matrosite is only partially disorganized, and the broken films appear to unite, or coalesce, forming a supporting skeleton, which prevents the semi-liquid mass from actually flowing. The cause of the different behaviour of the matrosite in each case is difficult to explain. The relative amounts of gelosite, retinosite and matrosite present, and the size of the particles, are much the same in both the Barigan and Joadja torbanite, although the latter gives a greater yield of oil. This indicates some fundamental difference in the nature of the oil-producing constituents in each material. Furthermore, the Joadja torbanite possesses a bright, silky lustre, while the Barigan material is dull. According to the explanation already discussed, for the presence of bright lustre, this means that there is a difference in the hardness of the matrosite in the two types of torbanite. Thus the different behaviour of the matrosite in each case appears to be due to differences in the nature of the matrosite and the oil-producing macerals, rather than variations in the quantity of these constituents.

*Optical Properties.*—Certain of the optical properties of the gelosite and retinosite undergo changes when torbanite is heated. The anisotropic nature of these constituents, previously recorded by the writer (Dulhunty, 1939), is not affected by heat till the temperature reaches the vicinity of 400°C., when the power of double refraction is reduced, and the polarization laminae become less distinct. Only a trace of double refraction remains at 425°C.; and it completely disappears after the material has been heated at 450°C.

The refractive index of gelosite and retinosite is not affected below 350°C., but it increases when torbanite is heated at higher temperatures. The values for unheated gelosite lie between 1.536 and 1.550, and for retinosite between 1.545 and 1.558. After heating at 450°C., the refractive index of gelosite increases to the vicinity of 1.570, and of retinosite to about 1.590. At 475°C., which is well within the zone of thermal decomposition, the values for gelosite and retinosite increase to about 1.650 and 1.680 respectively.

The natural colours of gelosite and retinosite, as seen by transmitted light, become slightly lighter at temperatures up to 425°C., then commence to assume darker shades at higher temperatures. After heating at 475°C., when the matrosite structure breaks down, and the decomposing mass tends to flow, the gelosite and retinosite remain translucent, but become very dark brown in colour. It will be noted that both the reflected and transmitted colours of the translucent constituents behave in a similar manner, becoming lighter up to 425°C., and then darker with increasing temperature.

*The Relation between Expansion and Temperature.*

The writer has already described special apparatus devised for the accurate determination of linear expansion in torbanite, and noted that the amount of expansion varies in different directions in relation to the bedding plane (Dulhunty, 1941). The coefficient of expansion varies greatly for specimens of different quality in any one deposit, and also for specimens of the same quality from different deposits. In any one specimen, however, it is always maximum at right angles to the bedding, and minimum in a parallel direction.

To consider, in the first place, the behaviour in the direction normal to the bedding: Expansion occurs immediately the temperature is raised above that of the atmosphere, and continues to the point of collapse, when the structure of the torbanite breaks down, and coking commences—usually between 450° and 475°C. The relation between the amount of expansion and temperature varies for torbanites from different deposits. Fig. 2 illustrates this relation for specimens from six deposits representing the main variations in type among the New South Wales' torbanites. The standard method used

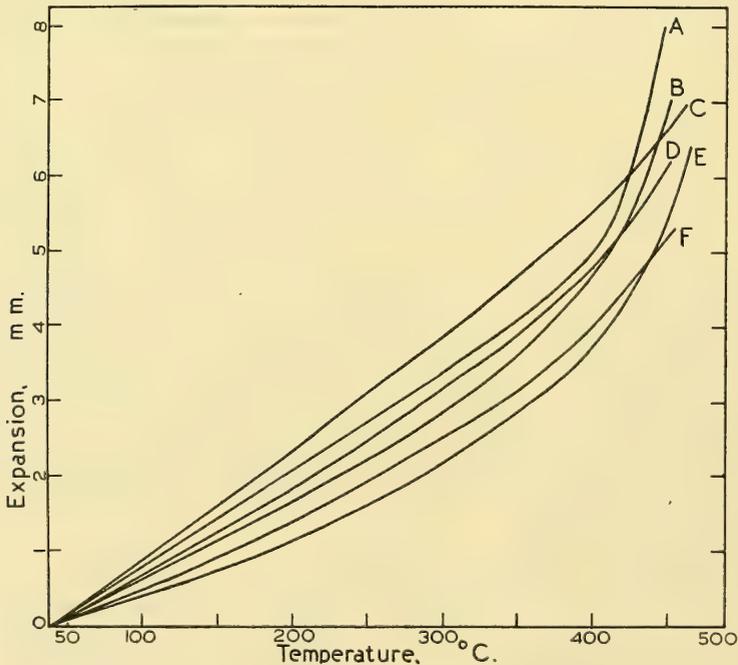


Fig. 2.—Curves showing relation between temperature and expansion, in direction normal to bedding, for six different torbanites. Lettering of curves: A, Airly; B, Coolaway Mt.; C, Glen Davis; D, Joadja; E, Baerami; F, Barigan.

in obtaining the data for these curves consisted of increasing the temperature at a uniform rate of about 10°C. per minute, and keeping it constant for five minutes at intervals of 100°C., where readings of the expansion were made. In each, the expansion is more or less proportional to temperature up to 300°C. Between 300° and 400°C. it is proportional for all specimens except Baerami, Barigan and Coolaway Mountain, which

show a greater rate of increase in expansion. Above 400°C. the rate of increase is much greater in all cases, giving a curve approximating to a hyperbola, especially for Baerami and Coolaway Mountain. The Airly material shows a sudden change in the rate of increase in the vicinity of 400°C. In no case has a curve been obtained, for a direction normal to the bedding, in which the rate of increase has fallen off with increase in temperature. The actual amount of expansion at the point of collapse, between 450° and 475°C., varies from 2 to 20 per cent., but usually lies in the vicinity of 10 to 15 per cent. Some portions of the Glen Davis and Airly deposits have given results between 18 and 20 per cent.

In directions parallel to the bedding the relation between expansion and temperature approximates more closely to a direct proportion, and the change in the rate of increase of expansion at high temperatures is much less marked than in the case of the direction normal to the bedding. Fig. 3 illustrates the relation between temperature and expansion in parallel directions for specimens from the six deposits mentioned above (note that the scale used for expansion in Fig. 3 is twice that used in Fig. 2). The

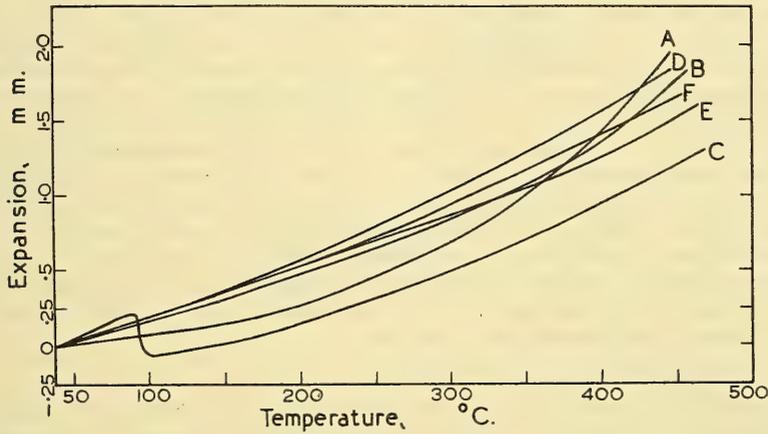


Fig. 3.—Curves showing relation between expansion and temperature, in directions parallel to bedding, for six different torbanites. For lettering of curves see Fig. 2.

curves for Barigan and Joadja are very close to a direct proportion; but the Airly and Coolaway Mountain materials show a greater rate of increase at the higher temperatures.

If the curves obtained for the expansion-temperature relation in each direction are compared (Figs. 2 and 3), it will be noted that there is no constant relation between the forms of the two sets of curves. This difference between the amounts of expansion in each direction is best indicated by quoting ratios obtained by dividing the amount of expansion in the normal direction by the amount parallel to the bedding, at different temperatures. Table 3 gives such ratios at three different temperatures for torbanites from eight deposits, including the six for which expansion curves have been discussed.

TABLE 3.

Table showing ratios of expansion in normal direction to expansion in parallel direction at different temperatures.

Specimen.	300°C.	400°C.	450°C.
Baerami .. .. .	2.8	2.7	3.2
Glen Davis .. .. .	8.0	5.8	5.9
Barigan .. .. .	3.6	3.1	3.5
Joadja .. .. .	3.6	3.1	3.6
Coolaway Mountain .. .. .	3.9	3.5	4.0
Airly .. .. .	5.7	3.4	4.2
Tong Bong Mountain .. .. .	5.5	4.7	4.8
Wollar .. .. .	6.0	4.2	4.9

The value of the ratio varies from 2·7 to 8·0. In each case the value at 300°C. is higher than at 400°C., but at 450°C. it may be either higher or lower than at the first two temperatures. There is a general tendency for the torbanites of highest quality to have the lowest values, but this does not hold good in all cases, as the value for Baerami is lower than that for Coolaway Mountain, although the latter is of much higher quality. In general, however, the specimens from Glen Davis, Airly, Wollar and Tong Bong Mountain are of lower quality than the other deposits shown in the table, although they possess the highest values for the ratio.

The actual amount of expansion at the point of collapse for parallel directions seldom exceeds 5 per cent., and usually lies between 3 and 4 per cent. Baerami and Airly torbanites expand to almost 5 per cent. at 450°C., while Tong Bong Mountain and Wollar torbanites possess an expansion of 3·2 per cent., and Glen Davis 3 per cent. Actually the limits of variation of total expansion, at any temperature parallel to the bedding, are much smaller than those for the normal direction.

The more or less proportional relation between rate of increase in expansion and temperature in parallel directions was obtained for all deposits tested, with the exception of Glen Davis. This material behaves in a most unusual manner. When heated it expands until the temperature reaches 80°C., then it actually contracts, while the temperature rises above 120°C., remains practically constant to the vicinity of 140°C., and then continues to expand at a normal rate proportional to the temperature up to 450°C. Tests have been made on specimens taken from various positions in the seam, between the top and the base, and all exhibit the same phenomenon. The amount of contraction which takes place between 80° and 120°C. is as much as 1·3 per cent. of the original length, and represents up to 16 per cent. of the total expansion at 450°C. As yet no satisfactory explanation has been found for this unusual behaviour. The only other known change, which occurs in torbanite between 80° and 120°C., with which it could be connected, is the loss of hygroscopic moisture; but other torbanites containing greater amounts of moisture than the Glen Davis material do not show any tendency to contract between the temperatures concerned.

#### *The Development of Permanent Deformation when Heated.*

As a result of carrying out expansion tests on numerous specimens of torbanite from fourteen different deposits, it was found that permanent expansion normal to the bedding, and permanent contraction in a parallel direction, resulted from heating in every case. In the standard method adopted for examining this property, rods of torbanite 40 mm. in length were cut from each specimen, both parallel and normal to the bedding. Each rod was heated to 38°C. and its length determined; then heated to 100°C. at the rate of 10°C. per minute, and held at constant temperature for 5 minutes; the expansion measured and then cooled at the same rate to 38°C., and the length again determined. This procedure was repeated with the same rod at temperatures of 200°, 300°, 400° and 500°C.; the amount of permanent linear deformation caused by heating to each successive temperature, and the total expansion at that temperature, being obtained from the two readings taken each time. From these results diagrams can be constructed for each torbanite, showing the behaviour in directions normal and parallel to the bedding, when heated successively to the temperatures mentioned above. Fig. 4 is the diagram obtained for the Coolaway Mountain torbanite. The curves A and B indicate the amount of expansion at any particular temperature, in normal and parallel directions, respectively; and the cooling curves from different temperatures in each case are shown by broken lines. If a rod, cut either parallel or normal to the bedding, is heated to any one temperature, and cooled repeatedly, it will expand and contract each time along the cooling curve from that particular temperature.

The amount of permanent expansion developed, normal to the bedding, at 450°C. varies considerably for torbanites from different deposits. Some of the torbanite from the Wollar deposit develops as much as 11 per cent. of the original length, while the Glen Davis and Barigan materials seldom develop more than 3·5 per cent. and the majority of the torbanites lie between 4 and 7 per cent. Parallel to the bedding, the amount of permanent contraction normally lies between 1·5 and 2·5 per cent. of the original length, some of the Joadja material developing as much as 3 per cent.

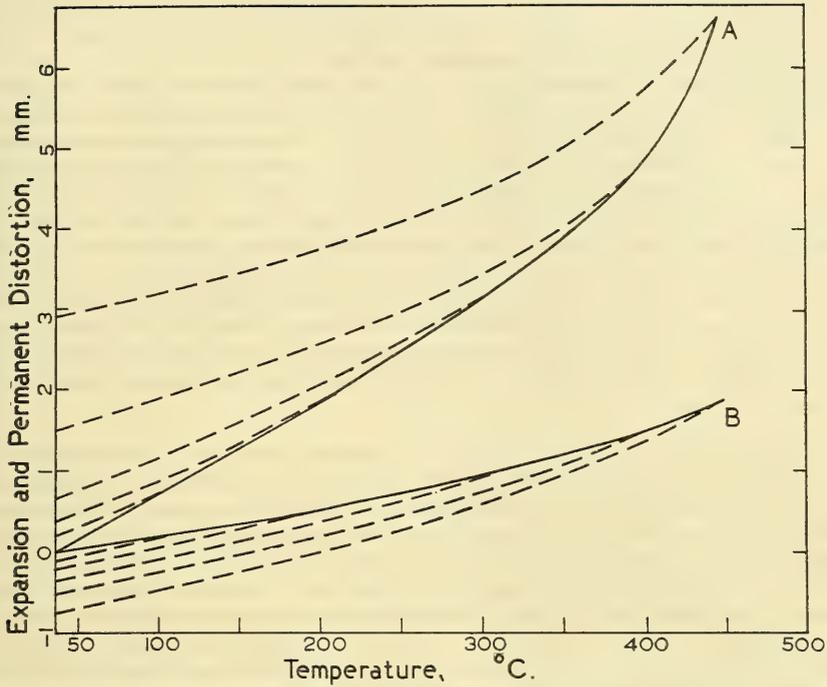


Fig. 4.—Diagram showing development of permanent deformation at different temperatures for Coolaway Mountain torbanite. A, normal to bedding; B, parallel to bedding.

The relation between the amounts of permanent expansion and contraction, developed in normal and parallel directions, respectively, for specimens from different deposits, is best illustrated by means of a series of curves obtained by plotting the amounts of linear deformation against the temperatures at which they are developed for the different torbanites. Fig. 5 shows a number of curves obtained in this manner. In directions parallel to the bedding, a certain amount of permanent contraction is developed at all temperatures up to 300°C., and in most cases up to 450°C.; but there are several exceptions such as Airly, Tong Bong Mountain and Glen Davis in which the amount of

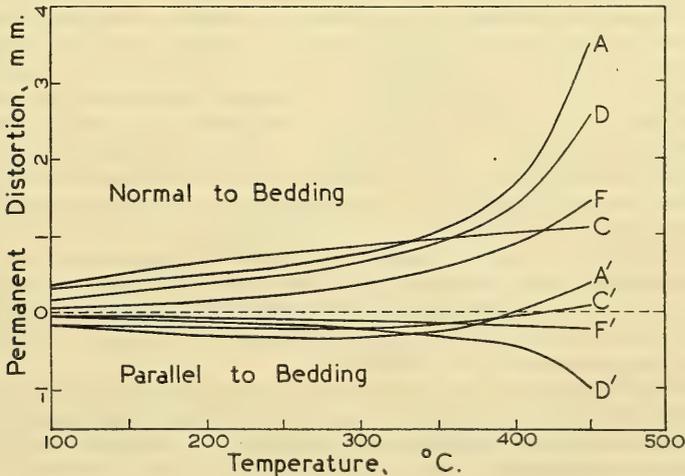


Fig. 5.—Diagram illustrating development of permanent deformation, normal and parallel to bedding, at different temperatures. For lettering of curves see Fig. 2.

permanent contraction is reduced when the temperature rises above 300°C., and at 450°C., a small amount of permanent expansion may result. This is illustrated by the curves for Glen Davis and Airly torbanites in Fig. 5.

The Airly material develops permanent contraction to 300°C., where it represents 1 per cent., then it diminishes to 400°C., at which temperature the rod on cooling returns to its original length; finally, at 450°C., 1 per cent. of permanent expansion is developed. This, however, is unusual; normally the rate of increase of permanent contraction becomes greater between 300° and 450°C., although in the case of Barigan torbanite, it remains constant above 400°C. For the direction normal to the bedding, Fig. 5 illustrates the rapid development of permanent expansion at temperatures up to 100°C., then a rate of increase more or less proportional to temperature up to 350°C., after which it becomes much greater to 450°C. The Glen Davis torbanite is the only exception, its rate of increase remaining proportional from 200° to 450°C. Parallel to the bedding, the rate of increase of permanent contraction is approximately proportional in all cases to 300°C., above which it may decrease, increase, or remain constant, as already discussed.

#### *Possible Causes of Expansion and Permanent Deformation Phenomena.*

The linear expansion of torbanite at temperatures up to 400°C. is due to the same causes as those which produce expansion in most solids when heated. The differences in amounts of expansion, in directions normal and parallel to the bedding at any given temperature, are evidently due to the fact that each minute, disc-shaped particle of gelosite expands to a greater extent in the direction of its short axis than it does in the plane of its longer axes. This property may be a result of the fact that the small masses of gelosite, each representing a colony of unicellular algae, were compressed to flat disc-like shapes when the deposits were first buried by the deposition of overlying sediments. The flattening of the masses indicates that the pressure, during the earlier stages of burial, was greatest in a vertical direction, and considerable strain must have been caused within each mass of gelosite. During the later stages of consolidation, after thick deposits had accumulated above the torbanite beds, the pressure was probably hydrostatic, and did not cause uneven strains. Thus the present shape of the gelosite discs, and their power of greater expansion at right angles to the plane of their longer axes, probably developed during the early stages of consolidation, when pressure distribution was uneven.

The phenomenon of permanent linear deformation, produced by heating torbanite at temperatures up to 350°C., may be due to one of several causes. As already described, it is always positive in the direction normal to the bedding, and negative in the parallel direction. The main cause appears to be a result of some physical effect rather than a chemical change, and the increase in deformation is roughly proportional to temperature up to 350°C.; and in some cases a greater amount is produced below 200°C. than between 200° and 350°C. Above 350°C., the deformation is influenced by chemical changes, as will be discussed later. The physical cause of permanent deformation, at lower temperatures, may be the fact that the deposits were compressed by forces operating at right angles to bedding during the early stages of consolidation, and that each mass of gelosite was subjected to stress directed inwards in the direction normal to the bedding and outwards in the parallel direction. If such stresses still exist in the torbanite, there may be a tendency for each mass of gelosite to regain its original shape when heated, which would result in the shorter axes of the discs becoming longer, and the longer axes becoming shorter. This would cause positive and negative deformation in directions normal and parallel to the bedding respectively. Consequently the development of permanent deformation may be due to the lasting effects of unequal pressures which existed when the deposits were first buried.

An alternative explanation is suggested by the arrangement of the gelosite discs, and the possible effects of strain due to heating in the expansion measurements. The small discs lying parallel to the plane of the bedding are pressed close to each other with their margins overlapping. While the temperature is being increased, the material on the outside of the test rods would expand before that at the centre, causing internal tensional strain and external compression. These strains may cause the discs to slide

over each other, where their margins overlap, to a very small extent. Such movement would have the effect of reducing the dimensions parallel to the bedding, and causing an increase at right angles, as actually occurs when permanent deformation develops. The films of matrosite would not expand so much as the gelosite, causing a certain amount of internal strain. This may also contribute to a sliding or shearing movement between the discs of gelosite.

*The Evolution of Volatiles at Different Temperatures.*

The principal chemical changes which occur during the thermal decomposition of torbanite are accompanied by the evolution of volatile hydrocarbons. For the purpose of investigating the part played by chemical changes in the effects of heat on the physical properties of torbanite, determinations were made of the relative amounts of volatiles driven off at different temperatures, in the case of specially selected specimens, which had been used in studying changes in physical properties. In the standardized method used for making these determinations, rods of torbanite were used, 40 mm. in length and 7 mm. square, contained in porcelain boats. Rods were used in preference to powdered material, as the conditions would approximate more closely to those involved in examining changes in physical properties, and to the fragmentary torbanite used in commercial treatment. The rods were inserted into an electric furnace, preheated to the required temperature, allowed to remain at constant temperature for 10 minutes, then removed and weighed after cooling. Determinations were made at intervals of 50°C., from 150°C. to 600°C. Specimens from eight different deposits were tested, together with a specimen of ordinary coal. The results, from 350° to 600°C., for three of the torbanites representing the general limits of variation, and the specimen of coal, are illustrated graphically in Fig. 6.

It will be noted that the torbanites give up their volatiles over a particularly small range in temperature compared with coal. It was found that the torbanites with the steepest curves between 425° and 500°C. contain the smallest amounts of humosite (vascular plant remains), give the highest yields of oil, and exhibit the greatest tendency to fuse during retorting. In these respects the three torbanites concerned in Fig. 6 possess the following properties:

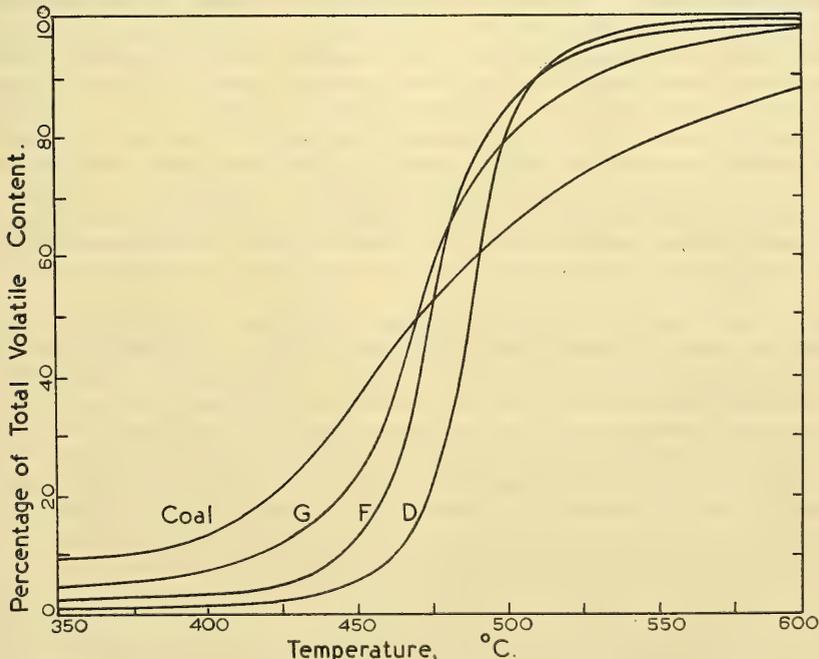


Fig. 6.—Diagram showing evolution of volatiles at different temperatures. For lettering of curves see Fig. 2. G, Wollar.

- Curve D. Joadja. Oil yield, 170 gallons per ton. Complete fusion during retorting. Only smallest trace of humosite.
- Curve F. Barigan. Oil yield, 130 gallons per ton. No fusion during retorting, but fragments show slight tendency to cohere. About 1.5 per cent. of humosite.
- Curve G. Wollar. Oil yield, 80 gallons per ton. No fusion during retorting, and no coherence of fragments. About 3 per cent. of humosite.

It is not suggested that the small differences in the amounts of humosite are responsible for the different rates at which the volatiles come off, or the oil yields, but rather that these three features, together with the tendency to fuse during retorting, all accompany changes in the nature of the gelosite, retinosite and matrosite, and were determined by differences in the environmental conditions, which existed during the deposition of the deposits. The varying steepness of the curves in Fig. 6, representing the temperature range of the evolution of volatiles, suggests a gradation in type, or the existence of an homologous series, from coal to a torbanite such as the Joadja material.

*The Relation between the Evolution of Volatiles and Physical Changes.*

The results illustrated in Fig. 6 indicate that no chemical changes of any consequence occur in torbanite at temperatures below 350°C.; and it is not until about 425°C. is reached that the more important changes, connected with thermal decomposition, begin to take place. Thus it may be concluded that any changes occurring in physical properties below 350°C. must be due entirely to physical effects, while changes which take place above 400°C. may be due to either chemical or physical effects, and in some cases to both.

The changes in natural colour, to lighter shades with increasing temperature up to 425°C., are evidently the result of physical effects, while the sudden darkening of the colour above that temperature is due to chemical changes. In the case of changes in the colour of the streak, it is evident that physical effects have no influence, and the darkening, which takes place above 350°C. must be of a chemical nature. The reduction of lustre above 350°C. appears to be the result of chemical change, while the development of secondary lustre above 300°C. in naturally-dull torbanites is due to physical softening of the gelosite. The texture of torbanite is not affected by heat below 350°C.; and the development of cracks parallel to the bedding in some torbanites is probably associated with the evolution of volatiles. In connection with the increase in flexibility, and decrease in breaking strength of torbanite when heated, it is evident from the results given in Table 2 that physical causes operate up to 350°C., after which chemical causes play an important part. The changes which occur in micro-structure are of a physical nature; but the fact that no alteration takes place until 400°C. is reached suggests that they are caused by chemical changes in the gelosite, especially above 450°C. The refractive index of gelosite is not affected by heating at temperatures below 350°C.; and it retains its powers of double refraction until a temperature of 425°C. is reached. Consequently these properties are only changed by chemical alteration of the gelosite.

The curves shown in Fig. 2, illustrating the amount of expansion at different temperatures, indicate a more or less proportional relation up to 350°C., above which temperature the curves become much steeper. It is evident that the expansion below 350°C. is due to physical causes; and the greater rate of increase at the higher temperatures suggests the additional influence of chemical changes. This is particularly marked in the case of Airly torbanite, while the Glen Davis material shows only slight increase due to chemical effects. The development of permanent deformation is another property in which the varying influence of chemical changes above 350°C. is particularly well marked, as illustrated by the curves in Fig. 5. The positive deformation of Airly, Joadja and Barigan torbanites increases rapidly in the vicinity of 400°C., while the curve for Glen Davis is not affected at all. In directions parallel to the bedding, the deformation of Airly and Glen Davis torbanites changes from negative to positive in the vicinity of 400°C., when the influence of chemical changes is superimposed on the physical effects, while the negative deformation for Joadja increases, and that for Barigan remains unchanged.

*The Application to Field Problems of the Relation between Expansion and Volatile Content.*

It has already been mentioned that the linear expansion of torbanite varies greatly for specimens of different quality in any one deposit, and also for specimens of the same quality in different deposits. If the expansion at 300°C., in the direction normal to the bedding plane, is determined for a number of specimens of varying quality from the same deposit, it is seen that there is a relation, within certain limits of variation, between the amount of expansion and the volatile content. When the specimens are arranged on a diagram in which the expansion in millimetres is plotted against the percentage of volatile content, it will be found that their positions approximate to a straight line, and the limits of deviation form a zone in which all specimens, from the particular deposit concerned, will fall. Furthermore, it has been found that the zones characteristic of different deposits, occupy different positions on such a diagram, and the width of each zone also varies. A diagram of this nature, showing the zones for five different deposits, is illustrated in Fig. 7. It will be seen that the gradient, width, and position of each zone, are different.

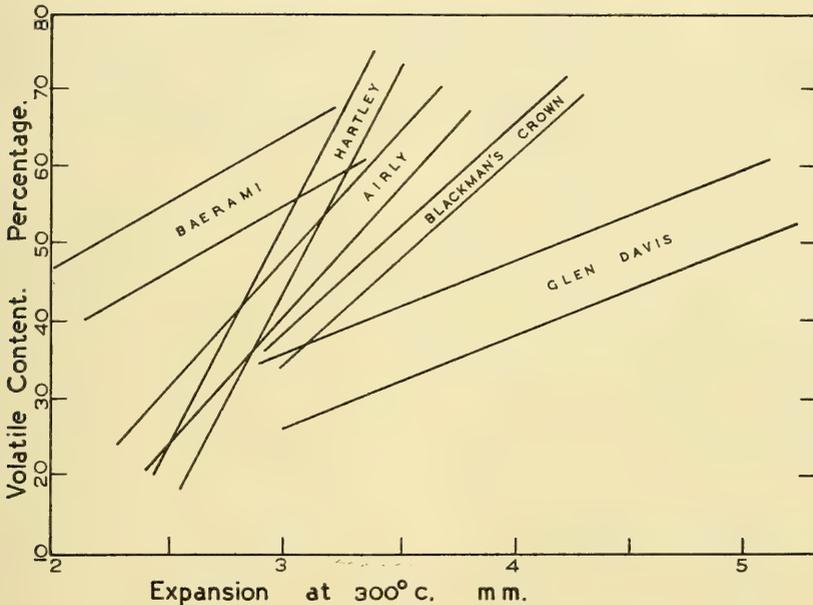


Fig. 7.—Volatile-expansion relation diagram, showing characteristic zones of different deposits.

Once the zone for a certain deposit has been established, the diagram can be used for estimating the quality of additional specimens, within specific limits of error, by determining the amounts of expansion at 300°C. A more important use of such diagrams, however, is to be found in their application to field problems, involving the correlation of outcrops, and the characterization of deposits occurring on closely associated horizons in the same area.

In such cases as the outcrop of torbanite on approximately the same horizon in two valleys, separated by a range capped with Triassic sandstone, the correlation of the outcrops can be effected by determining the volatile-expansion relation for specimens of varying quality taken from either side of the range. If they fall within the same zone, it may be concluded that they belong to the same deposit, which is therefore continuous between the two valleys. If, on the other hand, they fall into two separate zones, it is evident that the outcrops do not belong to the same horizon, and the two separate deposits must overlap in the concealed area between the valleys. Stratigraphical determinations, based on the above method, revealing the presence of one or more deposits in a confined area, may have important results in connection with available

reserves of torbanite. Such situations are not uncommon in the Western Coalfield of New South Wales; for example, three deposits of torbanite occur on separate horizons within 70 feet of strata at Narrow Neck near Katoomba.

Expansion-volatile relation diagrams may also be used in prospecting an area for torbanite deposits. If all the drift blocks, found in the streams draining a certain area, are tested for expansion and volatile content, and plotted on a diagram showing the zones for known deposits, the presence of any unknown deposit, which has been dissected by the drainage system concerned, will be revealed immediately.

*Acknowledgements.*

The writer wishes to make grateful acknowledgement of financial assistance made available by Sir George Davis for the construction of apparatus used in obtaining many of the data embodied in this paper. He also acknowledges the cordial co-operation of National Oil Pty. Ltd. at Glen Davis, and Standard Oil Co. at Baerami; and helpful discussion with members of the Geology Department, Sydney University, and the Geological Survey of New South Wales.

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ON THE ANATOMY AND FUNCTIONAL ADAPTATION OF THE THORAX AND PECTORAL GIRDLE IN THE WALLAROO (*MACROPUS ROBUSTUS*).

By W. BOARDMAN, Australian Institute of Anatomy, Canberra.

(Plate xii; nine Text-figures.)

[Read 26th November, 1941.]

The work which forms the subject of this paper arose, in the first instance, out of the plan of these laboratories to test by experimentation, such as were thus approachable of the several theories which have been advanced to explain departures from normal thorax shape commonly observed in man. Whilst it is agreed that a proportion of these defects may result from the action of hereditary factors, at least some are, in all likelihood, attributable to physiological irregularities of a nutritional origin—rickets, for example—which lend themselves more readily to investigation by the experimental method. Conclusions drawn from work on the common quadrupedal laboratory animals can be of only limited value, owing to the different architectural and mechanical factors encountered in the thorax and pectoral girdle. One or other of the higher primates would, of course, provide the necessary combination of requirements, but the difficulties attendant upon their acquisition and maintenance, suggested the advisability of turning to the endemic marsupial fauna for a suitable substitute. After a preliminary survey it was decided to examine in further detail the wallaroo (*Macropus robustus*) as representative of the widely spread family Macropodidae. In the kangaroos is presented the peak of development in the saltatory mode of progression, so much so that the use of the fore limb as an adjunct to locomotion has been greatly curtailed. Thirteen ribs, of which seven find attachment to the sternum as in man, a clavicle, and posture which is, to say the least, "semi-erect", go far to provide the structural features demanded. Moreover, the kangaroo can in a limited degree raise the hand above the head (Mackenzie, 1918).

In the first part of the paper an account of the anatomical findings is recorded, together with comparative notes so that it becomes, in effect, a summation of present information on the points investigated.\* Howell (1926) has directed attention to the fact that "the internal anatomy of all but a few mammals has been woefully neglected" except "the rarer and more spectacular" species. This is as true of the Australian Marsupialia as of the mammals of any other country, and it is intended that the observations herein recorded should comprise a contribution towards elimination of these defects in our knowledge. In the second portion, data established in the systematic account are used as a basis for discussion in obtaining an evaluation of the status and significance of the various features of the wallaroo chest (and, as far as justified, of the macropod chest in general), comparisons being drawn with the conditions found in typical quadrupeds on the one hand and the higher primates on the other.

The vexed question of terminology has been met by using, whenever possible, names in current use in works on human anatomy. For structures which have no equivalent in man the names used by Leche (in Bronn) were adopted. For descriptive purposes the kangaroos have been regarded as quadrupedal so that, generally, terms such as "ventral" and "dorsal" are used in preference to "anterior" and "posterior" respectively. In the matter of taxonomic nomenclature, no good purpose would at present seem to

\* I have not had access to Vrolik on *Dendrolagus inustus* (Ontleedkundige Naspringen omtrent *Dendrolagus inustus*. *Verh. Akad. Wet. Amst.*, v, 1857), nor to Meckel's volumes on vertebrate comparative anatomy.

be served by referring to animals described by previous workers under any name other than that which they themselves used.

Three specimens (a young and an adult female and an adult male) were dissected as the basis of the investigation. They were collected at Gudgenby in the Australian Capital Territory. Where necessary to clarify specific points dissection of other mammals has been carried out, and full use made of the extensive collections housed in this Institute. Dimensions recorded in the text refer to conditions as found in the adult male, unless stated otherwise, and all illustrations are from this specimen.

#### *General Form of the Chest.*

The general form of the wallaroo chest (Plate xii) is that of a truncated cone flattened along the dorsum from the angles of the ribs medially. From the second rib caudally the side walls of the thorax are remarkably straight, the greater or lesser degree of convexity common in mammals being absent. The first costal arch is so much smaller than the second that between them the tapering is more marked than in the rest of the chest. At the level of the first rib there is also a difference in the shape of the cross-section bounded by the costal arches, namely, from a bluntly pointed heart-shape to the quadrilateral outline characteristic of the superior aperture. In the ventral wall the first, second and third segments of the body of the sternum are approximately in the same straight line. The craniodorsal slope of the manubrium is more accentuated in accord with the small size of the first rib and its cartilage. Similarly the fourth sternebra, and to a greater extent the xiphisternum, change direction so that the rate of increase of the dorso-ventral diameter of the thorax is lessened.

Internally the chest displays the usual well-marked groove bounded by the dorsal curve of the ribs and the forward projection of the vertebral bodies; behind the fifth rib the groove gets shallower owing to increasing obtuseness of the angles of the ribs. As living specimens could not be obtained for examination, no details are available relative to the curvature of the spine. The intercostal spaces widen from the dorsal attachment of the rib ventrally, and the second, third and fourth spaces are conspicuously wider than the first and those caudal of them.

The *superior aperture* of the thorax is in the form of a quadrilateral, the dorsal side of which is made up of the body of the first thoracic vertebra and the neck of the first rib on each side, the lateral boundaries by the shafts of the ribs, and ventrally there are the rib cartilages and the intervening manubrium sterni. The U-shaped section bounded by the vertebra and ribs, slopes caudo-ventrally; at its junction with the rib the rib cartilage makes a right angle and is then directed medially and cranially to its union with the manubrium. The manubrium sterni is drawn out into a peak cranially, the summit of which is opposite the junction between the last cervical and first thoracic vertebrae. The *inferior aperture* is comparatively large and heart-shaped in cross-section.

Figures for the *thoracic index*\* (see Table 1), based on a series of three preserved specimens (a young and an adult female and an adult male), are in each case less than 100, indicating a chest which is flattened from side to side. The series is too small for significance to be attached to the well-marked differences which are present in the indices of the three individuals. However, it is noteworthy that in the male the index is less than in the adult female, this being the opposite of the condition usually found in man (Cunningham, 1937). It will be seen that the value given for the adult female points to a chest almost circular in cross-section, whilst, as was to be expected, the young female (in this case about half grown) displays a chest form in which there is a considerable degree of side to side flattening.

Additional measurements were carried out on each specimen at the level of the second and fourth sternocostal articulations, and the figures so obtained treated in

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\* In making measurements for the calculation of the thoracic index "the diameters are taken at the level of the xiphisternal joint". The expression here used,  $\frac{\text{Transverse diameter} \times 100}{\text{Dorso-ventral diameter}}$ , is that of Fourmentin, who appears to have been first to define the index (Davenport, 1934); other workers have used the reciprocal form.

the same way as in arriving at the standard thoracic index, thus giving numerical expressions for change in cross-section. In the adult male and female there is little or no alteration in the index at the various levels, indicating a straight-sided thorax, the diameters of which increase proportionally craniocaudally. In the young example, however, the changes in value of the index show a chest which has relatively a greater degree of side to side compression cranially than caudally.

TABLE 1.

*Lengths (in cm.) of the transverse and dorso-ventral diameters of the wallaroo thorax at various levels. The data obtained from measuring at the level of the seventh sterno-costal joint represent the thoracic index.*

Specimen.	Young ♀.			Adult ♀.			Adult ♂.		
Sterno-costal articulation ..	2	4	7	2	4	7	2	4	7
Transverse diam. ..	6.0	7.5	8.5	10.5	12.0	14.0	11.5	12.5	14.0
Antero-posterior diam. ..	10.0	11.5	12.5	11.5	13.0	15.0	13.0	14.25	16.0
Trans. diam. × 100 ..	60	65	68	91	92	93	88	88	88
Dorso-ventral diam.									

The *axilla* in the wallaroo is merely a narrow chink which lies between the thorax and medial side of the root of the arm; it is filled by areolar and fatty tissue. Dorsally the lateral and medial walls converge and meet at a very acute angle. The lateral wall is formed by the proximal part of the biceps, the scapula and subscapular muscle, the medial wall by the muscles clothing the chest. A floor to the space is provided by the pectoral muscles, the anterior fold being composed of the superficial pectoral and the narrow edge of the pectoralis quartus, the caudal border of the latter extending beyond the caudal border of the former. Caudally the axilla is sealed, partly by the latissimus dorsi, partly by the overlying skin muscle (*panniculus carnosus*).

A large lymph gland takes up much of the axillary space; it lies within the anterior fold and when the contents of the axilla are being examined, this gland effectively conceals from view the various nerves and vessels.

#### *The Skeleton.*

Owen's (1877) account and excellent figures of the skeleton of *Macropus rufus*, a near relative of *Macropus robustus*, leave little to be desired, and the agreement between the two falls short only in minor details. For the present purpose, however, some further comment is required on the ribs and their cartilages.

The *ribs* comprise thirteen pairs, the most common marsupial and invariable macropod number. Of them the seventh is the longest, there being a progressive decrease in size both above and below this level; the reduction is more marked cranially and terminates in a first rib which is small and stout. The curvature of the ribs in their dorsal half presents a gradually increasing radius from before backwards, so that the hollow formed by the forward projection of the vertebral bodies and the backward sweep of the ribs, gets gradually shallower. The first rib presents an external surface which is practically straight from the tubercle to the ventral extremity. A craniocaudal flattening is markedly in evidence in the first five ribs, particularly in the region of the angle; this is general in kangaroos (Leche, p. 333).

There are likewise thirteen pairs of costal *cartilages*. That of the first rib is quadrilateral in outline, short and stout, and twice as wide as those further back; it is ventrally convex and the extremity of the rib is markedly widened for its reception. A continuation from the craniomedial angle of the cartilage coalesces with a projection of the manubrium sterni on its lateral border caudal to the sternoclavicular articulation. The remaining rib cartilages are normal. A gradual increase in the length of the cartilages occurs from the second to the fifth, so that their costochondral articulations lie along a line which is only slightly inclined away from the sternum. With the sixth the increase is greater, so that the line becomes directed caudodorsally at an angle of

about 115° with the sternum. The seventh and eighth cartilages are about the same length, the ninth and tenth progressively shorter, the eleventh, twelfth and thirteenth merely pointed tips attached to the floating ribs.

The upper seven cartilages are attached to the sternum. As mentioned above, the first is implanted on the lateral aspect of the manubrium sterni. The second to the fifth is each in contact with two segments of the sternum, and the sixth articulates with the border of the last segment of the body of the sternum towards its caudal end. The seventh pair is attached one on each side of the bluntly-pointed extremity of the same segment as the sixth, so that the two joints, while not in contact medially, are included in a common joint capsule; the line of articulation of the xiphisternum with the body passes across these two joints dorsally. With the exception of the first, which is a synchondrosis, the chondrosternal articulations are diarthroses. The capsules are tight and the joint cavities small; there is no enlargement of the articular ends of the cartilages. The cartilages of the "vertebro-chondral" ribs, namely, the eighth, ninth and tenth, are held in position by the internal intercostal muscles, together with a more superficial layer of muscle which runs from the end of one cartilage to the cartilage above, the direction of the fibres being diagonally across those of the underlying intercostals (see description of intercostals, p. 359). There are no joints between adjacent cartilages. In one specimen (Fig. 4) the tip of the eighth cartilage on the right side is bound to the seventh cartilage by a continuity of their perichondrium. Owen (1841, p. 398), referring to kangaroos, comments that: "The cartilages of the six false pairs are long and bent towards the *sternum*, but do not join it, nor are they confluent, but have a gliding motion one over the other." Carlsson (1914), however, says that the three ribs following the seventh unite with it in *Dendrolagus dorianus*. The three pairs of floating ribs which lie free in the flank have cartilaginous portions which appear as short pointed tips.

#### *The Muscles of the Shoulder Girdle and Upper Arm.*

*M. supraspinatus*.—The supraspinatus which is much smaller than the infraspinatus arises by fleshy fibres from most of the supraspinous fossa medial of the neck of the scapula, the investing layer of deep fascia, and the suprascapular ligament. It proceeds laterally beneath the acromion to be inserted by mostly fleshy fibres onto the greater tubercle of the humerus. From its insertion the muscle is bisected along the direction of its fibres from the superficial to the deep surface by an aponeurotic partition traceable for about 3 cm. on the deep surface, less superficially; many fibres on each side of this division are inserted onto it in bipennate fashion. The insertions of the supraspinatus and infraspinatus are continuous on the greater tubercle; lateral to the great scapular notch their adjacent borders are in close contact and there is a considerable intermingling of fibres.

Innervation is by the suprascapular nerve.

*M. infraspinatus*.—The infraspinatus is about twice as bulky as the supraspinatus and arises from the infraspinous fossa of the scapula, the area of origin extending to the neck of the bone and also from the strong fascia which invests it. It is inserted, partly fleshy, partly tendinous, onto the great tubercle of the humerus, the insertion as mentioned above being continuous with and behind that of the supraspinatus.

Innervation is by the suprascapular nerve which proceeds from the supraspinous to the infraspinous fossa by way of the great scapular notch.

According to Meckel (mentioned by Wilson, 1894) and Carlsson (1915), in most marsupials the supraspinatus is larger than the infraspinatus. In all the macropods, except *Hypsiprymnodon* (Carlsson, 1915), the reverse seems to be general. Macalister (1870) says that in the Great Kangaroo the two muscles are about equal. The infraspinatus is also the larger in *Phascolarctos*.

*M. omohyoideus*.—In the wallaroo this muscle takes origin, as usual, from the hyoid bone and is inserted onto the superior margin of the scapula immediately medial of the attachment of the serratus ventralis. There is no central tendon.

*M. deltoideus* (Fig. 1).—The relationships and attachments of the deltoid are similar to those found in man. It has an extensive origin from the ventral border of the lateral two-thirds of the clavicle (except at its acromial end), the lateral border of the acromion, the whole length of the spine of the scapula and the fascial investment

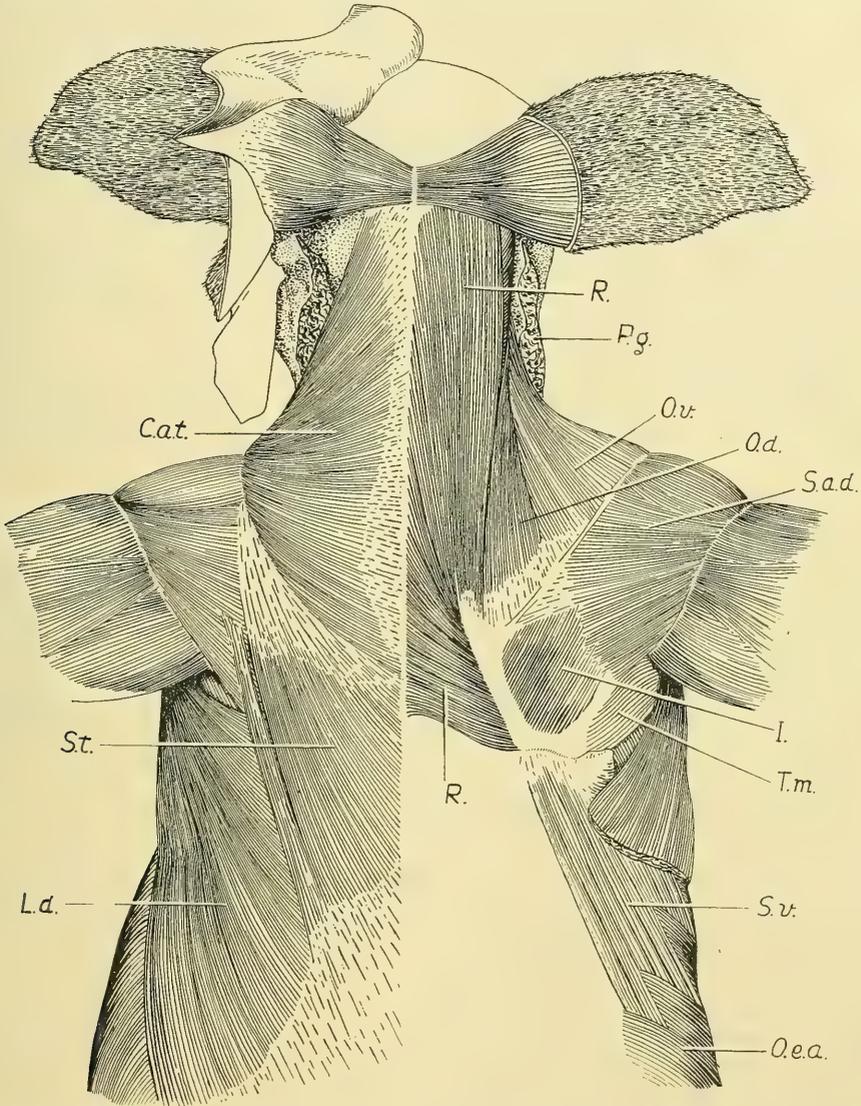


Fig. 1.—Dissection of the back to show the vertebro-scapular muscles. The trapezius has been removed from the right side. *C.at.*, clavo-acromiotrapezius; *I.*, infraspinatus; *L.d.*, latissimus dorsi; *O.d.*, pars dorsalis of omo-cleido-transversarius; *O.e.a.*, obliquus externus abdominis; *O.v.*, pars ventralis of omo-cleido-transversarius; *P.g.*, parotid gland; *R.*, rhomboides; *S.a.d.*, spino-acromio-deltaoides; *St.*, spintrapezius; *S.v.*, serratus ventralis; *T.m.*, teres major.

of the infraspinatus. The origin is by fleshy fibres from the clavicle, acromion and lateral two-thirds of the spine of the scapula; along the medial third of the spine of the scapula attachment is obtained through a flat triangular tendon which lies upon and adheres closely to the fascia over the infraspinatus. Dorsally the fleshy fibres terminate along a line parallel with the vertebral margin of the scapula and passing through

the point where fleshy is replaced by tendinous attachment on the spine. It will thus be seen that the deltoid covers only the lateral two-thirds of the infraspinatus. Insertion is to the deltoid tuberosity in the proximal half of the humerus. The portion originating from the clavicle is bound to its neighbour only by loose connective tissue, and is readily separable from the clavicle down to the insertion on the humerus; its lateral border is overlapped slightly by the adjacent border of the rest and larger section of the muscle. It will be seen, then, that in the wallaroo the deltoid is divisible into a *spino-acromiodeltoideus* and a *clavodeltoideus*.

The axillary nerve supplies the whole of the muscle.

The deltoid in marsupials is often bipartite or tripartite. In the Macropodidae, however, there is usually a high degree of fusion of the constituent parts to form a continuous muscle. This unsegmented arrangement has been recorded for *Macropus major* and *M. minor* (Cuvier and Laurillard), *M. bennetti* (Macalister, 1870), *Dendrolagus* (Carlsson, 1914) and *Petrogale* (" . . . fused as in man"—Parsons, 1896). Windle and Parsons (1898) imply a like condition in *Macropus rufus*, but Carlsson (1915) describes a tripartite muscle in *Hypsiprymnodon*. In the wallaroo, then, we have an intermediate condition in which fusion is incomplete.

*M. teres minor*.—The teres minor is small and for most of its length in contact with the infraspinatus. Its origin, partly fleshy, partly tendinous, is from the fascia investing the caudal border of the infraspinatus opposite the long head of the triceps. Insertion, by fleshy fibres, is to the humerus immediately distal of the insertion of the infraspinatus.

Innervation is through the circumflex nerve.

A teres minor is present throughout the Macropodidae, usually fused to some extent with the infraspinatus.

*M. teres major*.—The teres major arises from a short length of the axillary margin of the scapula immediately lateral to the inferior angle, from a narrow adjoining area of the subscapular fossa and on the dorsal side of the scapula from the fascia investing the infraspinatus. In other words, at its origin the muscle is excavated to embrace the borders of the scapula and infraspinatus. Insertion is under cover of the biceps and by a broad flat tendon about 18 mm. wide which is attached to the medial lip and floor of the distal portion of the inter-tubercular groove of the humerus; the tendon lies deep to part of the narrow tendon of the latissimus dorsi (see description of this muscle *infra*). A few fibres are inserted onto the subscapularis.

The nerve to this muscle arises from the lower of the posterior cords of the brachial plexus.

*M. subscapularis*.—Except for a small area at the inferior angle, the subscapularis arises by fleshy fibres from the subscapular fossa generally. The tendon of insertion is broad and powerful and is attached to the lesser tubercle of the humerus; some deep fibres directly overlying the humerus have a fleshy insertion.

Innervation is by the subscapular nerve which enters the muscle on its ventral surface near the humerus.

*M. biceps brachii*.—The fleshy belly of the biceps is readily separable into two components, viz., a deep, flattened spindle-shaped portion and a bulkier superficial layer which is broad and thick. The latter is concave on its deep surface where it fits closely over the former, and the proximal half is compressed where it is traversed by the pectoral mass. The origin is at first sight single, taking place by what appears as a narrow flattened tendon arising from the tip and medial aspect of the coracoid process of the scapula and including a small portion of the margin of the glenoid cavity; it lies entirely outside the capsule of the shoulder-joint and proceeds distally along the intertubercular groove of the humerus. By careful dissection, however, the partly-fused components of the tendon may be resolved into a superficial layer which provides attachment for the superficial section of the biceps, and a narrower deep layer connected with the fibres of the deep division of the muscle. Insertion is double, the deep layer (gleno-ulnar) being attached to the coracoid process of the ulna, the superficial (coraco-radial) to the radial tuberosity.

The nerve to the biceps arises from the outer cord of the brachial plexus and appears as a branch of the outer head of the median.

Division of the belly of the biceps, either partly or completely, occurs throughout the Marsupialia; in the Macropodidae separation is complete. The tendon of origin may be fused or double. In the Great Kangaroo and Bennett's Wallaby (Macalister, 1868) and in *Macropus rufus* (Windle and Parsons, 1898) the origin is double; in *Petrogale* (Parsons, 1896), *Dendrolagus* (Carlsson, 1914) and *Hypsiprymnodon* (Carlsson, 1915) it is single. Parsons (1896, p. 696) comments that "Meckel's account of the muscle in the Great Kangaroo seems to correspond with my own", that is, possesses one broad head. In all, the tendon is outside the capsule of the shoulder-joint.

*M. coracobrachialis*.—In the wallaroo the coracobrachialis is a very small muscle, for the most part obscured by the head of the biceps and the coraco-clavicular ligament. As in all macropods hitherto examined, including *Hypsiprymnodon* (Carlsson, 1915), it represents a coracobrachialis brevis (rotator humeri). It arises by a narrow tendon from the coracoid process of the scapula medial of, and closely bound to, the coraco-clavicular ligament and medial border of the tendon of insertion of the biceps. Its belly is narrow and flattened and crosses the tendon of the subscapularis to a fleshy insertion on the "surgical" neck of the humerus just distal of the lesser tubercle.

*M. dorso-epitrochlearis*.—This muscle is small and thin. It rises from the medio-distal portion of the ventral border of the latissimus dorsi, that is, from its fleshy part. The fleshy fibres fall short of the olecranon and are inserted into the superficial fascia which invests the medial surface of the brachium.

#### *The Muscles of the Thorax.*

*M. panniculus carnosus* (Fig. 2).—The cutaneous muscle of the trunk in close contact with, and exposed by removal of the skin, is well developed and occurs in the form of a thin sheet, which envelops most of the thorax and abdomen caudal of the level of the scapula. This muscle has, with a few exceptions, received scant notice by workers on Australian marsupials, so that data for comparison are lacking. Tobler (1902), however, has given a good account of the condition as met with in *Macropus bennetti* (= *Wallabia rufogrisea*\*) and my observations on the wallaroo show a similar arrangement. The terminology used by Langworthy (1932) seems the most suitable for descriptive purposes. He designates as the *cranial portion* the section of the muscle inserted with the pectorals onto the humerus, and as the *caudal portion* the fibres which have both origin and insertion in superficial fascia. In the wallaroo the cranial and caudal portions of the cutaneous muscle form a continuous layer, the cranial division, however, being identifiable not only by its humeral insertion, but also by its greater thickness.

The cranial portion is triangular in shape, the apex being directed towards the axilla, into which it proceeds as a narrow strip of muscle 1 cm. or less wide, under cover of the lateral border of the superficial pectoral. The cranial-most fibres cross the inferior angle of the scapula and are joined by a narrow slip of muscle inserted into the fascia covering the deltoid and probably representative of the omo-brachial section of the cutaneous muscle, such as occurs, for example, in the horse. From the axilla the fibres diverge, proceeding in a general dorsocaudal direction and find attachment to the skin along a line some 3-4 cm. lateral to the tips of the spinous processes and through a thin aponeurosis about 4.5 cm. long. The cranial border of this portion of the muscle is thicker than the rest, and within and in the vicinity of the axilla, is readily separable into two layers, each of which provides a distinct lamina to the double tendon of insertion onto the humerus. The most superficial fibres provide the deeper layer of the tendon, presenting in consequence a twisting similar to that which appears in the pectoralis major of some mammals (man and the wallaroo for instance). The more superficial layer of the tendon lies deep to, and is for the most part so closely blended with, the tendon of the pectoralis quartus that separation is impracticable.

\* See Iredale and Troughton, A Check-list of the Mammals Recorded from Australia. *Aust. Mus. Mem.*, vi, 1934, p. 49.

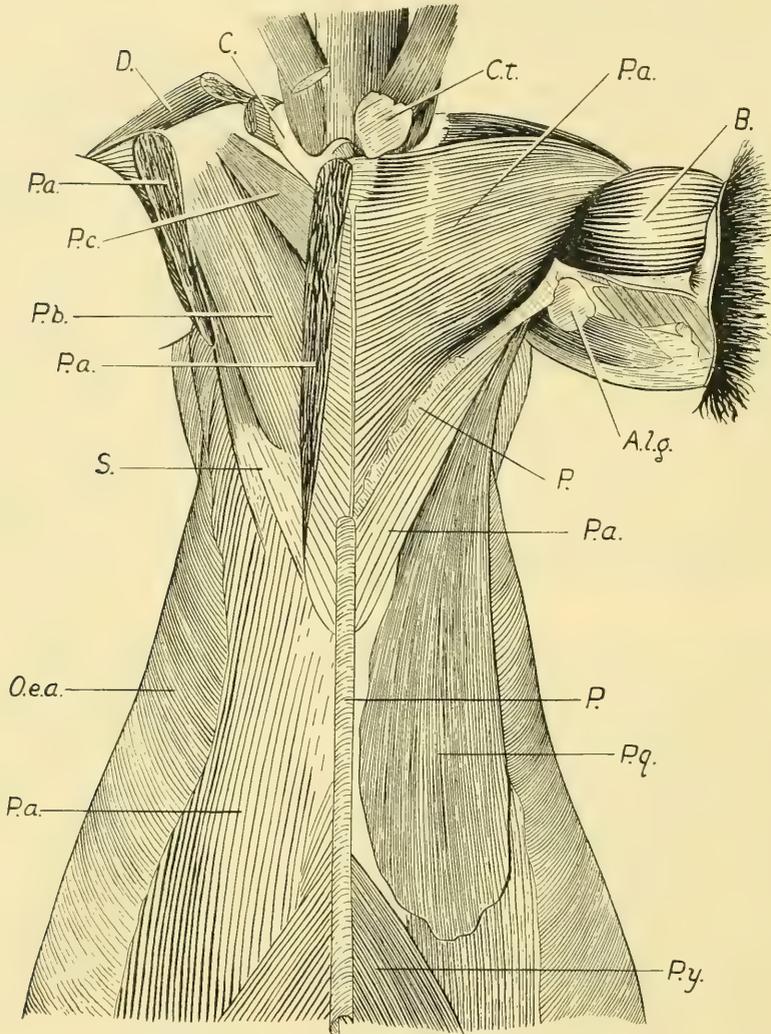


Fig. 2.—The pectoral group of muscles. On the right side most of the superficial layer has been removed. *A.l.g.*, axillary lymph gland; *B.*, biceps; *C.*, clavicle; *C.t.*, cervical thymus; *D.*, clavodeltoideus; *O.e.a.*, obliquus externus abdominis; *P.*, cut edge of panniculus carnosus; *P.a.*,  $\alpha$  pectoral; *P.b.*,  $\beta$  pectoral; *P.c.*,  $\gamma$  pectoral; *P.q.*, pectoralis quartus; *P.y.*, pyramidalis; *R.a.*, rectus abdominis; *S.*, supracostalis.

The caudal portion of the muscle, though thinner than the foregoing, is much more extensive. Its origin is of considerable length, running from the axilla along an irregular line across and parallel with the fibres of the superficial pectoral to the mid-ventral line at the junction of the third rib cartilage with the sternum, thence, along the mid-ventral line as far back as a point about 10 cm. below the xiphisternum. Over the superficial pectoral the origin is from its investing deep fascia; in the mid-ventral continuation of the origin in the thoracic region it is from a narrow aponeurosis which unites the muscles of the left and right sides, in the abdominal region from the linea alba. The fibres sweep back describing a wide ventrally concave arc to their insertion on the fascia of the gluteal region and the skin covering the fold between the thigh and abdomen. Along the back the muscle is united to the skin at a distance of 3-4 cm. from the mid-dorsal line by a membranous aponeurosis continuous with that of the cranial portion; the aponeurosis is traceable back to the sacral region.

As in *Didelphys* (Langworthy, 1932), *Macropus bennetti* (Tobler, 1902) and other marsupials which have been investigated, innervation is through the anterior thoracic nerve. Two main branches are in evidence, the larger of which, accompanied by blood-vessels, proceeds caudally on a course not far lateral to, and parallel with, the sternum. The other enters the superficial layer of the double part of the cranial portion of the muscle near the commencement of its tendon of insertion.

*The Pectoral Group.* (Fig. 2.)

In the present unsatisfactory state of our knowledge of the homologies of these muscles in the lower mammals, the question of nomenclature can only be overcome by the use of what is at best a temporary expedient. Of the several alternatives which appear in literature, the symbols used by Parsons (1896) in describing the pectorals of *Petrogale xanthopus* seem least productive of misconception. In this nomenclature the superficial mass is designated  $\alpha$ , the caudal and cranial divisions of the deep layer  $\beta$  and  $\gamma$  respectively, whilst the muscle frequently referred to as the pectoralis quartus becomes  $\delta$ . Parsons suggested that the pectoralis  $\beta$  and  $\gamma$  together constituted a pectoralis minor. Earlier Cunningham (1882) and Windle (1889) had given the matter careful consideration and decided that the  $\beta$  division alone is homologous with the pectoralis minor; Leche agreed with this separation and the conclusion seems most in accord with present knowledge. The pectoralis major is then, regarded as made up of two layers, the  $\alpha$  and  $\gamma$  divisions as described below.

*a Pectoral.*—This, the superficial and most powerful part of the chest musculature, is triangular in general shape, thickest at the cranial end, the thickness diminishing gradually as the caudal border is approached. The cranial-most fibres are at right angles to the sternum as they proceed laterally to their insertion on the humerus; further back an increasing degree of obliquity is apparent, the most caudal fibres being sharply inclined to the mid-ventral line; a narrow strip of the muscle at the caudal end tends to be separable. The adjacent  $\alpha$  pectorals form a continuous fleshy sheet across the ventral aspect of the thorax; there is no sternal furrow and the thickness of the muscles is such that in preserved specimens the sternum is not readily palpable. Cranially the muscle is in contact with the clavicular portion of the deltoid, the caudal border of which fits into a groove in the cranial border of the pectoral. The  $\beta$  and  $\gamma$  divisions are not visible till the  $\alpha$  layer is reflected, the cranial border of which also overlies the origin of the sternocleidomastoid. Tough fibrous tissue binds it to the capsule of the sterno-clavicular joint and the medial end of the clavicle. Laterally the border of the muscle is rounded on account of the "twisting" undergone by the caudal fibres.

The  $\alpha$  pectorals have their principal origin in, and are separated by, a median fibrous raphe which is attached to the ventral face of the sternum, from the cranial tip of the manubrium to the junction between the third and fourth sternebrae. Further origin, which forms a conspicuous feature of the caudal end of the muscle, is from the underlying expanded membranous attachment of the supracostalis, by a small flattened tendon at the caudal angle of the pectoral, and cranial of this by two further successive broad laminae from the deep surface of the pectoral. No fibres could be detected arising from "the inner part of the clavicle" as recorded by Parsons in *Petrogale*.

The pectoral mass as a whole is inserted onto the lateral lip of the intertubercular groove of the humerus, from the greater tubercle distally along the shaft for about three-fifths of its length. The insertion of the  $\alpha$  division extends over about half of the total for the muscle group. It is noteworthy that the fibres of its caudal two-fifths are "twisted" in such a way that their attachment, which is by a thin flattened tendon, is deep to the rest of the muscle, and occupies the more proximal position on the humerus; for the most part the tendon is closely adherent to the overlying muscle. The fibres of the cranial portion are gathered together as a thickened, blunt, fleshy spearhead which has an insertion, mostly fleshy, but in part tendinous, onto the humerus medial to the insertion of the deltoid and continuous with the insertion of the caudal two-fifths (*v. supra*). Some of the superficial fibres are inserted onto the deep fascia of the arm. Distally the insertion is in intimate contact with that of the deltoid and also with the origin of the brachialis.

*β Pectoral*.—The  $\beta$  division of the pectoral group is a strong flattened strip, oval in cross-section and tapering slightly towards its insertion. Its origin is fleshy from the ventral aspect of the first sternebra and the second and third costal cartilages immediately lateral of the sternum; the caudal border of the muscle lateral of its attachment to the third costal cartilage is united to the broad tendon of origin of the underlying supracostalis. Insertion is to the humerus by a thin flattened tendon which is continuous distally with the proximal portion of the  $\alpha$  tendon (that is, from the caudal-most  $\alpha$  fibres) and extends on the humerus proximally to the limit of the pectoralis insertion.

*γ Pectoral*.—This is the short flattened strip of muscle which proceeds from the manubrium cranio-laterally towards the "surgical" neck of the humerus. The subclavius lies immediately deep to it and its cranial border is, for almost its whole length, in contact with the caudal border of the clavicle. The origin is by fleshy fibres from the ventral face of the manubrium sterni, caudal of the clavicular facet almost to the caudal extremity of the bone; a median ventral bony ridge separates the left and right  $\gamma$  divisions from each other. The muscle tapers to a narrow flat tendon of insertion which joins the humerus superficial to the tendon of the  $\beta$  division; at their insertion onto the humerus the proximal border of the  $\gamma$  tendon is some 7 mm. more distal than that of the  $\beta$  tendon.

*M. pectoralis quartus*.—This, the most caudal of the pectoral muscles, is spatula-shaped, thin generally (very thin at the caudal end) and tapers cranially. In a fully-grown specimen its medial border is overlapped by nearly the whole length of the caudal border of the  $\alpha$  pectoral. The caudal end is rounded and lies upon the rectus abdominis and may or may not encroach to a limited extent onto the cranial end of the pyramidalis; it approaches the mid-ventral line opposite the end of the body of the sternum, whilst the caudal limit is about opposite the middle of the xiphoid cartilage. Origin is from the aponeurosis of the obliquus externus abdominis which invests the rectus and pyramidalis. Insertion is by a thin narrow tendon which lies deep to the insertions of the other pectoral components and is attached to the humerus opposite the point where the  $\alpha$  and  $\beta$  tendons adjoin.

The greater portion of the pectoral mass, exclusive of the pectoralis quartus, is innervated by the lateral anterior thoracic nerve. The medial anterior thoracic nerve, equivalent to the middle and posterior pectorals of Windle (1889, p. 347), which receives a large branch from the first named, supplies principally the panniculus carnosus, but sends fine filaments to the caudal portion of the  $\alpha$  and possibly  $\beta$  pectorals. The pectoralis quartus receives its nerve-supply as a branch of the principal stem to the panniculus.

The whole pectoral system of muscles is supplied by branches of the anterior thoracic artery which leaves the axillary artery medial of the connection between the lateral and medial anterior thoracic nerves.

With the exception of *Hypsiprymnodon* (Carlsson, 1915) the quadripartite composition of the pectoral mass occurs in all macropods hitherto described, namely, *Aepyprymnus* (Windle, 1889), *Dendrolagus* (Carlsson, 1914), *Petrogale* (Parsons, 1896), *Macropus rufus* (Windle and Parsons, 1898); Cuvier and Laurillard have figured the condition in *M. major* (Plates exciii and exciv) and *M. minor* (Plate clxxxi). This complex arrangement occurs in other marsupials, for example, in *Cuscus* (Cunningham, 1882), and would seem to represent the highest degree of pectoral differentiation met with in the group.

*M. supracostalis* (Fig. 3).—The supracostalis (known also as the transversus costarum and rectus thoracis) is a thin strip of muscle about 3 cm. wide which runs from the side of the sternum dorsocranially to the first rib. It takes origin by a broad aponeurosis from the ventral aspect of the sternum just lateral of the mid-ventral line, the attachment extending between the levels of the third and sixth sterno-costal joints. A narrow slip of the aponeurosis on the caudal border of the muscle falls short of the sternum and is attached to the underlying rectus abdominis; similarly a few fibres from the cranial border are attached to the tendon of the rectus. Near the

sternum the extensive aponeurosis, which has an area approximately half of that of the whole muscle sheet, is only with difficulty separable from those portions of the rectus and the membranous investments of the internal intercostals which lie deep to it. Insertion is by fleshy fibres onto the outer surface of the first costal arch from just lateral to the sterno-costal joint for about three-quarters of the length of the rib and its cartilage. The supracostalis lies deep to the pectoral mass and scalenus posterior, superficial to the rectus abdominis, and is apparently in the same layer as the obliquus externus abdominis, but separated from it.

The supracostalis has received scant notice in marsupial literature. Macalister (1870) recorded it in the wombat and Tasmanian devil. The only account I have noticed of its presence in the Macropodidae is that of Parsons (1896) on *Petrogale*; his observations differ little from the condition seen in the wallaroo.

*M. subclavius*.—In the wallaroo the subclavius is a powerful, cylindrical muscle which arises from the cranial border of the cartilage of the first rib and is inserted along almost the whole length of the caudal surface of the clavicle. The fibres of insertion are confined to the clavicle, showing no disposition to form a sternoscapularis by extension onto the acromion process, such as occurs in a number of marsupials. The other macropods in which the muscle has been noted all show similar attachments and limitation.

The nerve to the subclavius arises from the front of the upper cord of the brachial plexus in the usual way. No connection was observed between it and the phrenic, such as is figured by Harris (1939).

*Mm. serratus anterior and levator scapulae*.—As is common in marsupials, these two muscles are in the same layer, forming a continuous sheet so that the exact boundary between them is difficult to determine. They will therefore be treated together as though comprising a unit.

Origin is from the transverse processes of the four hinder cervical vertebrae, and thence along the lateral aspect of the thorax by fleshy slips from the outer surface of the ribs as far back as the sixth. Its three caudal slips interdigitate with the three cranial-most slips of the origin of the obliquus externus abdominis. The fibres of the muscle are arranged fan-wise and converge to their insertion on the scapula. That section of the muscle which takes origin from the transverse processes of the fourth and fifth cervical vertebrae, is inserted onto the medial angle of the scapula and about 1.5 cm. of the contiguous superior margin. Slips from the fifth and sixth ribs are inserted onto the inferior angle, while the larger middle section of the muscle sheet occupies the costal aspect of the vertebral border of the scapula. The cranial border of the serratus abuts the cranial border of the omo-cleido-transversarius (*pars dorsalis*) which lies superficial to it. Except for two or three centimetres nearest the scapula the two borders are closely adherent and not readily separable, so that the superficial muscle appears as a fold of the serratus.

Parsons (1896) in his account of these muscles in *Petrogale xanthopus* apparently includes with them what is here described as the dorsal part of the omo-cleido-transversarius, that is: "The slip which rises from the transverse process of the atlas [and] is inserted into the inner third of the spine of the scapula." The condition here described for the wallaroo is typical of the arrangement in macropods.

*Mm. intercostales externi* (Fig. 4).—Cranial to the tenth rib the ventral limits of these muscles are either at or in the immediate vicinity of the union between the bony and cartilaginous sections of the ribs. In the case of the floating ribs, that is, the eleventh to the thirteenth, the muscle extends ventrally from the tip of the rib below to the rib above, the direction of the fibres being almost at right angles to that of the rib; in the space bounded by ribs twelve and thirteen, the external intercostal is merely a narrow slip.

On the ventral aspect of the thorax some of the muscles, especially those occupying the intercostal spaces cranial of the sixth rib, exhibit a tendency in adjacent muscles for the superficial fibres to be continuous by passing over the intervening rib. In this fashion some fibres may pass over a second rib in addition, thus forming a continuous

sheet associated with three external intercostals (cf., the arrangement in *Echidna*—see Leche in Bronn, p. 770). The anterior intercostal membrane is very thin.

In connection with the external intercostals mention must be made of a well-defined, continuous, fairly thick band of muscles which unites adjacent ribs at their angles. Fibres, the direction of which is with the long axis of the body, run from rib to rib similar in arrangement to the intercostal series; some fibres unite alternate angles. The band, which is superficial to the external intercostals, extends back to the space between ribs ten and eleven; it lies deep to the iliocostalis lumborum and iliocostalis dorsi and is in close association with their costal attachments. Medially, attachment to the ribs is continuous with the insertions of the levatores costarum. The components of this muscle band would appear to bear the same relationship to the external intercostals as the Mm. infracostales (Leche in Bronn, p. 770) probably do to the internal intercostals.

A further peculiarity associated with the external intercostal layer is seen in connection with the eighth, ninth and tenth of the asternal ribs (these correspond to the vertebro-chondral ribs in man, but are not united through their cartilages to the cartilage of the seventh rib). Each of the ribs mentioned is connected with its predecessor by a slip of muscle superficial to, and with fibres running diagonally across, the internal intercostals (Fig. 4). A similar arrangement has been recorded in the dog (Bradley, 1927).

*M. transversus thoracis*.—This takes origin from the lateral borders of the dorsal surface of the sternum from a point cranial of the union between the first and second

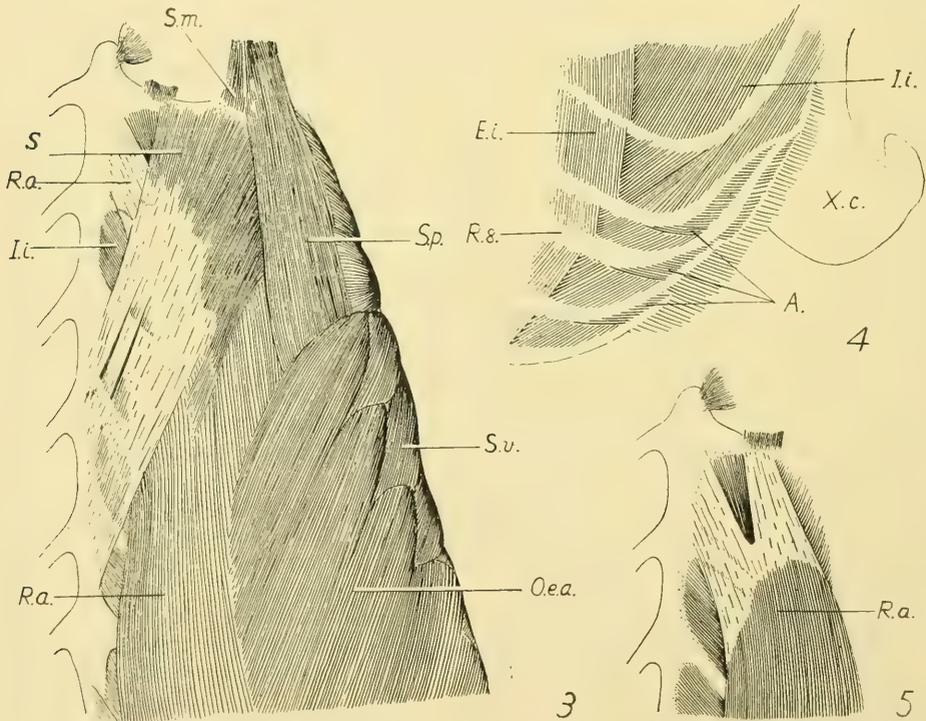


Fig. 3.—The thorax from the left side to show the relationships of the supracostalis and rectus abdominis. *I.i.*, internal intercostal; *O.e.a.*, obliquus externus abdominis; *R.a.*, rectus abdominis; *S.*, supracostalis; *S.m.*, scalenus medius; *S.p.*, scalenus posterior; *S.v.*, serratus ventralis.

Fig. 4.—The intercostal muscles associated with the cartilages of the vertebro-chondral ribs. *A.*, supernumerary muscles; *E.i.*, external intercostal; *I.i.*, internal intercostal; *R.8.*, eighth rib; *X.c.*, xiphoid cartilage.

Fig. 5.—The cranial end of the rectus abdominis illustrating its tendinous attachment to the first rib and the ventral face of the manubrium sterni. *R.a.*, rectus abdominis.

segments of the body to the junction between the xiphoid process and its cartilage. The fibres generally are directed cranio-laterally, but towards the caudal limit of the muscle their direction changes, becoming first lateral and finally caudolateral. Insertion is onto the rib cartilages as far as, and occasionally somewhat beyond, their union with the extremities of the bony ribs and, in addition, onto the fascial layer which extends between the ribs deep to the internal intercostals. The insertion extends from the second rib cartilage to the fascia between the sixth and seventh with a few fibres onto the seventh cartilage. The muscle is strong and thicker caudally (that is, immediately in front of the diaphragm) than further forward. It increases in width from the second rib, the increase being in accord approximately with the lengthening of the rib cartilages.

Macalister (1870) records the presence of this muscle in *Macropus giganteus* and *M. bennetti*.

*M. scalenus* (Fig. 3).—Although classified with the neck muscles, the scalenes are of interest in the present study by reason of their thoracic attachments and relationship to the brachial plexus. In the wallaroo the scalene complex lies dorsal of the brachial plexus and subclavian artery so that there is no scalenus anterior. Most writers on the anatomy of the Macropodidae have distinguished a scalenus brevis arising from the first rib and a scalenus longus dorsal to this and from ribs further back. These correspond respectively to the *medius* and *posterior* divisions of human anatomy, and this nomenclature will be used in the following account.

The broad and thick *scalenus medius* comprises the major portion of the muscle. It arises by fleshy fibres from the dorsal half of the cranial border of the first rib. The insertion, also fleshy, is to the transverse processes of the fourth to seventh cervical vertebrae. As in man the muscle is pierced by both trunks of the long thoracic nerve. A small slip which is here regarded as belonging to the scalenus medius arises from the first rib superficial to, but distinct from, the principal origin and opposite its lateral portion. It proceeds cranially to be inserted by a narrow strip of tendon onto the transverse process of the fourth cervical vertebra; on its deep surface its fibres are augmented by a fourth small cranially-directed slip which arises under its cover from the transverse processes of cervical vertebrae six and seven.

The *scalenus posterior* takes the form of a conspicuous flattened band which, in its course across the ribs, is approximately parallel with the sternum; there is a decrease in width from the thoracic attachments cranially. The middle part of the muscle comprising about half of its width, arises from the cranial side of the outer surface of the fourth rib by a thin flattened tendon which lies deep to the slip of the serratus ventralis to the same rib. The remainder of the origin is from the upper edge of the third rib by two smaller slips—a very slender and membranous one, continuous with the dorsal border of the muscle, the other, somewhat larger, forming the ventral border and springing from the rib by fleshy fibres. Some superficial fibres of this latter slip are received across the intervening external intercostal muscle (to whose surface they are closely applied) from an attachment on the fourth rib medial of the main origin. The cranial-most slip of the obliquus abdominis externus is superficial to the caudal extremity of the posterior scalene. Insertion is in part to the transverse process of the fourth cervical vertebra by a single slender round tendon embedded in and piercing the scalenus medius, and partly by fibres to this last-named muscle.

The absence of an anterior scalene seems to be general in marsupials. The dorsal part of the complex is separable into the usual two portions, at least at the rib attachments. There are few records of these muscles in Macropodidae. Parsons (1896) observed them in *Petrogale xanthopus* and later Windle and Parsons (1898) in *Macropus rufus*. Neither of these two papers, however, mentions a complexity of the cervical insertion comparable with that described above in the wallaroo.

#### *The Muscles of the Abdomen.*

Brief mention must be made of those muscles of the abdominal wall, which, to a greater or lesser degree, extend onto the thorax.

*M. obliquus externus abdominis* (Fig. 3).—The origin of the external oblique extends along most of the thorax and thence caudally to a point immediately above the upper extremity of the ilium. In the thoracic region it arises by fleshy slips from the outer surface of all the ribs except the first and second; the first three slips interdigitate with those of the serratus anterior. The abdominal portion takes origin principally from the lumbodorsal fascia. The muscular fibres are directed caudally and ventrally and overlap the lateral border of the rectus abdominis by 2–3 cm. along a line which is approximately parallel to the mid-ventral line. Insertion is to the marsupial bone and linea alba, attachment to the latter being through a tough strap-shaped aponeurosis which is with difficulty separable from the rectus abdominis and pyramidalis muscles which lie beneath. As in man, this aponeurosis enters into the formation of the ventral layer of the sheath of the rectus. There are no tendinous inscriptions present such as Carlsson (1914) has recorded in the thoracic portion in *Petrogale penicillata*, and Parsons (1896) in *Petrogale xanthopus*.

*M. rectus abdominis* (Figs. 2, 3, 5).—This muscle runs as a broad strip from the pubis to the first rib and manubrium sterni. At about the middle of the abdomen the recti diverge so that in their course cranialwards the medial borders are separated from the mid-ventral line by a centimetre or more. The thoracic portion of the muscle band which lies upon the ribs and passes over their articulations with the cartilages, gradually narrows towards the head till between the levels of the second and third sterno-costal joints the fleshy fibres terminate along an irregularly convex line to be replaced by a wide, flat tendon of insertion (Fig. 5). The tendon is divided from before backwards for about three-quarters of its length resulting in the formation of two distinctly separated heads of which the medial and larger is inserted onto the ventral face of the manubrium between the first and second sterno-costal joints, the lateral narrows slightly to an insertion on the outer surface of the first rib and lies beneath the medial border of the supracostralis. As in *Dendrolagus* and *Hypsiprymnodon* (Carlsson 1914 and 1915 respectively) tendinous inscriptions are not present (this is usual in marsupials). Parsons (1896) noted "a few indistinct intersections" in *Petrogale xanthopus*.

#### The Muscles of the Back.

*M. trapezius* (Fig. 1).—The general disposition and relationships of this muscle are much the same as in man. About opposite the second thoracic vertebra, however, there is interposed a triangular aponeurosis, the sharp apex of which just or very nearly reaches the mid-dorsal line, so that it divides the muscle into two parts and serves as a tendon of insertion of the lower component. The upper portion, the caudal fibres of which are readily separable from the cranial margin of the aponeurosis, is regarded as a *clavo-acromiotrapezius*, the lower as a *spinotrapezius*.

The *clavo-acromiotrapezius* arises from the ligamentum nuchae, caudal of the articulation between the atlas and occipital bone, and the tips of the spinous processes of the first and second thoracic vertebrae, together with the intervening supraspinous ligaments. Attachment is by a thin flattened tendon of varying width, except at the caudal limit where a few fleshy fibres are attached direct. Between the fifth cervical vertebra and a point just above the caudal limit of the muscle, the tendon forms with its fellow opposite a conspicuous oval expansion. From this extensive origin the fibres converge towards the spine of the scapula on which the majority is inserted. Considering the insertion from above downwards, it will be observed that a few of the upper cervical fibres are attached to the clavicle in its lateral fifth; the remainder of the muscle finds a fleshy insertion in a continuous line along the medial border of the acromion and the upper margin of the spine of the scapula.

The origin of the *spinotrapezius* which constitutes the second portion of the trapezius adjoins and appears to be a continuation downwards of that of the *clavo-acromiotrapezius*. It extends between the tips of the spines of the second and tenth thoracic vertebrae together with the included supraspinous ligaments. As far back as the spine of the fifth thoracic vertebra the origin is fleshy, but for the rest it is by a large triangular tendon, the fibres leading from which commence along an oblique line inclined at an angle of about 45° to the long axis of the body and approximately in line with the dorsal

limit of the fleshy fibres of the latissimus dorsi. Caudally the spinotrapezius is limited by a band of fibres about 0.75 cm. wide, distinct from the main muscle except for about 2 cm. beyond the tendon of origin; this proceeds cranio-laterally parallel with, and close to, the main muscle, and is inserted onto the fascia which invests the spinodeltoid over about the mid-point of the deeper lying infraspinatus. The remainder and major portion of the muscle is inserted through a triangular aponeurosis (mentioned above as separating the two major trapezius components) onto the spine of the scapula medial of its mid-point and opposite the insertion of the clavo-acromiotrapezius.

The trapezius generally is well developed except in the part inserted onto the clavicle and acromion where it is very thin. Most of the cranial border is hidden beneath the very extensive parotid gland which lies caudal of the ear in the lateral aspect of the neck. Caudally the spinotrapezius overlaps the upper edge of the latissimus dorsi; there is no area corresponding to the *triangle of auscultation* as described in man.

As usual, the trapezius is innervated by the accessory nerve which approaches the cranial edge of the muscle under cover of the parotid gland. On the deep surface of the trapezius the nerve is joined by a branch from the fourth cervical nerve.

In none of the accounts of the trapezius in macropods is there mention of division of the muscle sheet as described in the wallaroo, in which, however, the degree of division is much less than in *Caenolestes* (Osgood, 1921) and *Notoryctes* (Wilson, 1894). Macalister (1870) mentions that in *Sarcophilus* "the part of the muscle corresponding to the root of the spine of the scapula was weak and tendinous, and nearly divided the fleshy part into an upper and a lower trapezius".

*M. latissimus dorsi* (Fig. 1).—The fleshy portion of the latissimus, while thick and strong, is of relatively small area and does not overlap onto the abdomen such as commonly occurs in mammals. It lies between the line of posterior rami of the thoracic nerves and the digitations of the obliquus abdominis externus; the caudal limit does not extend beyond the space between the eighth and ninth ribs. It passes over but is not connected with, the inferior angle of the scapula, and the craniodorsal portion lies deep to the spinotrapezius.

The origin is from the superficial layer of the lumbodorsal fascia which is closely adherent to the underlying muscles and ribs. A wedge-shaped expanse of the fascia about 3 cm. wide at its narrowest part, separates the medial edge of the muscle from the mid-dorsal line. The cranial two-fifths of the fleshy fibres arise from the spinous processes of the fourth to the thirteenth thoracic vertebrae through the intervening fascia. There are no supplementary slips of origin from ribs, nor, as mentioned above, from the inferior angle of the scapula.

The muscle narrows and thickens as it proceeds cranio-laterally towards the axilla and is inserted by a narrow tendon into the bottom of the intertubercular sulcus of the humerus along a line continuous above with the insertion of the teres major. Except along its ventral border, the latissimus tendon overlies and is closely applied to, but separable from that of the teres major.

Innervation is by the thoracodorsal nerve which arises from the lower of the posterior cords of the brachial plexus.

Among Macropodidae, the vertebral origin of the wallaroo latissimus is a relatively lengthy one extending over ten thoracic spines; in *Dendrolagus* (Carlsson, 1914) it covers eight and in *Petrogale* (Parsons, 1896) only four, so that in the last named there is no overlapping by the spinotrapezius. The wallaroo differs from other members of the family in having no costal slips of origin.

*M. rhomboideus* (Fig. 1).—The rhomboid takes the form of a muscle sheet in which the only sign of segmentation is provided by a short tendinous partition, 1.5 cm. in length, attached to the medial angle of the scapula and serving indistinctly to separate the insertions of the vertebral and cranial portions. It arises in an unbroken line from the nuchal crest of the occipital bone, the whole length of the ligamentum nuchae and thence caudally from the tips of the spinous processes and included supraspinous ligaments as far back as the third thoracic vertebra. Attachment in the mid-dorsal line and to the nuchal crest is by a thin narrow aponeurosis which widens to form with its fellow a small V-shaped expansion superficial to the atlas and axis. Opposite

the scapula the fibres, which are here rather coarse and strong, are directed laterally and caudally. Above the scapula the fibres are finer and the muscle thinner; in the middle of the strip they are parallel with the long axis of the body, whilst those lying medial and lateral of them converge towards the medial angle of the scapula. The insertion is divisible into two portions. All the fibres from the dorsomedial line, that is, from the occiput to the caudal limit of the muscle, enter into a fleshy insertion along the total extent of the vertebral margin of the scapula. The remainder, which arise from the nuchal crest, are inserted by a small flattened tendon which passes over the medial angle of the scapula to be inserted onto its dorsal surface superior to the base of the spine and between the vertebral margin and medial limit of the tendinous insertion of the pars dorsalis of the omo-cleido-transversarius.

It would seem that the rhomboid, though fused into a single muscle sheet, may be regarded as comprising, in the portion arising from the nuchal crest, a *rhomboideus capitis*, whilst the rest is equivalent to the major and minor divisions recognized in human anatomy. An undivided rhomboid is the more common condition in marsupials and occurs in all Macropodidae so far known, with the exception of *Macropus giganteus* and Bennett's Kangaroo, in both of which, according to Macalister (1870), there is a faintly separable *rhomboideus capitis*. In his description of the muscle in *Petrogale*, Parsons (1896) makes no mention of fibres arising from the occipital bone, so that a *rhomboideus capitis* is presumably absent; in *Macropus rufus*, Windle and Parsons (1898) describe fibres from the occipital bone in one of their specimens, but note their absence in the other.

*M. omo-cleido-transversarius*.—Due to the fact that it may be single or double and may appear in close association with the levator scapulae, this muscle has been noticed in literature under an extensive list of synonyms. Leche (pp. 731-4) clarified the situation by designating, when the muscle appeared double, a *pars ventralis* and a *pars dorsalis*. The double condition is clearly defined in the wallaroo.

The *pars ventralis*, commonly known as the acromio-trachelian (Parsons) or omo-atlantic (Macalister), has the general facies of a right-angled triangle, the right angle being at the acromio-clavicular joint. It is thick towards the middle, thinner at the borders; the ventral border is obtusely rounded. Origin is from the transverse processes of the second to the fourth cervical vertebrae by slips partly fleshy, partly tendinous. The insertion is continuous onto the lateral half of the spine of the scapula and the lateral border of the acromion; a few of the most ventral fibres are inserted on the cranial aspect of the clavicle at its acromial end. Attachment is fleshy except for about 1.5 cm. dorsally, where it is by a thin flattened tendon continuous with that of the pars dorsalis. The whole of the pars ventralis lies deep to the trapezius and its dorsal border overlaps to a slight extent the ventral border of the pars dorsalis. The accessory nerve crosses the muscle superficially on its way to the trapezius.

The *pars dorsalis* is not so powerful as the pars ventralis. It arises by fleshy fibres from the transverse process of the atlas and is inserted onto the superior border of the medial half or so of the spine of the scapula and into the angle which the spine makes with the vertebral margin bounding the supraspinous fossa. The insertion is by a thin flattened tendon about 1 cm. deep which is adherent to the underlying fascial investment of the supraspinatus.

As mentioned in the description of the ventral serratus (*v. supra*), the cranial border of the pars dorsalis is in close contact with the cranial border of the serratus for most of its extent.

The omo-cleido-transversarius appears to be double in all Macropodidae, with the exception of the Tree-Kangaroos, *Dendrolagus* (Carlsson, 1914), in which the dorsal part is absent. Cuvier and Laurillard (Plate clxxxviii) figured a double muscle in *Macropus major*, and Carlsson (1914) records the double condition in *Petrogale penicillata* and *Aepyprymnus*. Parsons (1896) in describing the "acromio-trachelian" in *P. xanthopus* says that "it is entirely covered by the trapezius, onto which some of its superficial fibres are inserted". In Macalister's account (1870, p. 154) of Bennett's Wallaby and the Giant Kangaroo it is claimed that the "omo-atlantic" (= pars ventralis)

"is inserted into the anterior fourth of the scapular spine and into the whole length of the clavicle"; in the wallaroo (*v. supra*) some fibres were observed inserted into the acromial end of the clavicle.

*M. serratus dorsalis cranialis* (Fig. 6).—The cranial dorsal serratus appears as a thin sheet of muscle having the shape of a parallelogram divided longitudinally into a medial half comprising the aponeurotic tendon of origin and a lateral half made up of

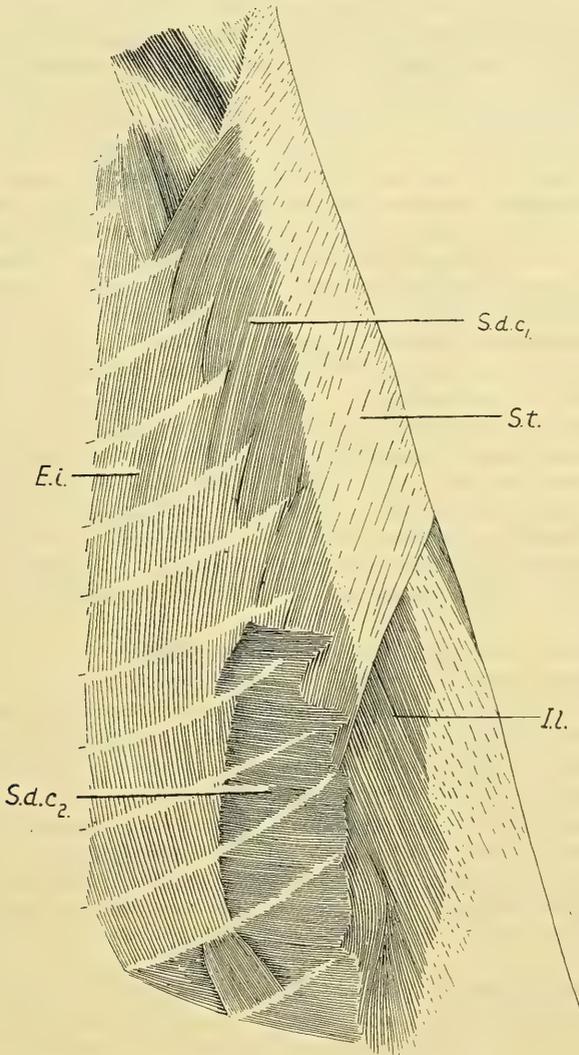


Fig. 6.—Dissection to show the relationships of the dorsal serrati. *E.i.*, external intercostal; *I.l.*, iliocostalis lumborum; *S.d.c.*, serratus dorsalis cranialis; *S.d.c.*<sub>2</sub>, serratus dorsalis caudalis; *S.t.*, the broad tendon of origin of the serratus dorsalis cranialis.

fleshy fibres. The muscle and its tendon lie deep to the lumbodorsal fascia. It arises by the long narrow tendon already mentioned from the ligamentum nuchae caudal of the level of the spine of the second cervical vertebra, and the tips of the spines of the thoracic vertebrae back to and including the ninth. The tendon displays a slight increase in width from before backwards. Insertion is by fleshy slips to the external surfaces of the third to eleventh ribs lateral of the iliocostalis. The direction of the fibres is parallel to that of the external intercostals; the first and last slips are weaker than the others.

*M. serratus dorsalis caudalis* (Fig. 6).—The caudal portion of the dorsal serratus layer is thicker than the cranial portion. It arises from lumbodorsal fascia, the fibres running approximately parallel with those of the internal intercostals. The dorsal limit of its fleshy fibres is roughly along a line which follows the curvature of the lateral border of the iliocostalis lumborum. Insertion, partly fleshy, partly membranous, is to the external surfaces of ribs eight to thirteen, the ventral-most portion of the attachment to the rib lying deep to the corresponding slips of the obliquus abdominis externus. Where the fibres cross the underlying ribs (in passing to their rib insertion), there is a discontinuity as though by the intervention of obliquely placed tendinous intersections through which the muscle sheet is bound to the outer surfaces of the ribs. The three cranial-most slips overlap the three caudal-most slips of the cranial division.

The wallaroo has two dorsal serratus muscles as described above. They are both well developed and readily separable from each other. In *Petrogale wanthopus*, however, Parsons (1896) records the absence of the caudal member of the pair. Cuvier and Laurillard figure (Plates clxxxvii and clxxxviii) two muscles in *Macropus major*, but there is no overlapping of the one by the other. In the koala (Macalister, 1872, and Young, 1882) and wombat (Macalister, 1870) the two muscles form a continuous sheet. Leche has summarized the manner of their occurrence in *Dasyurus*, *Didelphys* and *Phalangista*; in all three a cranial and caudal division are present.

*The Diaphragm.*—I am unaware of any but brief mention of the diaphragm in marsupials, and there seems to be no account of it in the Macropodidae. Young (1882) in a short discussion of the occurrence of the muscle in the koala says “. . . the oesophagus is situated between the muscular fibres derived from the crura but behind their junction, so that, like the aorta, it is practically behind the diaphragm”. This would suggest that there are no muscle fibres separating the aortic from the oesophageal hiatus and that there is no splitting of the right crus for the passage of the oesophagus. The condition in the wallaroo approaches more closely the arrangement found in the Primates.

The dome of the diaphragm is symmetrically disposed about the median plane; there is no shallow median depression (such as occurs in man) to interrupt the continuity of the curve from one side to the other. As in mammals generally it consists of a central tendon which serves for the insertion of a peripheral zone of radially disposed fleshy fibres arising from the ribs (*pars costalis*), xiphoid cartilage (*pars sternalis*), and upper two lumbar vertebrae (*pars lumbalis*).

The central tendon has the general form of an isosceles triangle, the apex of which is truncated where the fleshy fibres of the *pars sternalis* of the muscular portion pass into it, and the base is interrupted for its whole length by the fleshy *pars lumbalis*. Dorsally the *pars costalis* and *pars lumbalis* are separated by the central tendon except where the two adjoin and decussate for about 1 cm. ventral of the trigonum lumbocostale.

The sterno-costal portion of the fleshy periphery arises by the *pars sternalis* which is markedly thicker than the rest, and a *pars costalis* the thickness of which decreases from its confluence with the *pars sternalis* dorsally. The *pars sternalis* arises by a single broad strip of muscle from the dorsal surface of the cranial third of the xiphoid cartilage. The *pars costalis* arises from the internal surfaces of the seventh to thirteenth costal arches inclusive; from the seventh to the tenth it is from the rib cartilages; in the case of the tenth the attachment extends dorsally to the costo-chondral articulation. Behind the tenth arch the origin is from both cartilage and rib with a diminishing proportion of cartilage till, in the case of the thirteenth costal arch, it is from the bony rib alone. The *pars costalis* is inserted into the lateral border of the central tendon.

The lumbar portion of the muscular part of the diaphragm is roughly rhomboidal in shape, the ventral tip lying to the left of the venacaval foramen, the dorsal angle on the second lumbar vertebra, this latter being split into the right and left crura by the passage of the aorta dorsally. The origin of the *pars lumbalis* is from the ventral

surface of the bodies of the first and second lumbar vertebrae by means of the right and left crura which are separated dorsally by the passage of the dorsal aorta.

The *right crus* is much the larger of the two and constitutes three-fifths or more of the lumbar portion of the diaphragm. It arises by a flattened tendon more or less parallel to the median plane attached dorsally to the ventral surface of the bodies of the first and second lumbar vertebrae and the intervertebral fibro-cartilage through the anterior longitudinal ligament of the vertebral column. This vertical raphe extends through about half of the crus and ceases when the fibres split to form the oesophageal hiatus. The majority of the fleshy fibres rise laterally from the tendon (which is exposed medially opposite the aorta) and from the lateral aspect of the ventral face of the body of the first lumbar vertebra and the fibro-cartilage between it and the second. From about a level immediately ventral of the aorta, fibres arise from it medially. It will thus be seen that the bundle constituting the right crus has a bipennate structure. From this origin the fibres fan out to their insertion in the central tendon, a few of the most lateral arching across the large psoas minor and participating in the formation of the ventral boundary of the trigonum lumbocostale.

The *left crus*, like the right, takes origin from both the first and second lumbar vertebrae, but it does not extend quite so far along the vertebrae either caudally or cranially. It forms the left boundary of the aortic hiatus and its medial fibres ventral of the aperture cross—mostly caudally—those of the lateral aspect of the right crus.

The fibres from the crura on the right and left sides pass over the psoas muscle forming a lumbo-costal arch. Lateral of the psoas there is a well-defined trigonum lumbocostale, bounded ventrally by the lateral fibres of the crus and the dorsal-most fibres of the corresponding costal portion with which they decussate. There is no attachment of the crura to the transverse processes of the lumbar vertebrae.

The *hiatus oesophagus* is situated at the ventral border of the pars lumbalis in the median plane and surrounded (though weakly ventrally) by fleshy fibres derived from the right crus. The *hiatus aorticus* calls for no comment; no middle arcuate ligament was observed. The *foramen venae cavae* pierces the central tendon, lying to the right of the median plane and just ventral of the fleshy fibres of the right crus.

#### *Digestive System.*

The oesophagus, the only part of the alimentary canal concerned, is of moment in so far as its relations to the other thoracic viscera are noteworthy. In the upper part of the thorax it lies slightly to the left of the median plane. Proceeding caudalwards a wide sweep towards the right is described, the mid-dorsal line being crossed opposite the third intercostal space. It is in contact dorsally with the left longus colli and the medial border of the right; the trachea lies ventrally and to the right and in preserved specimens the impression of the cartilaginous bars is conspicuous on its right ventro-lateral aspect. Passing behind the aortic arch and still trending towards the right, it comes to lie directly dorsal to the trachea at the point where it bifurcates, and to the right of the descending aorta. Beyond the origin of the bronchi it again begins to cross towards the left and, about half-way along the thoracic course of the descending aorta, assumes its normal position ventral to it.

#### *Respiratory System.*

The respiratory system in marsupials has received not infrequent notice in the literature of the group and parts of it such as the anatomy of the larynx are comparatively well known. In the absence of an account of the lungs and pleurae *in situ*, I have taken advantage of the excellent preservation of the adult male of the series dissected to present these structures in some detail.

*The Trachea and Bronchi.*—Within the thorax the trachea lies somewhat to the right of the mid-dorsal line and proceeds caudalwards with a slight inclination towards the right. As far back as the head of the fourth rib its dorsal face is pressed against the concavity formed by the right longus colli and the right side of the oesophagus, which latter in this region lies ventral of the left longus colli. Opposite the head of the fourth rib the left side of the trachea is, in preserved specimens, marked by a broad shallow groove due to the passage of the aortic arch.

The tracheal rings are incomplete dorsally, and in the region immediately above the commencement of the bronchi, one free end tends to overlap the one opposite; Parsons (1896) has recorded a similar condition in *Petrogale xanthopus* in which "the cartilaginous rings form rather more than complete circles, so that one end overlaps the other on the dorsum". In the marsupials generally, incomplete rings seems to occur more usually than those which are complete; among Macropodidae, *Halmaturus* (Leche, p. 1137) is alone in having them undivided.

*The Mediastinum.*—The general disposition of the mediastinal pleurae and their relationship to the dorsal and ventral body walls is described below. It remains briefly to indicate the arrangement of the contents of the mediastinal cavity as seen *in situ* through the pleurae prior to their removal. For descriptive purposes the cavity is conveniently divided into *precardial*, *cardial* and *postcardial* regions.\*

The *precardial mediastinum* lies cranial of a transverse plane which passes through the fifth thoracic vertebra at the level of the attachment of the ribs and the cranial end of the second sternebra. In its ventral half the cavity is obliterated by apposition of the left and right pleural boundaries. Viewed from the right side the trachea is the most conspicuous and most dorsal feature. The right superior vena cava lies immediately ventral of the trachea and in its course from the superior aperture of the thorax to the heart this vessel is directed obliquely from the right of the trachea towards its mid-ventral line. The right vagus nerve is also visible lying on the ventral surface of the trachea, following and slightly hidden by the right side of the vena cava. The right phrenic nerve is conspicuous on the ventral surface of the vena cava.

Except for a short distance immediately cranial of the heart the trachea is not visible when the precardial mediastinum is viewed from the left, owing to its being hidden by the great vessels arising from the aortic arch. The left superior vena cava lies ventrally and to the left of the great vessels; the left phrenic nerve lies on its right dorsal aspect.

The *cardial mediastinum* is much bulged on both right and left sides by the enclosed heart, dorsal of which lies the group of blood-vessels and bronchial tubes which comprises the root of the lung. On each side the phrenic nerve crosses the lung root ventrally. From the right, the oesophagus is visible dorsal of the lung root, and the right vena azygos is also readily seen between the oesophagus and body wall. The azygos vein crosses the trachea cranial of the lung root to unite with the vena cava of its own side; the right vagus nerve passes between it and the trachea on its way to the dorsal aspect of the lung root. From the left side the thoracic aorta and aortic arch are the most dorsal of the cavity contents that are visible. The left vena azygos is disposed similarly to the right but, to join the vena cava, the aorta is crossed instead of the trachea.

Between the pericardium dorsally and the sternum ventrally there is a well-marked *ventral (= anterior) mediastinum*.

In the *postcardial mediastinum* the ventral and greater portion of the septum is pushed well to the left for the accommodation of the intermediate lobe of the right lung, at the same time obliterating the cavity in the portion involved. Dorsally the pleural layers diverge to form a cavity which is smaller than that of either the precardial or cardinal sections. A vena azygos is visible from both sides. The aorta lies to the left of the middle line; ventral of it, is the oesophagus which is obliquely placed so that, followed from its emergence from behind the right bronchus, it crosses the aorta from right to left.

*The Pleurae.*—The *cupula pleurae* is not visible among the structures at the root of the neck, its summit on both sides being hidden behind the broad cartilage of the first rib. It receives support by attachment to the deep surface of this cartilage and to the sternal end of the bony portion of the rib, as well as being loosely connected by connective tissue to the deep surface of the sternothyroid muscle. Ventral of the trachea and great vessels which pass to the neck from the thorax, the medial limits

\* The terminology here adopted is that used in Bradley's "Topographical Anatomy of the Dog". 2nd Edition, 1927.

of the adjacent cupolas are separated for only a short distance behind the manubrium sterni before becoming closely apposed to form the ventral portion of the precardial mediastinum.

Along the *vertebral line of reflection* on the right side, the pleura is reflected onto the trachea and root of the lung and more caudally onto the dorsal aorta and oesophagus. Opposite the dorsal aorta reflection is from the mid-vertebral line, opposite the trachea somewhat to the right. On the left side cranial of the aortic arch reflection is onto the innominate artery, the left vagus and left superior vena cava, for the rest onto the aortic arch and thoracic aorta; reflection is to the left of the mid-vertebral line.

The *sternal line of reflection* on the right side commences at the right border of the manubrium sterni immediately below its articulation with the cartilage of the first rib, and proceeds diagonally across the manubrium and body of the sternum to a point on the left at the lower border of the third rib cartilage somewhat medial of its mid-point. The line then swings back to the right in an arc skirting the right border of the third sternebra and part of the fourth, continuing round towards the left till it meets the line of reflection on the left side, which is then followed. The line of reflection on the left side is the same as that on the right from the manubrium to the third rib from whence the right pleura turns to the right, but the left continues in the same direction in a fairly straight line to a point behind the junction between cartilaginous and bony portions of the sixth rib. Its course is then directly caudally to the diaphragm.

The *diaphragmatic line of reflection* follows in general the attachments of the diaphragm to the lower ribs and cartilages, and as these have received attention under that muscle it is unnecessary to detail them here.

As mentioned above, ventral of the right superior vena cava and phrenic nerve, from cranial of the pericardium to the base of the cupula pleurae, the sheets of pleurae bounding the precardial mediastinum are in contact so that the mediastinal cavity is obliterated. The cardiac mediastinum has the usual relations. In the postcardial mediastinum, there is also elimination of the cavity by contact of the opposite pleurae, except dorsally where they divide to include the oesophagus, dorsal aorta, etc.; this is due to displacement brought about by the position of the azygos lobe of the right lung. The *fold of the vena cava* (plica venae cavae) is a delicate double pleural sheet which envelops the inferior vena cava dorsally, giving off a subsidiary fold for the accommodation of the right phrenic nerve and accompanying blood-vessels. Its ventral origin is along a line directed from the left border of the xiphisternum cranially and laterally to the apex of the heart; from this base the general direction of the sheet is obliquely dorsally and towards the right. It blends with the portion of the right pleura investing the pericardium, and caudally has origin from the pleura adherent to the diaphragm, so that there is formed a partition with a free dorsal border which allows the passage of the intermediate (azygos) lobe of the right lung between it and the dorsal body wall, but serves to separate this lobe from the body of the lung.

Hartmann-Weinberg (1924) described the occurrence of openings in the postcardial mediastinum between the aorta and oesophagus which permitted communication between the right and left pleural cavities. These openings were found in *Didelphys marsupialis* and *Perameles garragassi*, but their absence is inferred in Macropodidae. Jazuta (1932) confirmed their presence in the opossum. No trace of such apertures was found in the wallaroo. It is interesting to note the condition in the horse, of which Sisson (1927) says: "The posterior mediastinum is very delicate ventral to the oesophagus, and usually appears fenestrated; when these apertures are present, the two pleural cavities communicate with each other."

*Lungs*.—The right lung has nearly twice the bulk of the left, the difference in volume (from figures obtained by displacement) being expressed by the ratio 11:6. The two lungs are completely separated the one from the other, there being no area of adhesion caudal of the hilum as in some mammals.

The *left lung* (Fig. 7) is elongate, and, due to the extent and depth of the cardiac impression, laterally flattened. Lobation with its consequent division of the lung

substance is very little in evidence. A division between the apex and the remainder is indicated by a shallow fissure ventrally in the dorsocaudal corner of the cardiac notch; a similar shallow fissure incises the dorsal border opposite the cranial boundary of the cardiac notch. The cardiac notch appears as an extensive rhomboidal gap in the ventral border; it is narrower dorsally and lies within the span of the third to fifth ribs, thus leaving exposed a corresponding area of the pericardium which lies in direct contact with the chest wall. The *apex* is relatively large and obliquely truncate

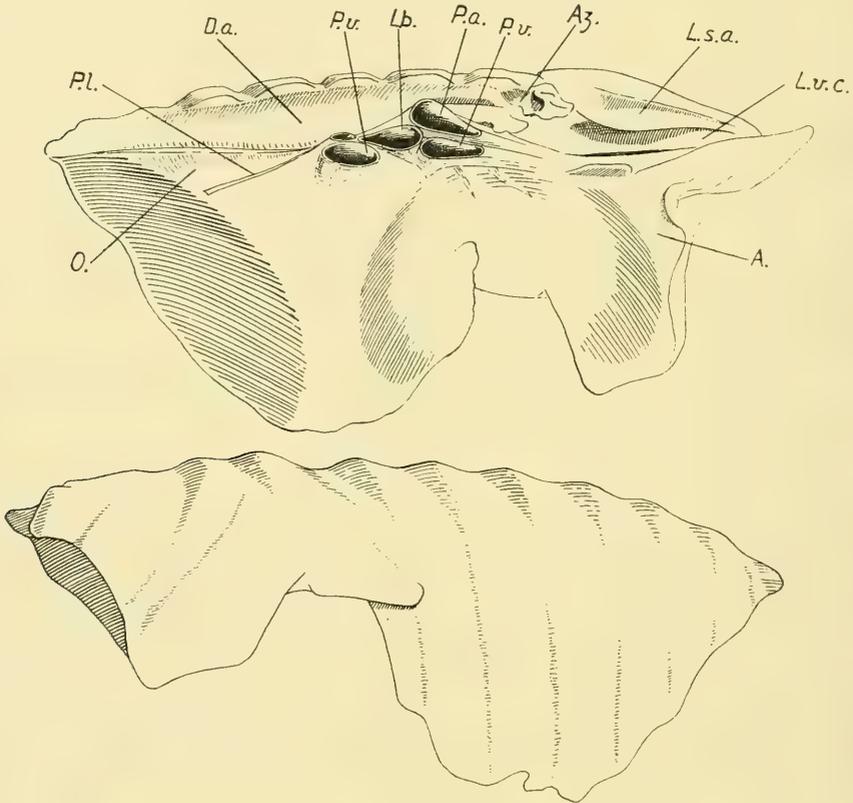


Fig. 7.—Above, medial surface of left lung hardened *in situ*; below, the same specimen from the lateral aspect. A., apex of lung; L.b., left bronchus; P.a., pulmonary artery; P.l., pulmonary ligament; P.v., pulmonary vein. The following grooves and impressions are indicated: Az., azygos vein; D.a., dorsal aorta; L.s.a., left subclavian artery; L.v.c., left anterior vena cava; O., oesophagus.

cranially. On the medial aspect of the dorsal border of the body of the lung there is the deep impression caused by the thoracic aorta, and ventral to it and caudal of the hilum, that made by the oesophagus. Cranial of the hilum, but at a more ventral level than the aorta, there is a deep groove for the reception of the left vena cava, and dorsal of this a shallow depression which marks the course of the left subclavian artery. There is also a groove formed by the left vena azygos cranial of the hilum.

The pulmonary artery is the most dorsal of the structures comprising the *root of the lung* with the bronchus lying caudal and ventral of it. In the angle formed by the bronchus and the artery, and closely adjoining both, lies the superior pulmonary vein, the superficial branches of which are visible for some distance on the surface in the cardiac depression before entering the lung substance. The primary bronchus enters the lung and proceeds to its base along a line parallel to the dorsal border. At the hilum a large branch originates, and this gives rise to two divisions; one, slightly the larger,

is the apical bronchus, and the other is directed at right angles to the long axis of the lung towards the ventral border and supplies the section which corresponds to the cardiac lobe. The branch of the pulmonary artery which accompanies the apical bronchus lies dorsomedially to it, but in the remainder of the lung the main branches of the artery take up a dorsal position. The pulmonary veins have their usual ventral disposition; of the two veins the hinder drains the lung caudal of the cardiac notch, the other the apical lobe together with the "cardiac lobe" region.

The *left pulmonary ligament* (Fig. 7) commences at the caudal aspect of the inferior pulmonary vein and skirts the ventral edge of the impression made by the oesophagus. It is reflected onto the lung from the pleura investing the lateral aspect of the oesophagus.

In its cranial third the *right lung* (Fig. 8) is thin and laterally flattened, but the rest is thick, especially dorsally. Viewed from the costal aspect it is triangular in outline with a well-defined cardiac notch. There is one major fissure and this cuts into the ventral border behind the cardiac notch dividing the lung to the hilum and representing the line of demarcation between the apex and body of the lung. There is another shallower incision on the lateral basal border. Between the two incisions mentioned, the body of the lung is produced ventrally to a peak which corresponds to the cardiac lobe of other mammals. This "cardiac lobe" is accommodated within a pouch formed between the fold of the vena cava and the diaphragm, that is, it lies between the diaphragm and heart, extending across the mid-ventral line for a short distance into the left half of the chest, relations similar to those of the intermediate lobe (*v. infra*). On its medial surface there is a small flap, triangular in cross-section, between which and the body of the lung the posterior vena cava passes. The right lung has an *azygos* (= *intermediate*) *lobe* which arises from the medial aspect of the dorsal region caudal of the hilum. It is an irregularly pyramidal process, triangular in cross-section, attenuated and tapering, and concave cranially and caudally where it fits against the pericardium and diaphragm respectively; caudally it is partly separated from the main lung by a shallow fissure. The posterior vena cava, right phrenic nerve and fold of pleura associated with these structures are lodged in a groove on the medial face of its base. The usual position is occupied between pericardium, diaphragm and oesophagus and is in relation ventrally to the "cardiac lobe" though separated from it by the intervening fold of the vena cava. The *apex* is laterally flattened and presents cranially a thin semi-circular edge. It is separated from the body of the lung by the fissure mentioned above.

Running across the dorsal aspect of the base of the azygos lobe and the contiguous surface of the main lung, there is a wide groove for the oesophagus, and dorsal to this towards the basal border the impression of the thoracic aorta is visible. Cranial of the hilum on the dorsal mediastinal surface there is the broad impress of the right half of the trachea and ventral of this that of the right superior vena cava. The groove for the right vena azygos is very distinct cranial of the hilum where it crosses the trachea on its way to discharge into the right superior vena cava.

Among the constituent parts of the root of the right lung, the bronchus occupies the most dorsal position; the pulmonary artery is immediately ventral, and the pulmonary veins are arranged in a semicircle from caudal of the bronchus round to a position ventral to the pulmonary artery. A small branch each of bronchus, artery and vein proceeds to the intermediate lobe. On entering the lung the primary bronchus gives off a large apical branch to the apex which forms a relatively considerable fraction of the total lung bulk. As in the left lung a further large branch leaves the stem bronchus at right angles to the long axis and proceeds towards the ventral border to supply the "cardiac lobe". The stem bronchus is directed normally to the base of the lung. The artery which accompanies the apical branch lies medial to it, that which follows the stem bronchus lies on its dorsal side, and that which accompanies the large branch of the stem bronchus to the ventral border lies alongside, but cranially. The vein accompanying the large ventral bronchial branch is parallel

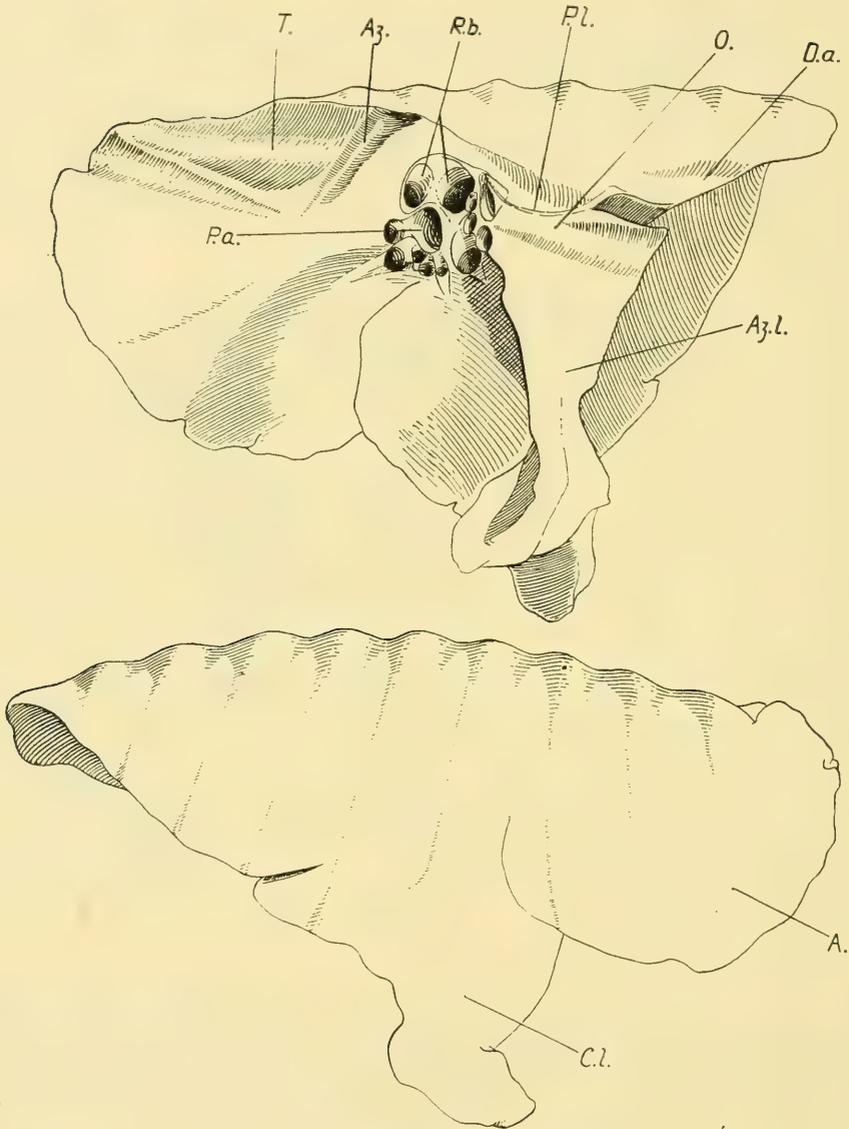


Fig. 8.—Above, medial surface of the right lung (hardened *in situ*, and from the same specimen as the figured left lung); below, its lateral aspect. *A.*, apex of lung; *Az.l.*, azygos lobe; *C.l.*, cardiac lobe; *Pa.*, pulmonary artery; *Pl.*, pulmonary ligament; *R.b.*, right bronchus. The following grooves are indicated: *Az.*, azygos vein; *D.a.*, dorsal aorta; *O.*, oesophagus; *T.*, trachea.

and close to the artery, but cranial of it; the other veins have their usual superficial medial disposition.

The right *pulmonary ligament* (Fig. 8) is reflected onto the surface of the lung from pleura investing the ventral aspect of the oesophagus.

Speaking generally the macropods show little development of deep fissures dividing the lung substance into lobes. Notches, however, of greater or lesser depth are common, and it would appear that the position of these is usually indicative of incipient lobulation. This absence of lobulation is especially true of the left lung; Owen (1868, p. 577) describes two lobes "in another kangaroo", but apart from notches the Macropodidae

generally may be said to have a unilobate left lung. In the wallaroo the right lung is bilobate. Owen (1868) describes a four-lobed condition in a kangaroo and records "two or three deep fissures" in the Potoroo. In other species in which the condition of the right lung has been mentioned, for example *Macropus major* and *M. parryi* (Owen, 1868), and *Petrogale xanthopus* (Parsons, 1896), there are only notches present in the ventral margin. Sonntag (1921, p. 872) says that "in the Macropodidae, of which *Dendrolagus ursinus*, *Macropus bennetti* and *Macropus giganteus* were examined, both lungs have deep median sulci dividing them into anterior and posterior parts, but these are not entirely separated from one another".

Parsons (1896, p. 714) mentions of *Petrogale xanthopus* that "on neither side is there any eparterial bronchus". If this is so, it is probably unique among marsupials in which there is, in general, an eparterial bronchus on the right side (Aeby's type IIA). In the mature wallaroo the presence of an eparterial (apical) bronchus on the right side is quite clear.

#### The Thymus Gland.

The following description was drawn up from the dissection of a fully-grown adult male and differs only in minor details from the conditions found in the two females examined. The gland (Fig. 9) takes the form of a flattened mass composed of two principal and readily separable parts, a right and a left. It is greyish-brown in colour and lies upon the innominate artery and the roots of its branches, together with the portions of the trachea which are exposed between these vessels. It is confined within

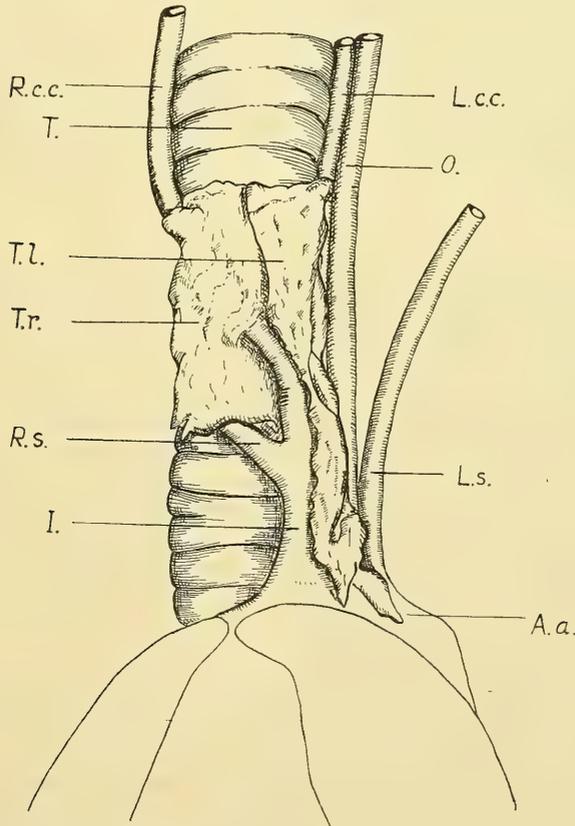


Fig. 9.—Ventral view of the trachea with the branches of the arch of the aorta and the thymus gland. *A.a.*, aortic arch; *I.*, innominate artery; *L.c.c.*, left common carotid; *L.s.*, left subclavian artery; *O.*, oesophagus; *R.c.c.*, right common carotid; *R.s.*, right subclavian; *T.*, trachea; *T.l.* and *T.r.*, left and right lobes of the thymus.

the precardial mediastinum except for two caudally directed narrow lobes which overlap the pericardium (*v. infra*). The gland extends from a point about opposite that which divides the manubrium sterni into a cranial two-thirds and a caudal third back to the arch of the aorta. The left part is slender and lies in the groove between the trachea and oesophagus, more caudally between the innominate artery and oesophagus, so that it obscures the root of the left common carotid and the left side of the innominate. It narrows caudally and terminates on the arch of the aorta between the roots of the left subclavian and innominate arteries; this termination is bifid, the more medial of the two slips being attached to the pericardium by strands of connective tissue, the other by connective tissue and fine blood-vessels to the left anterior vena cava where it is joined by the vena azygos. The right section is broader and shorter; it lies in close contact with its neighbour medially and is placed so that it crosses the right common carotid and subclavian arteries, but does not extend caudally to their origin from the innominate artery. The right and left portions of the gland are bound together and to the underlying arteries and trachea by fatty connective tissue.

The gland is abundantly supplied with nerves from the stellate ganglion of the sympathetic system and the vagus. A pair of small oval cervical thymus glands was observed in the root of the neck, one on each side of the mid-ventral line and lying superficial to the caudal end of the sterno-cleido-mastoid.

It will be seen that in the adult wallaroo the thoracic thymus is of large size. In two examples of *Macropus bennetti* dissected by Symington (1898) one (an eight-year-old individual) had no thymic tissue in the thorax. Windle and Parsons (1898) record of *Macropus rufus* that "the thymus in A occupies its usual situation: it consists of two lobes, each of which is about 75 mm. in length". Their specimen A was a young animal taken from the pouch, B a fully-grown example, lack of mention of the thymus of which possibly indicates its involution. Johnstone's observations (1898) were confined to the condition of the thymus in pouch specimens. Otto recorded the presence of a thoracic thymus in *Macropus giganteus* and *M. leporoides*, but was unable to find it in *Petrogale penicillata*.

#### *The Nervous System.*

For the present purpose it has been considered necessary to depict the topography of the thoracic portions of the phrenic and vagus nerves in some detail. The brachial plexus in marsupials is already well known (Thomas, 1930; Miller, 1934; Harris, 1939) so that only points of interest for comparative purposes have been recorded in the wallaroo. In addition, the sympathetic system has been discussed in so far as the stellate ganglion is concerned.

The *right phrenic nerve* enters the superior aperture of the thorax on the ventral aspect of the right superior vena cava to which it is loosely bound by connective tissue. In this relationship to the vein it proceeds caudalwards through the precardial mediastinum and then enters the cardiac mediastinum to traverse the pericardium along a line just ventral of the root of the lung. The remainder of its course to the diaphragm is within a small accessory fold of the fold of the vena cava, so that the nerve follows the course of the posterior vena cava lying along its ventral aspect and somewhat to the right. On the right side the phrenic nerve is the most ventral of the contents of the precardial mediastinum.

The *left phrenic nerve* enters the chest on the medial aspect of the left superior vena cava, but immediately assumes a position on its dorsal side which is kept during the passage of the nerve through the precardial mediastinum; as on the right, the nerve is in close contact with the vena cava. After traversing the arch of the aorta, at about the level when the vena cava receives the left vena azygos, that is, opposite the commencement of the descending aorta and within the cardiac mediastinum, the nerve moves round the vein medially passing between it and the pericardium investing the left atrium, so that it comes to lie ventrally on the vein. The pericardium is crossed, the nerve being loosely attached to it by connective tissue and separated from the root of the lung by the vena cava. In the postcardial mediastinum it passes

to the diaphragm between the right and left mediastinal pleurae, which are here in contact with each other.

In the neck the vagi accompany the common carotid artery and cervical sympathetic trunk of their respective sides, the three being bound together by connective tissue.

The *right vagus nerve* enters the superior aperture of the thorax lying on the right side of the trachea. It crosses the subclavian artery ventrally medial of the origin of the internal mammary and passes into the precardial mediastinum; just before reaching the subclavian artery the recurrent (laryngeal) nerve branches off, hooks round the artery in the angle formed by it and the internal mammary, and proceeds cranialwards. The nerve continues its course in the precardial mediastinum on the lateral aspect of the trachea; it passes dorsal of the vena azygos as it arches across the trachea to join the vena cava, and beneath the azygos changes direction, proceeding from thence caudodorsally to the dorsal portion of the root of the lung, where it breaks up to form the posterior pulmonary plexus.

In the upper part of the neck opposite the thyroid gland the *left vagus* and left common carotid lie in the V-shaped groove formed between the longus colli and trachea. Further back, about half-way down the neck, the oesophagus appears from beneath the trachea and separates it from the longus colli, so that the vagus and carotid then continue their downward course upon the oesophagus. The chest is entered dorsal of the anterior vena cava and ventral of the subclavian artery. In the neck the vagus is situated lateral to the common carotid and this relationship is maintained in the precardial mediastinum till just before the carotid unites with its fellow of the right side; thence the nerve passes ventral of the left lobe of the thymus gland which overlies the root of the left common carotid and the groove between the innominate and oesophagus. It then passes over the arch of the aorta, gives off the recurrent (laryngeal) nerve and reaches the dorsal aspect of the root of the lung by way of an opening bounded by the vena azygos ventrally, the inner curve of the aortic arch laterally, and the pericardium medially. It forms as usual the posterior pulmonary plexus. The recurrent (laryngeal) nerve after hooking round the aorta opposite where it is crossed by the vagus, proceeds upwards in the thorax towards the neck, lying on the ventral face of the trachea towards its left side within the groove formed between the trachea and oesophagus.

A main nerve stem issues from each posterior pulmonary plexus. That on the right continues through the thorax on the right face of the oesophagus, but moves round to its dorsal aspect and is joined by a large branch from the left vagus before piercing the diaphragm. The left vagus passes along the left side of the oesophagus; opposite the head of the ninth rib it gives off a large branch which passes round the oesophagus dorsally to unite with the right vagus as described above. The principal part of the left nerve then proceeds along the oesophagus ventrally and in this position traverses the diaphragm.

The *brachial plexus* in the wallaroo has been investigated by Harris (1939). I have compared my specimens with his account and figure, and find practically point for point agreement. In none of the three I examined, however, did there appear to be a connection between the phrenic and the nerve to the subclavius. The two heads of the median did not join till they entered the distal half of the brachium. As Harris points out, there is no branch to the plexus from the fourth cervical nerve. Parsons (1896) has given a useful survey of the plexus in *Petrogale xanthopus*.

*The Sympathetic System.*—The cervical trunk of the sympathetic passes through the neck in close contact with the vagus, both these nerves being enclosed in a sheath of connective tissue which lies along the dorso-lateral aspect of the common carotid artery. Just before entering the thorax the sympathetic trunk diverges laterally from the carotid, traversing obliquely the oesophagus on the left side and the trachea on the right and then, passing deep to the root of the vertebral artery, joins the cranial end of the stellate ganglion. This important ganglion is large and has an irregular outline, but is generally elongate and lies obliquely across the lateral half of the longus colli, so that its long axis is directed in a dorsocaudal direction when traced from

before backwards; its situation is under cover of the first rib and opposite the dorsal portion of the space between the first and second ribs. The inferior cervical ganglion and the first and second thoracic ganglia are indistinguishably blended into its formation. Large rami connect with the first and second thoracic nerves. An ansa subclavia with the usual relations is present on each side.

#### *Blood Vascular System.*

*The Heart.*—The wallaroo heart differs only in detail from Owen's (1868) description of the organ in the kangaroo and Parson's (1896) later and fuller account of it in *Petrogale xanthopus*. The right auricular appendix shows no sign of bifurcation as described by both authors.

*Position of the Heart.*—The heart lies between planes which transect the thorax at the level of the upper border of the third rib cartilage and the lower border of the sixth respectively, where they articulate with the sternum. It is not symmetrically disposed about the median plane, about three-fifths of its bulk lying to the left. From the base the long axis is directed caudally, ventrally and slightly to the left. The apex which is very bluntly pointed, lies opposite the central tendon of the diaphragm somewhat to the left of the median plane.

*Pericardium.*—The pericardium has the same shape as the heart which, in preserved specimens, it loosely invests. It is pierced by the left anterior vena cava opposite the cranial end of the ventral aspect of the left lung root and by the right anterior vena cava lateral of the cranial end of the ascending aorta. The posterior vena cava, after traversing the fold of the right pleura which is provided for it, enters the pericardium caudal of the root of the right lung in approximately the same frontal plane as the entry of the right anterior vena cava, so that the ventral components of the lung root represented by the right pulmonary veins and the more dorsally-placed pulmonary artery intervene between the two. The extension of the pericardium onto the aorta proceeds to a point about midway between the origins of the innominate and left subclavian arteries so that the innominate root also is for a short distance enclosed in pericardium. There are no connections of a ligamentous nature with the sternum such as is represented by the sterno-pericardial ligaments in man. Ventrally the heart is held in position principally by the ventral attachments of the mediastinal pleurae, the small space between the pericardium and dorsal surface of the sternum being occupied by loose connective tissue. Sonntag (1921, p. 865) makes the statement that "the *Pericardium* adheres to the diaphragm in all marsupials except *Trichosurus vulpecula*, and it adheres to a variable extent to the sternum and ribs". Earlier Cunningham (1882, p. 150) had recorded that in the Thylacine "posteriorly the fibrous layer presents a slight attachment to the diaphragm", but "in the *Dasyure*, *Phalanger* and the *Phascogale* the fibrous pericardium presents no direct attachment to the anterior surface of the diaphragm. In *Cuscus*, however, a distinct fibrous band passed between these structures." In the wallaroo the pericardium was found to be separated from, and not in any way connected to, the diaphragm, the apex of the heart being anchored caudally by the left and right mediastinal pleurae which are in contact with each other in this region.

*The Aorta and its Branches* (Fig. 9).—Within the thorax the aorta is divisible into ascending and descending parts linked by the arch. The ascending aorta, which lies wholly within the pericardium, originates at the base of the left ventricle and issues from the confines of the heart bounded on the left by the left atrium, on the right by the right atrium and the more deeply situated pulmonary artery. Its direction is cranialwards with a slight inclination ventrally and to the left; the left side of the trachea lies dorsal to it. The arch of the aorta swings in a sharp even curve to the left, crosses the oesophagus, and, opposite the fifth intercostal space and dorsal of the root of the left bronchus becomes the descending aorta; the right half or less of the arch from which the innominate artery springs is included within the pericardium. The descending aorta passes caudalwards through the thorax immediately ventral of the bodies of the vertebrae somewhat to the left of the mid-dorsal line.

From the arch of the aorta two great vessels originate—on the right a large innominate artery, and about 1 cm. to its left, the left subclavian artery. The innominate rises from the arch ventral to the left border of the trachea where it abuts the oesophagus. It proceeds cranialwards for some 2.5 cm., ventral to the groove between the trachea and oesophagus. About 1.25 cm. from its origin, that is, at the middle of its length, it gives off the right subclavian artery, and then continuing straight on finally divides to form the right and left common carotids at the level of the head of the first rib. The right subclavian is directed cranio-laterally across the ventral face of the trachea, its course being parallel with that of the right common carotid which lies cranial to it. In the neck the right common carotid continues its course at the side of the trachea, the left between the oesophagus and trachea. The recurrent branch of the left vagus nerve, after hooking round the arch of the aorta, travels to the neck ventrally on the trachea and dorsal of the innominate and left common carotid. The left subclavian artery arises as a separate vessel, leaving the aortic arch where it becomes caudally directed, that is, about opposite the head of the fourth rib; its point of origin is in the median plane. On its left and dorsally lies the caudal end of the left longus colli, and on its right is the oesophagus which forms the floor of the space between this subclavian and the innominate viewed from the ventral side. As discussed elsewhere, the roots of the great vessels are to a large extent concealed by the thymus gland which lies on their ventral surfaces.

After the second, each intercostal space receives an artery in the usual way from the descending aorta. The first pair of aortic intercostal arteries supplying the third space are considerably longer than the succeeding members of the series; they arise opposite the head of the fifth rib from the dorsal surface of the aorta at the commencement of its descending part, and, proceeding cranio-laterally, dorsal first to the longus colli and then to the sympathetic trunk, so reach the intercostal space.

Pearson (1940) has summarized present knowledge on the variations in origin of the arteries arising from the aortic arch in marsupials. With the exception of *Halmaturus* (Bennett's Wallaby) (see Parsons, 1902, p. 394) and *Bettongia* in which three arteries spring from the arch, two is the rule in Macropodidae, namely, an innominate which by branching forms the two common carotids and the right subclavian, and the left subclavian which arises independently. The wallaroo belongs to Pearson's subdivision in which we find "the innominate long, with the right subclavian given off some distance from the base, behind the origins of the right and left common carotids". A similar condition was recorded by Parsons (1896) in *Petrogale xanthopus*, but in his later paper (1902) on the branches of the aortic arch in mammals a *Petrogale* is figured with the left common carotid leaving the innominate stem before the right subclavian. This last arrangement occurs in *Trichosurus vulpecula* (Sonntag, 1921).

*Venae Cavae*.—There are two anterior caval veins, a right and a left. Within the precardial mediastinum that on the right lies ventrally on the trachea and is directed towards the ventral side of the lung root. It debouches into the right atrium after receiving laterally the right vena azygos which crosses the trachea to join it. The phrenic nerve lies on its ventral aspect. The left anterior vena cava is the most ventral of the structures within the precardial mediastinum on its left side. In this region the subclavian and common carotid arteries, vagus and phrenic nerves and the thymus gland all lie dorsal to it. After crossing the arch of the aorta and receiving the left vena azygos the vein describes an arc to the right, round the base of the heart first between the left atrium and pulmonary veins and then between the latter and the left ventricle; it empties into the caudal end of the right atrium. The posterior vena cava after piercing the diaphragm traverses the fold of the vena cava and joins the left anterior vena cava where it enters the right atrium.

*Venae Azygos*.—The azygos veins are paired, that on the right being slightly the larger of the two. In the thorax they lie along the ventral aspect of the bodies of the vertebrae, one on each side of the descending aorta and ventral to the aortic intercostal arteries. Opposite the head of the sixth rib the right azygos turns sharply ventrally, crosses the trachea and empties into the right anterior vena cava just before it

pierces the pericardium. The left azygos turns similarly opposite the head of the fifth rib, and crossing the aorta at about the junction of its arch and descending part, communicates with the left anterior vena cava. Intercostal veins having the usual relationships to their accompanying arteries and nerves run from the intercostal spaces (caudal of the third) and open separately into the azygos of their own side.

Beddard (1907) investigated the azygos veins in marsupials and described their condition in a considerable range of macropods. Pearson (1940) has extended the data on the subject. The nearly equal veins present in the wallaroo approach what is regarded as the primitive arrangement of the vessels.

#### DISCUSSION.

"Amongst mammals there are two forms which carry their bodies in a really peculiar manner, these are the kangaroo and man" (Keith). Both types have been subjected to profound functional modification of the hinder end of the body—particularly in the structure of the limbs—for specialized methods of progression. In both the fore limbs have been released to a greater or lesser degree from their primitive function of supporting the cranial end of the thorax; in man this process has led to complete emancipation of the fore limb, in the kangaroos to a partial emancipation. The accompanying postural changes are, however, associated with structural adaptations which extend beyond those which are so obvious in the hind limbs and affect practically every part of the body. It is customary to designate the members of the family Macropodidae "semi-erect" as contrasted with man, the ultimate in bipedal uprightness. The general comparison implied is nominal since the evolutionary lines are so widely separated, and the mechanism underlying the postural changes differs so greatly in the two types. In the macropod, pectoral girdle and thorax modifications have been less profound than in the hinder end of the body, and structure has not been greatly varied by the requirements of a specialized function of the fore limb. It is of interest to institute a comparison with typical pronograde and orthograde types to assess the effect of the alteration in the orientation of the long axis of the body which has taken place side by side with the evolution of saltatory locomotion.

*General Form of the Thorax.*—The absence of curvature in the side walls of the wallaroo chest is one of its most marked features; also, in the semi-erect position, there is little or no thoracic curvature in the spinal column so that the thorax as a whole is conical in shape. These points are well brought out in the two radiographs (Plate xii); in the injected specimen from which they were made, the lungs had not collapsed so that, in all likelihood, a fairly faithful representation of the thorax (at least in one phase of its movement) is presented. Most published figures and museum examples of the articulated macropod skeleton show a ventrally-directed concavity in the line of the dorsal vertebrae, but the accuracy of such specimens of the articulator's art is doubtful, particularly as they are usually set up with the fore limbs well raised. Without examination and radiographs (preferably made on living specimens) of a selection of species of the family, it is not possible to say whether or no these observations on the form of the chest in the wallaroo are true of macropods in general. From my experience of several species in captivity and in the field, I am inclined to regard the wallaroo as typical in this respect. Absence of curvature, especially in the side walls of the thorax basket, is contrary to what is found in pronograde quadrupeds and man. It appears to be a skeletal modification (probably peculiar to animals in which progression by saltation is highly developed) caused by the caudalwards shift of the centre of gravity of the thorax as an integral part of the general shift in the same direction of the centre of gravity of the body as a whole. This migration of the mass of the thoracic viscera (mostly in the lungs) has brought about a considerable relative enlargement of the caudal end of the thorax at the expense of the cranial end and middle zone and has thus tended to eliminate curvature of the side walls. At the same time a very wide inferior aperture and a small superior aperture have been produced.

There are several points of importance in connection with the arrangement and form of the ribs. The general displacement caudalwards of the thoracic viscera

(*v. supra*) has been accompanied by a caudalwards movement of the ventral ends of the ribs so that they come to be articulated with the spinal column more obliquely than in quadrupeds generally, though less than in man; this obliquity is very noticeable in the case of the first rib. In man the inclination of the ribs, especially in expiration, is obvious and is correlated with orthograde posture; in typical quadrupeds, on the other hand, the hoops formed by the ribs tend to hang in a vertical plane as though suspended from the vertebral column. It will be seen, then, that in the wallaroo the angle which the ribs make with the spinal column is intermediate in size between the near-right angle found in pronograde quadrupeds such as the dog and the platypus and that characteristic of the higher primates. There seems little doubt that postural change in the wallaroo is associated with this alteration in rib inclination.

*Thoracic Index.*—Apart from the measurements made for taxonomic purposes, little statistical data referring to recent mammals other than man has been accumulated. There is an exception to this, however, in the thoracic index which has been made a subject of investigation by a number of workers principally for the purpose of tracing its changes with age and sex in man and seeking an explanation for the occurrence and distribution of narrow and broad chests in the various groups of the Mammalia. As might be expected, there is a notable lack of uniformity on the part of the various authors in making the measurements required. Davenport (1934), who listed the index in a large number of animals (including some marsupials), obtained his data from articulated museum skeletons. This author, in view of the exaggerated length of the vertebral spines of some mammals, selected points so as to omit the spine from the sagittal diameter (incidentally, his measurement extends dorsally only to the ventral head of the rib so that more than the spine is in reality subtracted). Such a procedure precludes comparison with results obtained from living material in which the length of the spinous process must be considered, and, though Davenport was aware of this, I think he underestimated its importance. Also, skeletons in museum collections have the possibly important disadvantage that often there is no record of their sex. In my series of wallaroos the two diameters were measured on a transverse plane passing through the xiphisternal joint and meeting the long axis of the vertebral column at right angles. The figures were obtained shortly after injection and were made with a pair of anthropometry callipers (Flower's type); the dorso-ventral diameter was taken between the superficial surface of the sternum and the line connecting the tips of the spinous processes. As mentioned elsewhere, the diameter was used as the divisor in computing the index following Fourmentin's original definition. The results (adult male 88, adult female 93, young female 68) are embodied in the table on p. 351. The difference between the adult male and female may be indicative of sexual dimorphism. An index of 68 for the young female (less than half grown) is very low and connotes a thorax with a high degree of lateral flattening. Davenport (1934) appears to be the only worker who has measured a kangaroo, and his figure, 119, for a species of *Macropus* is considerably in excess of the highest for the wallaroo (*M. robustus*), that is, 93 in the adult female. To make an adequate comparison the sagittal diameter of the chest of an articulated specimen of *Macropus rufus* housed in the osteological collection of this Institute was measured using both Davenport's points of reference and those advocated in this paper. This enabled an approximate correction factor to be estimated which, when applied to Davenport's result, brought about a reduction to 90. Looked at broadly with the limited data available and considering the thoracic cross-section as embracing the relevant section of the vertebral column and its associated muscles, it would seem that the adult wallaroo (which is probably typical of macropods in this respect) possesses a chest nearly circular in cross-section, such flattening as occurs being from side to side; the flattening is much less than in most quadrupeds. Weisgerber (quoted by Duckworth, 1904) gives an average index of 76 for a series of sixteen carnivores; the points used in measurement are not specified. Figures for man vary with age, sex and health; according to Weisman (1938) the value for a normal adult male is 149 (it is usually lower in females). Weisgerber's average figure for a group of twenty-seven Simiidae is 112. The wallaroo thus occupies an intermediate position. Chest shape is

sufficiently closely associated with habits (Davenport, 1934) for the suggestion to be advanced that the increase in index figure for the wallaroo arises from a structural adaptation in response to alteration in the forces operating on the thorax as a result of change in method of locomotion and posture.

*Muscles.*—Probably the majority of the more noticeable variations in the wallaroo chest and pectoral girdle are as much the legacy of previous arboreal life (it is generally agreed that the ancestors of the marsupials were tree inhabitants) as the outcome of changes which have taken place since a terrestrial life was adopted. Nevertheless, such changes are largely traceable to postural alteration, since the occurrence of variation can just as readily proceed from arboreal uprightness as a corresponding degree of terrestrial uprightness. The fore limb, being freed from participation in supporting the weight of the body or from acting as an adjunct to climbing activities, and at the same time not acquiring another function leading to other movements, would tend to show the somatic characteristics of a vestigial organ. In kangaroos, with the exception of the modern arboreal forms, the fore limbs, though weakly developed and relatively not much used as locomotory organs, are of great assistance to the animal in the slow progression practised during grazing. "When travelling slowly these animals move over the ground in a manner peculiar to themselves, swinging the legs forward between an arch formed by the arms and tail" (Le Souef and Burrell, 1926, p. 168). It will thus be seen that the fore limbs, though often and for considerable periods lifted clear of the ground, are not at all "emancipated" in the sense of the word as used when referring to man. Consequently the changes are not so great as might be anticipated by watching a kangaroo bounding along in full stride.

The pectoral girdle in the kangaroo is composed of a weakly-developed scimitar-shaped clavicle and a scapula which displays a marked increase in craniocaudal length in comparison with the extent of the Glenovertbral axis. Examination of a wide range of mammalian scapulae shows that this change in dimensions is common among arboreal and orthograde forms and usually gives rise to a relative increase in the size of the infra- as compared with the supraspinous fossa. In the terrestrial pronograde quadrupeds the scapula is not wide and generally has the fossae approximately equal or the supraspinous fossa the smaller. The shortness of the clavicles in the kangaroos causes the scapulae to be placed on the sides of the thorax (as in pronograde quadrupeds), so that they are almost parallel to one another, and anything comparable with the pronounced shoulder and flattened back of the primates, caused mostly by a pushing outwards and backwards of the ventral end of the scapula by the strutting action of the clavicle, is not present. The effect on fore limb mobility of the closeness of the scapula to the lateral walls of the thorax is obvious. Limb movement is almost entirely restricted to that of the vertical longitudinal plane, there being little scope for the side and rotatory motion which is a prominent feature of the primate fore limb. The restriction is reflected in the structure of the head of the humerus, the highest point of which is below the level of the tuberosities and is directed backwards approximately at right angles to the line passing through the condyles; this feature is essentially associated with the structure of the humerus in the terrestrial pronograde quadrupeds. Nevertheless, the range of movement possible to the arm is probably greater on the whole than in the average quadruped, which tends to move the fore limb only in the plane dictated by the requirements of locomotion. For instance, kangaroos have a limited ability to raise the hand above the head (Mackenzie, 1918). The anatomical basis of this lies in the highly-developed deltoid (which is thick and has an almost continuous origin along the spine of the scapula, round the acromion and onto the lateral two-thirds of the clavicle), and the relative shortening of the Glenovertbral axis of the scapula which makes its rotation—an integral part of arm movement—more easily effected. In the wallaroo the ventral serratus is well developed, but the trapezius, though having the same general arrangement as in the primates (it forms to all intents and purposes a single sheet) is very weakly developed where it is inserted onto the clavicle and acromion. Moreover, the

extension of the fibres onto the clavicle is limited, only the lateral fifth of the bone being involved. In man the upper portion of the trapezius is important "in elevating and rotating the acromion upwards", thus bringing about rotation of the scapula. This trapezius weakness in the wallaroo appears to be compensated for by the marked development of the ventral part of the omo-cleido-transversarius whose disposition fits it well to perform cranialwards rotation of the acromion. The fibres of the ventral part of this muscle have the same direction as those of the overlying trapezius and the insertion is continuous onto the lateral half of the scapular spine and the acromion with some of the most ventral fibres extending to the acromial end of the clavicle. The omo-cleido-transversarius as a whole probably imparts a strong translatory motion to the scapula. In the marsupials most records of the occurrence of the muscle appear to indicate the double condition, that is, a ventral and dorsal part; the extent of the insertion on the clavicle is very variable, and in several forms is much less than that described herein for the wallaroo. It is double in all kangaroos with the exception of the members of the genus *Dendrolagus* (*D. dorianus*, *lumholtzii* and probably *inustus*—Carlsson, 1914) and serves as a mark of distinction between the terrestrial and arboreal forms.

The remaining shoulder muscles call for little comment. The form of the head of the humerus and the manner in which the limb is bound to the side of the chest, make it unlikely that the humerus undergoes very much rotation, so that the principal function of the subscapularis, infraspinatus, supraspinatus and teres minor is to act mainly in keeping the head of the humerus in position. The teres minor is very weak.

In an animal such as man the pectoralis major (equivalent to the  $\alpha$  and  $\gamma$  pectoral of the wallaroo) has several functions largely the outcome of shoulder joint and pectoral girdle mobility. Together with the latissimus dorsi and teres major it is an adductor of the scapulo-humeral joint; it is responsible, with the serratus ventralis, for the ventral translatory movement of the scapula and is, in addition, an indirect forward rotator and depressor of the scapula (Steindler, 1935). Under certain conditions the pectoralis major and latissimus dorsi act as accessory muscles of respiration (Cunningham, 1937). In the wallaroo the pectoral mass is very well developed. The  $\beta$  division (probably homologous with the pectoralis minor of man) has a humeral attachment so that action on the scapula is indirect. At first sight, the occurrence of such a powerful pair of muscles across the ventral surface of the wallaroo chest seems somewhat anomalous. In tree-climbers the pectoralis major and the latissimus are the principal agents in drawing the body upwards when the hands have been fixed. No such function, however, is asked of these muscles in the terrestrial macropods. I am inclined to attribute the great development of the pectoral sheet primarily to its use in a manner comparable with that obtaining in typical quadrupeds, that is, as a ventral sling for the support of the thoracic end of the body and as an adductor of the fore limb. It will be remembered (*v. supra*) that in slow locomotion the fore limbs are extensively used. The wallaroo (and this applies to macropods in general) advances in slow movement by first fixing the fore limbs and tail so that they are in position to function as a tripod. The body and hind limbs are then elevated (so that the latter clear the ground) and drawn forward, causing the hind limbs to take up a position opposite and outside the fore limbs. Only then are the fore limbs and tail moved if necessary to be advanced for a repetition of the movement. It is thus clear that the pectoral mass is at times probably called upon to carry out more work than in the majority of quadrupeds, for not only must it take up much of the strain imposed on the fore limbs and tail when the hind limbs are free of the ground, but, in addition, it is the muscle in large part responsible for drawing the body through when the hind limbs are advanced (cf. the weak latissimus dorsi). Further, whereas in man the pectoralis major is only exceptionally utilized as an accessory muscle of respiration, it is likely that in kangaroos its function as such is of much greater frequency. In the wallaroo there is no clavicular part to the pectoral mass, the cranial-most fibres originating from the manubrium sterni and being directed at right angles to the long axis of the

body towards the humerus. A clavicular origin, however, has been recorded in the Macropodidae, for instance, by Parsons (1896) in *Petrogale xanthopus*.

The superficial pectoral in the wallaroo is particularly interesting in that it displays in a marked degree the so-called twisting of the caudal fibres which is responsible for their tendon of insertion finding attachment to the humerus proximal to that of the remainder and more cranial portion of the muscle. Very few workers who have dissected marsupials have recorded this peculiarity which is shared with man and most of the primates. Windle (1889) recorded only three cases from the Marsupialia, namely, *Phalangista vulpina*, *Dasyurus viverrinus*, and *Chironectes variegatus*. There does not appear to be any previous record of the occurrence in the Macropodidae. Owen's (1868) remarks would seem to indicate that the pectoralis major is "twisted" generally in marsupials. The feature is not restricted to the primates and marsupials, but is known to occur sparingly in several other orders of the Mammalia, especially in the Carnivora. The generally-accepted explanation that the tendon associated with the more caudal fibres (usually known as the "reflected portion") has twisted through an angle of 180° and thus gained a more proximal position of attachment on the humerus, does not seem to be a true picture of what has occurred. Harris (1939), for instance, says: "It would appear probable therefore, that the twisting of the tendon of the lowest portion of the pectoral is due to the gradual acquirement of a higher insertion on the humerus of the lowest fibres of the pectoral, which has thus doubled the tendon backwards, in order to give better leverage for depression of the humerus." Windle (1889) examined the available data and came to the conclusion that the apparently reflected portion of the pectoralis major was in reality a second more caudally placed part of what he calls the costal layer (the more cranial of the two being the pectoralis minor as understood in human anatomy), the caudal border of which had fused with the caudal border of the pectoralis major lying superficial to it, thus giving rise to a pocket open cranially. As Harris (1939) points out, by giving the fibres of the lower part of the pectoral a pull more nearly parallel to the long axis of the body, their power is accentuated so that the humerus may be depressed with greater force. This rearrangement is so much in accord with the requirements of the arboreal habit in which the pectoral mass and the latissimus dorsi are the chief agents in drawing the body upwards, that it appears rational to interpret its occurrence in terrestrial marsupials as a relic of arboreal activity, particularly useful to such kangaroos as possess it, in that greater power is required of the pectoral mass in the peculiar movements associated with slow locomotion.

It is curious that in the wallaroo neither the superficial pectoral layer nor the latissimus have supernumerary slips of origin from the costal arches, a fact which must weaken their action in modifying the shape of the thorax (as in respiratory movements, for example). In the case of the pectoral, connection with the ribs is precluded by the intervention of the rectus abdominus and supracostalis; it has, however, additional slips of origin from the latter.

*Respiration.*—Respiratory movements in mammals are designed to effect a rhythmic increase and decrease in the capacity of the thorax by means of muscle action and the intrinsic forces resident in the thorax basket. Attention must first be directed towards the means by which these movements are produced in four-footed animals and man, respectively. In quiet respiration in quadrupeds the fore limbs and scapula, by remaining relatively fixed, enable the muscles inserted thereto\* and attached also to the ribs to aid the external intercostals and intercartilaginous portions of the internal intercostals in drawing the ribs towards the shoulder girdle. During the movement the principal function of the diaphragm is to offer resistance to the increased pressure to which it then becomes subjected from the abdominal side. "This, for the most part, covers the range of activity of the diaphragm in the inspiration of most animals" (Wood Jones, 1926). An interesting fact concerning the extent of the necessity for action by the

\* Wood Jones (1926) includes the thoracic portion of the ventral serratus in this functional grouping, but other authors (Sisson, 1927, and Dukes, 1937) note its use only in forced inspiration.

diaphragm arose out of the work of Lemon (cited by Dukes, 1937), who discovered that dogs "in which the whole of the diaphragm was paralyzed by bilateral phrenic neurectomy ran and played like normal animals and after exercise could not be separated from normal dogs by those who were not acquainted with them". Thus, in dogs at least, the loss of the action of the diaphragm is not serious, and in any case it would seem that the muscles mentioned are the principal agents of inspiration. Expiration involves the return of the thorax to its original position by the effect of its own elasticity, the action of the interosseus portions of the internal intercostals and transversus thoracis muscles, together with those in the abdominal wall which exert pressure on the viscera and in consequence on the caudal face of the diaphragm. In quiet respiration of this type the amount of rib movement (especially in that part of the thorax bounded by the ribs which are united directly with the sternum) is not great; the abdominal movement is usually much more apparent.

In bipeds there has occurred an alteration of muscle function. The diaphragm becomes the most important of the inspiratory muscles, and when it contracts its descent causes enlargement of the thoracic cavity and a great increase in intra-abdominal pressure. In addition, the same sections of the intercostal muscles are active. In expiration, as in quadrupeds, the interosseus portions of the internal intercostals are involved, together with the muscles of the abdominal wall (rectus abdominis, internal and external obliques and transversus abdominis) which, by increasing the abdominal pressure and forcing the diaphragm upward toward the thoracic cavity, provide a strong expiratory "backstroke" (Steindler, 1935). The muscles (other than the intercostals) which in quadrupeds serve to elevate the ribs have, in man and other primates, "become muscles which produce added movements of the mobile fore limbs" (Wood Jones, 1926); they revert to their more primitive respiratory function during laboured breathing, especially when the fore limb is stabilized.

A considerable portion (perhaps most) of the locomotory activities of macropods are carried out with the fore limb free of the ground. This would automatically tend to lessen the inspiratory aid which such muscles as the great serrate and pectorals could render, since their pull on the ribs would, if at all evident, be greatly reduced with the fore limb in an unstable condition. It thus may be deduced that when leaping, a greater strain than usual being placed on the respiratory system, there would be a marked tendency for the inspiratory movements to be dependent on the diaphragm and relevant intercostals. In expiration under these conditions the abdominal muscles would probably be called upon to provide as much (or more) force on the abdominal contents as in man. Bearing these facts in mind and examining the musculature of the wallaroo as typical of macropods, considerable support was found for this view. The diaphragm is very well developed. In bipeds its dome is horizontal in position; in the wallaroo the degree of cranioventral obliquity is much less marked than in the pronograde mammals (Plate xii) and approaches the condition found in the orthograde primates. As pointed out by Keith (1923) attainment of the erect posture has been accompanied by this change in the orientation of the diaphragm and it would seem that in the wallaroo an intermediate condition is presented. The abdominal muscles in the wallaroo are strongly developed and the rectus abdominis, which is attached cranially to the first rib and the ventral surface of the manubrium sterni, is reinforced in its abdominal portion by a strong pyramidalis which lies superficial and in close contact with it; the rectus has no thoracic attachments exception those mentioned. This strengthening of the abdominal walls is, of course, associated with other than respiratory requirements. The caudalwards shift of the centre of gravity and the necessity for a firm counter to the tendency of the viscera to pull away from the diaphragm with each leap, have also, in all probability, been largely responsible. It is likely that the actual movement of leaping with the heavy pull which, on obvious mechanical grounds, must be rhythmically exerted on the caudal face of the diaphragm, is in itself an important factor in inspiration.

As mentioned above, there is comparatively little capacity for movements of expansion and contraction in the cranial end of the quadruped thorax. On the other

hand, in man, and in all orthograde primates, the apical region is of considerable respiratory importance, the ribs having been freed for movement by the caudal migration of the thoracic attachments of the rectus abdominis (Keith, 1923). In the wallaroo and all other macropods so far described the rectus still retains its primitive connection with the first rib, but restriction of this region by the rectus appears to be rendered less effective by the condition of the external intercostals. These muscles, cranial of the sixth rib, display a tendency for their superficial fibres to be continuous over two or three spaces. In addition, the second, third and fourth intercostal spaces are markedly wider than the first and those caudal of them (this feature is present, but not so obviously in man and probably in other mammals). The presumed outcome of such an arrangement could only be by the greater range of contraction of the external intercostals to increase the amplitude of rib movement in the area concerned, and so to enhance respiratory efficiency. The end result would appear to facilitate costal breathing, and represents a trend rather towards the human type and away from the quadrupedal type.

In connection with respiration one other feature in the structure of the thorax is worthy of mention. This is the manner in which the ventral ends of the cartilages continuous with ribs eight, nine and ten (Smith, 1916, would call these the respiratory ribs) are not successively bound by elastic tissue to the cartilage cranial of them, but lie free in the muscles. As has been previously mentioned (p. 360), the cartilage tips are united instead by bands of muscle in series with the external intercostals. It would appear that this arrangement gives much greater power of expansion and contraction throughout the zone of the costal arch, and may be regarded as an adaptation favouring increased respiratory efficiency in what is, in mammals generally, the more important region of the chest in breathing. The value of this structural modification will be patent when the underlying lung structure is considered (*v. infra*).

*Thoracic Viscera.*—The thoracic viscera show little or no significant change from the disposition and relationships observed generally in the pronograde mammals. The manner of fixation of the heart and the relationships of the pericardium have been discussed elsewhere in this paper (p. 376) and it has been shown that Sonntag's (1921) generalization that the pericardium is adherent to the diaphragm in all marsupials except *Trichosurus vulpecula* is incorrect. It might have been anticipated that with postural variation such as we see in macropods the pericardium would have shown closer association with the diaphragm, but even a pericardiophrenic ligament is not present in the wallaroo. Although the pericardium is not bound to the ribs or sternum except by loose connective tissue, the anchoring effect of the mediastinal pleurae is well marked. To this support by the pleurae must be added that of the great vessels cranially and the lungs laterally. Even then it is doubtful if the desired stability of the heart could be obtained without the support afforded by the azygos and cardiac lobes of the right lung. An azygos lobe to the right lung is a common occurrence in quadrupeds in which it occupies a median position between the heart and diaphragm. It has been postulated (*v. supra*) that the shift in position of the centre of gravity of the kangaroo body has caused a concentration of lung mass at the caudal end of the thorax, thus making this region of more than usual importance as a respiratory zone. The right lung, which is nearly twice as large as the left, has, in addition to a large azygos lobe occupying the subcardiac sinus, a large cardiac lobe (Fig. 8). By reference to the description of the fold of the vena cava, which forms the ventral boundary of the subcardiac sinus, it will be seen that the fold is obliquely placed across the median plane. Consequently, in addition to the sinus which houses the azygos lobe, there is another pocket between the ventral body wall and the ventral side of the fold of the vena cava which contains the cardiac lobe of the right lung. The heart is thus completely shut off from the diaphragm by lung tissue which forms a thick elastic buffer between the two structures, responsible, in all likelihood, for the absence of caudalwards displacement of the heart as an evolutionary trend correlated with change in posture. The mechanical advantage of having an organ such as the heart resting on a mass of elastic tissue during the violent shocks which the body as a whole sustains

in full saltatory movement, is apparent and to be regarded as adaptive to the method of progression and the orientation of the body.

#### SUMMARY.

An account is given of the anatomy of the pectoral girdle and thorax of the wallaroo (*Macropus robustus*), particular attention being directed to the muscles and the form and disposition of the viscera. Comparative notes from a survey of the literature are incorporated. The data obtained are used in an attempt to correlate certain aspects of structure with function. Comparisons are instituted where necessary with the conditions found in pronograde quadrupeds and orthograde primates.

Gravity shift is postulated as responsible for straightsidedness of the thorax and the heavy concentration of lung tissue at its caudal end.

The increase in the caudalwards obliquity of the ribs with the vertebral column is regarded as an adaptation due to postural change.

In considering the thoracic index it is shown that chest shape has evolved away from the keeled quadrupedal type towards the dorso-ventrally flattened type common to orthograde species.

The bones of the pectoral girdle and the head of the humerus are reported on briefly. Scapula proportions are observed to be similar to those found in mammals which have acquired "arboreal uprightness" and in orthograde forms. It is concluded that this is a postural modification. The shortening of the glenovertebral border of the scapula is correlated with the limited ability to raise the hand above the head which is possessed by macropods.

Arm movement in the wallaroo is examined from an anatomical standpoint and the ventral part of the omo-cleido-transversarius is suggested as a compensation for trapezius weakness in cranialwards movement of the acromion.

The function of the powerful pectoral mass is discussed in its relationship to the unusual method of slow locomotion practised by kangaroos. "Twisting" of the caudal fibres of the superficial pectoral is regarded as a relic of arboreal ancestry eminently useful to such macropods as possess it.

The probable respiratory situation in the Macropodidae is stated from consideration of the structural peculiarities and locomotory habits of the wallaroo. It is suggested that in saltatory movement the abdominal viscera are an active factor in augmenting inspiratory movements of the diaphragm. A respiratory significance is advanced for the external intercostal muscles associated with the wide second to fourth intercostal spaces, and also for the fact that the tips of the eighth to the tenth rib cartilages lie free in the muscles.

In the suspension of the heart the importance of the cardiac lobe of the right lung in joining with the azygos lobe to produce a support for the heart and a buffer between it and the diaphragm is discussed.

#### CONCLUSIONS.

From the discussion summarized above, it will be seen that the thorax and pectoral girdle of the wallaroo exhibit a number of structural modifications which are explicable if interpreted as associated with, and arising out of, the needs of postural change and peculiar locomotory habits. Some of these modifications (the orientation of the diaphragm and the obliquity of the ribs, for example) show a considerable degree of convergence when compared with the same features in orthograde primates. Some, such as the concentration of lung tissue at the caudal end of the thorax, may be peculiar to macropods and other saltatory forms. The relationship of the heart to the diaphragm is representative of a group of characteristics similar to those found in typical pronograde quadrupeds.

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## EXPLANATION OF PLATE XII.

Radiographs of the thorax which show the absence of curvature in the vertebral column and side walls. In A, the lateral view, the curvature of the diaphragm and the situation of the heart are clearly shown. Removal of the first rib on the right side has caused a slight displacement of the manubrium sterni. B is taken from the dorsal aspect.

## ON AUSTRALIAN DERMESTIDAE. PART I.

DESCRIPTIONS OF A NEW GENUS AND TWO NEW SPECIES; ALSO A NOTE ON THE  
GENUS ANTHRENUS.

By J. W. T. ARMSTRONG.

(Three Text-figures.)

[Read 24th September, 1941.]

*Introduction.*

This is the first of a short series of papers on Australian Dermestidae, a family, the Australian members of which have received very little attention during the last twenty-five years. With the exception of those in the South Australian Museum, they are not at all well identified in our collections. This is partially explained by the difficulty of identifying specimens, gummed on card, when many of the important generic and specific characters are on the under side.

I desire to express my thanks, for the loan of specimens, to the authorities of the South Australian, Australian and Macleay Museums, especially the first mentioned, who have sent me the whole of their collection (some 650 specimens), containing cotypes of most of Blackburn's species and two Lea types, without which it would have been almost impossible to make progress with such a difficult family. My thanks are also due to Mr. F. E. Wilson and Dr. K. K. Spence. I am greatly indebted to the late Mr. H. J. Carter for his encouragement and help. His death is a great loss to all who study Coleoptera. Thanks are also due to Mr. F. H. Taylor who prepared the microphotos of the antennae.

ANTHRENUS Geoffroy.

*Hist. Insect. Paris*, 1, 1762, 113; *Fauna Ins. Fridrichsdalina*, 12, 1764.

Of the several Australian species described before 1903 as belonging to this genus, all but one proved to be members of other genera (*vide* Blackburn, 1903, p. 172). *A. socius* Lea, of which the type is before me, has already been placed under *Trogoderma* in the Lea Collection and belongs to that genus. *A. ocellifer* Blackb., the only remaining species, is common in inland Australia. Arrow described a closely allied species, *A. frater*, from Tasmania in 1915. In the Lea Collection there are two specimens from Tasmania confused with *A. ocellifer* Blackb., that agree perfectly with Arrow's description. For these two species I now propose a new genus.

I know of two introduced species, *A. verbasci* L. (= *varius* F.) and *A. pimpinellae* F. There is a specimen of the latter, labelled "Townsville, Queensland, F. H. Taylor" in my collection. It is readily distinguished from the former by the broad transverse, unbroken band of pale grey scales at the base of its elytra.

Genus NEOANTHRENUS, n. gen.

Body compact, elliptical, densely squamose. Legs slender. Head visible from above. Pronotum anteriorly elevated, posteriorly angulate, abruptly narrowed in the anterior third. Mesosternum entirely bisected. Prosternum deeply and transversely excavated along the anterior margin to receive the antennae. Antennae short, 11-segmented, second segment large and subglobular, third to sixth transverse and moniliform, seventh and eighth moderately pectinate each bearing a stout seta, the remaining three forming a large, compact, sub-ovate, nearly cylindrical club.

This genus is close to *Anthrenus*, but is readily distinguishable by its oblong, much less rotund form, the extent to which the head is visible from above, and its anteriorly elevated pronotum. This latter characteristic and the densely squamose clothing differentiate it from *Anthrenocerus*, and its squamose body and the form of its antennae from *Orphinus* and *Trogoderma*.

Type, *Anthrenus ocellifer* Blackb.

Besides the two species previously described under *Anthrenus* (*A. ocellifer* Blackb. and *A. frater* Arrow), there are two undescribed species before me. Arrow has stated in his description of *A. frater* that this species and *A. ocellifer* Blackb. are the only two differing from other Anthreni in their "peculiar oblong shape, anteriorly elevated pronotum and abruptly clubbed 11-jointed antennae", so that it seems very probable that the genus is confined to Australia.

The four species of *Neoanthrenus* may be tabulated as follows:

- A. Form elongate, parallel; elytra scarcely wider than pronotum . . . . . *parallelus*, n. sp.
- AA. Form broader, elliptical; elytra noticeably wider than pronotum.
- B. Clothing consisting of smaller, more setiform scales . . . . . *frater* Arrow
- BB. Clothing consisting of larger and broader scales.
- C. Clothing nowhere fulvous, predominantly black . . . . . *niveosparsa*, n. sp.
- CC. Clothing largely fulvous . . . . . *ocellifer* Blackb.

NEOANTHRENUS FRATER (ARROW).

The two specimens before me are on loan from the South Australian Museum, so I do not feel justified in dissecting one, and therefore, since the antennae are partially concealed beneath the front edge of the prosternum, I am unable to examine the antennal joints, but, in view of the species being so close to *N. ocellifer* Blackb., I presume they are similar. (See Fig. 1A.)

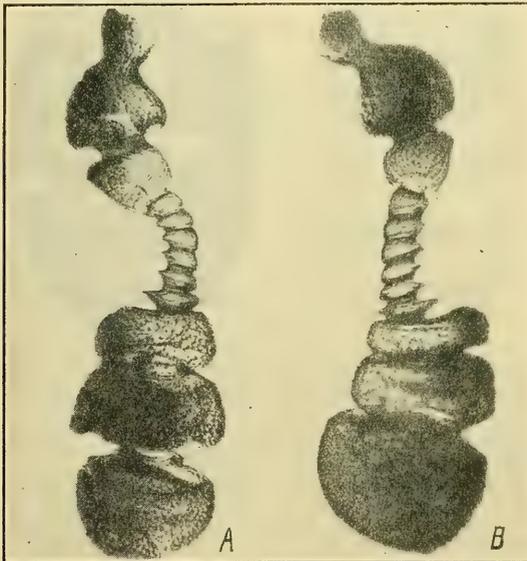


Fig. 1.—Antennae of *Neoanthrenus*. A, *N. ocellifer* Blackb.; B, *N. niveosparsa*, n. sp.

NEOANTHRENUS NIVEOSPARSA, n. sp. Figs. 1B and 3.

Elliptical, black, densely clothed with black and sparsely spotted with white scales, the latter inclined to form four rings on the elytra, two basal and two post medial, and becoming more extensive towards the margin of the pronotum; clothing of ventral surface white; densely punctate. Head visible from above. Pronotum transverse, at first gradually, then abruptly narrowed towards apex, convex, slightly depressed at base,

sides slightly emarginate, anterior angles obtuse, posterior acute, base biarcuate. Elytra expanded at shoulders, thence parallel for half their length, then evenly rounded to apex. Legs obscurely reddish. Antennae 11-segmented, first large and irregular, second large and subglobular, remainder transverse; seventh and eighth moderately pectinate, last three forming a massive club.

Length, 2.25-3 mm.; width, 1.25-1.75 mm.

Hab.—N.S.W.: Mullaley (H. J. Carter and the author); Galston (Dumbrell); Telegraph Point (the author).

Holotype in the author's collection, paratypes in the Australian, South Australian and Macleay Museums.

There are fifteen specimens of this species before me. In shape it is very similar to *Neoanthrenus ocellifer* Blackb., broader than *N. frater* Arrow, but from both of these, its predominantly black scales at once distinguish it. It shows little variation.

NEOANTHRENUS PARALLELUS, n. sp. Fig. 2.

Elongate, dark brown, clothed with closely packed scales, mostly ashy-white, but some brown tending to form an obscure pattern on the dorsal surface; closely and evenly punctate. Head visible from above. Pronotum transverse, sub-rectangular, convex, strongly depressed just in front of base; sides strongly emarginate, anterior angles obtuse, posterior slightly acute, widest at base which is biarcuate. Elytra scarcely wider than pronotum, one and one-half times as long as the combined width, parallel; posterior fifth evenly rounded to apex. Legs testaceous. Antennae 11-segmented, the terminal three segments forming a massive club.

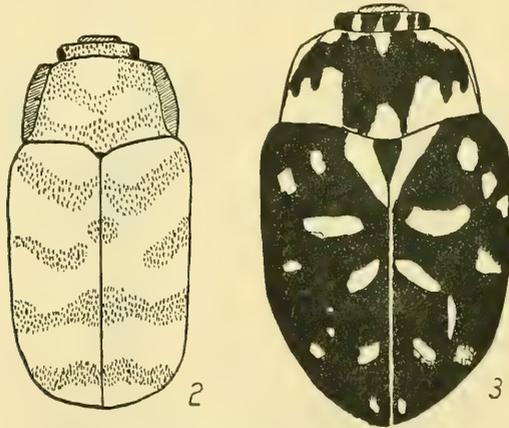


Fig. 2.—*Neoanthrenus parallelus*, n. sp.

Fig. 3.—*Neoanthrenus niveosparsa*, n. sp.

Length, 2.4-2.75 mm.; width, 1.1-1.2 mm.

Hab.—N.S.W., Lane Cove (ex Macleay Museum).

Holotype in the author's collection, paratypes in the Macleay Museum.

Six specimens before me are abundantly distinguished from the other three species by their pale and comparatively uniform colour and their elongate appearance, the sides being more parallel. The brown scales form an intricate pattern on the pronotum and four wavy, transverse, evenly spaced bands on the elytra, of which the first is interrupted at the suture and the second consists of two lateral, oblique patches and a pre-medial spot.

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## STUDIES IN TROMBIDIIDAE (ACARINA: TROMBIDIIDAE).

By CARL E. M. GUNTHER, M.D., B.S., D.T.M. (Sydney), Field Medical Officer,  
Bulolo Gold Dredging Limited, Bulolo, Territory of New Guinea.

[Read 29th October, 1941.]

## A. NEW GUINEA TROMBIDIID LARVAE: RECORDS OF NEW HOSTS AND LOCALITIES.

The following trombidiid larvae were taken in New Guinea between September, 1939, and March, 1940 (except the specimen from Manus, which was taken in 1935). I am deeply indebted to Mr. Tom Iredale, of the Australian Museum, for identifications of bird hosts.

1. TROMBICULA MINOR Berlese, 1905.
  - (a) *Principal host*: Bush fowl (*Megapodius reinwardt* Dumont, 1823), colonies on legs. Watut River valley.
  - (b) *Casual host*: Man. Watut River valley. (Seventy of these larvae have now been taken on eleven men.)
  - (c) *Casual host*: Pigeon (*Phlogaenas jobiensis* Meyer, 1875), Baiune.
  - (d) *Casual host*: Cat bird (*Ailuroedus melanocephalus* Ramsay, 1885), Bulolo.
2. SCHÖNGASTIA JAMESI Gunther, 1939.
  - (a) *Principal host*: Bush fowl, colonies on neck. Bulolo.
3. SCHÖNGASTIA BLESTOWEI Gunther, 1939.
  - (a) *Casual host*: Man. Manus, Admiralty Islands. (Fifty-five of these larvae have now been taken on nine men.)

This specimen was taken in 1935 by Dr. R. W. Cooper. I have to thank Dr. C. T. Backhouse, to whom Dr. Cooper gave it, for passing it on to me.
4. SCHÖNGASTIA TAYLORI Gunther, 1940.
  - (a) *Principal host*: Scrub wallaby (a local highland form of *Macropus (Thylogale) coxeni* Gray, 1866), colonies on legs. Watut River valley.
5. PARASCHÖNGASTIA BACKHOUSEI (Gunther, 1939).
  - (a) *Principal host*: Bush fowl, colonies on neck. Bulolo.
6. NEOSCHÖNGASTIA IMPAR Gunther, 1939.
  - (a) *Principal host*: Brown's rat (*Rattus browni* Alston, 1877), embedded between the scales all over the proximal fifth of the tail. Bulolo.
7. LEEUWENHOEKIA AUSTRALIENSIS Hirst, 1925.
  - (a) *Principal host*: Bush fowl, colonies inside ears. Bulolo.
  - (b) *Principal host*: Rufous shrike-thrush (*Caleyia megarhyncha* Quoy and Gaimard, 1830), colonies inside ears. Bulolo.
  - (c) *Principal host*: *Paradisaea minor* Shaw, 1809, colonies inside ears. Bulolo.
  - (d) *Principal host*: Whistler (*Pachycephala* sp.), colonies inside ears. Bulolo.
  - (e) *Principal host*: Stephan's pigeon (*Chalcophaps stephani* Pucheran, 1853), colonies inside ears. Baiune.
  - (f) *Principal host*: Cat bird (*Ailuroedus melanocephalus* Ramsay), colonies inside ears and on legs. Bulolo. Specimens up to  $667\mu \times 500\mu$  were taken on this host.
  - (g) *Principal host*: Pitta (*Pitta mackloti* Temminck, 1834), colonies inside ears. Baiune.
  - (h) *Casual host*: Fawn-breasted bower bird (*Chlamydera cerviniventris* Gould, 1850), Bulolo. Largest seen,  $723\mu \times 611\mu$ .
  - (i) *Casual host*: Ground thrush (*Eupetes caerulescens* Temminck, 1835), Baiune.

- (j) *Casual host*: Kingfisher (*Tanysiptera galeata* Gray, 1859), Baiune.  
 (k) *Casual host*: *Paradisaea* sp. (probably *P. raggiana*), Bulolo.  
 (l) *Casual host*: *Pitohui kirhocephalus* Lesson and Garnot, 1827. Bulolo.

B. LEEUWENHOEKIA AUSTRALIENSIS IN NEW GUINEA.

*Leeuwenhoekia australiensis* is, in Australia, a common parasite of man, and has been taken on the ears of a domestic cat; in the Celebes Walch found it on rats; but in New Guinea so far it has been taken only on birds. Of all the New Guinea mites it shows the greatest variability, particularly in the cheliceral teeth, the scutal measurements, and the body setae. Examination of a large number reveals a wide range, but all intermediate stages are present, and there is no doubt that only one species is represented. The following description is based on some forty specimens:

Genus LEEUWENHOEKIA Oudemans 1911.

*Ent. Ber.* 's-Grav., iii, No. 58, 137.

LEEUWENHOEKIA AUSTRALIENSIS Hirst 1925.

*Trans. Roy. Soc. Trop. Med. Hyg.*, xix, 150; Walch, *Geneesk. Tijdschr. v. Ned. Ind.*, lxxvii, 1927, 922; Gunther, this paper, p. 394; *L. australiensis* Hirst, 1929; Womersley, *Rec. S. Aust. Mus.*, v (2), 1934, 217. *L. australiensis* Hirst, 1925; Womersley, *Rec. S. Aust. Mus.*, vi (1), 1937, 82; Gunther, *Proc. Linn. Soc. N.S.W.*, lxiv, 1939, 73, 74, and 95. *Hannemania blestowei* [nom. nud.] Gunther, *Med. J. Aust.*, 1938, ii, No. 6, 202. *L. australiensis*, Gunther, this paper, p. 391.

Body usually oval, widest at level of coxae iii; sometimes with definite shoulders at level of coxae ii and tapering to a narrow rounded point; often with a shallow constriction behind coxae iii. Striations strong and fine, pitting on scutum, maxilla, and coxae. Colour pale orange to blood red. Newly hatched, L,\* 222 $\mu$ ; W, 209 $\mu$ ; largest seen, 723 $\mu$   $\times$  611 $\mu$ . Maxillary setae short, with five fine branches. Chelicerae stout, tapering abruptly to a fine sharp point. A row of 3 to 7 denticles along the dorsomedial side of the distal fourth; from 5 to 10 ventral denticles (usually one row of 5 or 6; when there are more than 6, there are 2 or 3 rows, but this is rare). A long nude seta on the base of each cheliceral sheath. Palpi rounded; a long curved seta with fine branches on the convex side, on ii; a similar seta, but very long and almost straight, on iii; on iv, a stout branched seta towards the apex and 2 nude setae near the base. Palpal claw bifurcate (trifurcate in 3 specimens), the medial element very long, stout, hooked at the end; the lateral element shorter, fine and straight. Appendiculum small and rounded, with one fine nude seta and four long branched setae. Scutum pentagonal, with a median anterior process; L, 65 $\mu$  to 75 $\mu$ ; W, 94 $\mu$  to 103 $\mu$ . Anterior process with parallel sides, rounded at the tip; L, 25 $\mu$  to 28 $\mu$ ; W, 10 $\mu$  to 12.5 $\mu$ . Anterior margin (except for the process) straight or slightly convex; anterior corners rounded; lateral margins diverging posteriorly, slightly concave; posterior margin strongly salient, the two halves straight, projecting to an obtuse rounded point; posterior corners rounded. The central portion of the scutum is occasionally raised, leaving the four lateral setae on a lower level than the others; in such a case the pseudostigmata are set in the posterior face of the raised portion. Scutal setae fine, with very short branches on all sides; the anteromedials 43 $\mu$  to 50 $\mu$  long, 13 $\mu$  to 19 $\mu$  apart, and set back from the anterior margin, in line with, or slightly behind the AL setae; AL, 38 $\mu$  to 53 $\mu$  long, in the anterior corners; PL, 63 $\mu$  to 78 $\mu$  long, in the posterior corners. Pseudostigmata two-thirds of the distance back, in line with or just behind the PL setae, 25 $\mu$  to 35 $\mu$  apart. Pseudostigmatic organs filiform, fine, with about 8 fine branches arranged roughly in pairs along the distal third; L, 50 $\mu$  to 63 $\mu$ . Ocular shield almost touching the scutum in newly-hatched specimens, up to 30 $\mu$  away in fully-engorged ones; 28 $\mu$  long, with its anterior margin opposite the anterior margins of the pseudostigmata. Eyes double, the anterior much the larger. Body setae 116 to 171, those of the dorsum with short branches on the convex side, the posterior setae with very short spine-like branches; those of the venter shorter and finer, with relatively longer branches. Dorsum, setae 58 to 83, in rows as follows: 2, 7 to 11, 2, 6 to 10, 2, 7 to 10, 2, 9 to 13, 2, 8 to 12, 6 to 10,

\* As in previous papers, L = length, W = width, AL = anterolateral, and PL = posterolateral.

4 to 6; rows 1, 3, 5, 7, and 9 are on the lateral margins of the body and are composed of somewhat stouter setae. In one case row 5 has 2 setae on one side. Row 11 is occasionally missing; row 12 is arranged in a semicircle or a square on the posterior pole of the body. Venter with 56 to 86 setae arranged irregularly over the posterior two-fifths, and one pair between coxae iii; there is no pair of setae between coxae i as is usual in the other genera of the family; instead there is an extra seta at the extreme tip of coxa i. The anus is situated two-thirds of the way back on the ventral surface. Legs relatively very long: i,  $340\mu$  to  $375\mu$ ; ii,  $265\mu$  to  $292\mu$ ; iii,  $375\mu$  to  $389\mu$ . Six elements in each leg, the first two and the last three retaining the characteristics of the corresponding segments in other genera. Leg setae long, fine, with a few long branches on the convex side. Coxal setae: on i, one at the anterolateral angle and one at the tip; one each on ii and iii. Bases of fifth segments all constricted. All tarsi long and tapering, the last two segments of iii especially long and slender. The spurs on tarsi i and ii fine and sharp; the dorsal nude seta on i prominent. No nude seta on iii. The lateral claws of the tarsi have a fringe of minute hairlets.

*Principal hosts:* Bush turkey (*Talegalla jobiensis* Meyer, 1874), Bush fowl (*Megapodius reinwardt* Dumont, 1823), Rufous shrike-thrush (*Caleyia megarhyncha* Quoy and Gaimard, 1830), *Paradisaea minor* Shaw, 1809, Whistler (*Pachycephala* sp.), Stephan's pigeon (*Chalcophaps stephani* Pucheran, 1853), Cat bird (*Ailuroedus melanocephalus* Ramsay, 1885), Pitta (*Pitta mackloti* Temminck, 1834); on all, colonies inside the ears, and on the cat bird colonies also on the legs. *Casual hosts:* Cassowary (*Casuarius casuarius* Linné), Pitohui (*Kirhocephalus* Lesson and Garnot, 1827, Fawn-breasted bower bird (*Chlamydera cerviniventris* Gould, 1850), Ground thrush (*Eupetes caerulescens* Temminck, 1835), Kingfisher (*Tanysiptera galeata* Gray, 1859), *Paradisaea* sp. (probably *P. raggiana*). *Habitat:* Bulolo and Baiune Rivers, Territory of New Guinea.

It will be seen that the New Guinea specimens agree with the Australian ones, but that there are slight differences between these and the Celebes specimens, mainly in the branching of the pseudostigmatic organs and the maxillary setae. These are of minor importance, and the general features of all groups come within the wide range of variation which appears to be possible in this species.

#### C. NOTES ON THE TROMBIDIID MITES OF THE NETHERLANDS EAST INDIES.

Most of the work on the Trombidiids of the Netherlands East Indies has been done by Walch. His surveys were very carefully and thoroughly carried out, and he is responsible for contributing much valuable information. However, on the question of the larval genera he adopted a conservative attitude; and while it must be granted that the larval genera of Oudemans, Ewing, and others are not permanent, nevertheless it cannot be hoped that many will be linked up with their corresponding adult genera for years yet, since the laboratory breeding of larvae to ascertain their adult form is a very difficult procedure. Meanwhile it is of the greatest practical importance in the study of the vectors of the *tsutsugamushibyō* group of diseases to have accurate means of distinguishing between all the various types of larvae, and for the convenience of workers in this field it is desirable to have all the known larvae accurately placed. This is the purpose of these notes; even though Walch brings some very convincing evidence that *Trombicula* and *Schöngastia* may belong to the same adult genus, and their very close association is proved by the fact that throughout the world members of these two genera alone attack man, yet so far only species of the genus *Trombicula* have been actually convicted as vectors. Hence for the present it seems more satisfactory to keep them apart.

The following list is intended to bring together all the East Indian mites under their correct larval genera. Where any species occurs in neighbouring areas, these are listed in parentheses.

#### Genus TROMBICULA Berlese 1905.

##### 1. TROMBICULA MINOR Berlese.

*T. minor* Berlese, 1905—*T. mediocris* Berlese, 1912—*T. pseudoakamushi* Hatori, 1919, after Walch, 1923, 1927.—*T. pseudoakamushi* var. *deliensis* Walch, 1924a.

JAVA, SUMATRA, CELEBES. (MALAYA, AUSTRALIA, FORMOSA, TERRITORY OF NEW GUINEA.)

2. TROMBICULA WICHMANNI (Oudemans).  
*Thrombidium wichmanni* Oudemans, 1905. *Microtrombidium wichmanni* Warburton, 1928.  
CELEBES, DUTCH NEW GUINEA. (BRITISH NORTH BORNEO.)
3. TROMBICULA DELIENSIS Walch.  
*Trombicula deliensis* Walch, 1923.  
SUMATRA. (MALAYA.)
4. TROMBICULA ACUSCUTELLARIS Walch.  
*Trombicula acuscutellaris* Walch, 1923. *Trombidium acuscutellare* Walch, 1927.  
SUMATRA. (MALAYA.)
5. TROMBICULA DENSIPILIATA Walch.  
*Trombicula densipiliata* Walch, 1923.  
SUMATRA.
6. TROMBICULA KEUKENSCHRIJVERI Walch.  
*Trombicula keukenschrijveri* Walch, 1924a.  
SUMATRA. (MALAYA.)
7. TROMBICULA RARA Walch.  
*Trombicula rara* Walch, 1924a.  
SUMATRA.

## Genus SCHÖNGASTIA Oudemans 1910.

8. SCHÖNGASTIA VANDERSANDEI Oudemans.  
*Thrombidium van der Sandei* Oudemans, 1905. *Microtrombidium vandersandei* Warburton, 1928. *Trombicula van der sandei* Walch, 1923, 1924a, 1924b, 1927. *Trombicula vandersandei* Patton and Evans, 1929.  
DUTCH NEW GUINEA.
9. SCHÖNGASTIA OUDEMANSI (Walch).  
*Trombicula oudemansi* Walch, 1923. (Capitate pseudostigmatic organs, Walch, 1923; chelicerae long and shaped like a saw, Walch, 1924a.)  
SUMATRA. (MALAYA.)
10. SCHÖNGASTIA SCHÜFFNERI (Walch).  
*Trombicula schüffneri* Walch, 1923. (Capitate pseudostigmatic organs and 5 or 6 cheliceral teeth, Walch, 1923.)  
SUMATRA.
11. SCHÖNGASTIA PSEUDO-SCHÜFFNERI (Walch).  
*Trombicula pseudo-schüffneri* Walch, 1927. (Capitate pseudostigmatic organs and saw-shaped extremity of chelicera, Walch, 1927).  
SUMATRA.

## Genus NEOSCHÖNGASTIA Ewing 1929.

12. NEOSCHÖNGASTIA SALMI (Oudemans).  
*Schöngastia salmi* Oudemans, 1922. *Schöngastia (Trombicula) salmi* (Oudemans) Walch, 1927. (Capitate pseudostigmatic organs but no cheliceral teeth, Walch, 1927.)  
JAVA.
13. NEOSCHÖNGASTIA INDICA (Hirst).  
*Schöngastia indica* Hirst, 1915. *Trombicula muris* Walch, 1923. *Schöngastia indica* Walch, 1927. *Trombicula indica (muris)* Patton and Evans, 1929.  
SUMATRA, CELEBES. (INDIA, MALAYA.)
14. NEOSCHÖNGASTIA GLOBULARE (Walch).  
*Trombidium (Trombicula?) globulare* Walch, 1927. (Capitate pseudostigmatic organs and a single cheliceral tooth, Walch, 1927.)  
CELEBES.

## Genus LEEUWENHOEKIA Oudemans 1911.

15. LEEUWENHOEKIA AUSTRALIENSIS Hirst.  
*Leeuwenhoekia australiensis* Hirst, 1925; Walch, 1927.  
CELEBES. (AUSTRALIA, TERRITORY OF NEW GUINEA.)

## Genus WALCHIA Ewing 1931.

## 16. WALCHIA GLABRUM (Walch).

*Trombidium glabrum* Walch, 1927. (Four scutal setae, capitate pseudostigmatic organs, Walch, 1927).

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 ———, 1925.—*Kitasato Arch. Exp. Med.*, vi, No. 3, 235.  
 ———, 1927.—*Geneesk. Tijdschr. v. Ned.-Ind.*, lxvii, 922.  
 ———, and KEUKENSCHRIJVER, N. C., 1924.—*Trans. 5th Bienn. Congr. Far East. Ass. Trop. Med.*, Singapore, 1923, 627.  
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THE DEVELOPMENT OF *Aedes (Pseudoskusea) concolor* TAYLOR IN  
RELATION TO SMALL QUANTITIES OF SALTS IN SOLUTION AND TO THE  
TEMPERATURE OF THE WATER.

By A. R. WOODHILL, Department of Zoology, University of Sydney.

[Read 26th November, 1941.]

*Introduction.*

In a previous paper (Woodhill, 1936) it was pointed out that further experiments on the effect of minute quantities of salts in solution should throw some light on the factors responsible for the limitation of the breeding places of *A. (P.) concolor*. In the following paper an account is given of experiments along these lines, together with the effect of different constant temperatures. The general technique of the experiments was similar to that previously described.

*Laboratory Experiments.*

Tables 1 and 2 give the details of the experiments with dilute solutions of salts, and Table 3 is a summary of the two preceding tables. The symbol S‰ or ‰ indicates grams of salts in solution per 1,000 grams of water. Table 4 gives the details of a series of experiments with sea-water and tap-water at constant temperatures of 70°F. and 80°F., and Table 5 is a summary of these results.

TABLE 1.

*First instar larvae of A. concolor, hatched in distilled water and transferred within twelve hours to various solutions plus food. Twenty larvae in each experiment. Constant temperature 70° F.*

No. of Exp.	Comp. of Water.	No. of 4th Instar Larvae.	No. of Pupae.	No. of Adults.	Mean per cent. Adults.
1		20	20	20	} 95
2		20	20	20	
3	Tap-water S‰ 0.06	19	19	19	
4		20	20	19	
5		20	20	17	
6	Dist. water	0		0	} 0
7	S‰ 0	0		0	
8		0		0	
9		0		0	
10		0*		0	
11	Dist. water	20	20	19	} 92
12	plus	20	20	19	
13	NaCl 0.095‰	20	20	18	
14	CaCl <sub>2</sub> 0.005‰	20	20	18	
15	S‰ 0.1	20	20	18	
16	Dist. water	20	20	19	} 94
17	plus	20	19	18	
18	NaCl 0.0475‰	20	20	19	
19	CaCl <sub>2</sub> 0.0025‰	19	19	19	
20	S‰ 0.05	20	19	19	
21	Dist. water	16	7	6	} 29
22	plus	20	6	6	
23	NaCl 0.02375‰	14	8	5	
24	CaCl <sub>2</sub> 0.00125‰	17	10	7	
25	S‰ 0.025	17	5	5	

\* All dead in first instar.

TABLE 2.

*First instar larvae of A. concolor, hatched in distilled water and transferred within twelve hours to various solutions plus food. Twenty larvae in each experiment. Constant temperature 70° F.*

No. of Exp.	Comp. of Water.	No. of 4th Instar Larvae.	No. of Pupae.	No. of Adults.	Mean per cent. Adults.
1		20	20	13	} 82
2	Dist. water	20	20	16	
3	plus	20	20	20	
4	NaCl 0.1‰	18	18	17	
5		19	18	16	
6		20	15	14	} 79
7	Dist. water	17	15	14	
8	plus	20	18	18	
9	NaCl 0.05‰	19	17	16	
10		19	19	17	
11		20	11	9	} 36
12	Dist. water	20	8	6	
13	plus	19	10	8	
14	NaCl 0.025‰	20	9	7	
15		17	8	6	
16	Dist. water	0*	—	—	} 0
17	plus CaCl <sub>2</sub>	0	—	—	
18	equivalent to	0	—	—	
19	NaCl 0.1‰	0	—	—	
20	in Cl content.	0	—	—	
21	Dist. water	0*	—	—	} 0
22	plus MgCl <sub>2</sub>	0	—	—	
23	equivalent to	0	—	—	
24	NaCl 0.1‰	0	—	—	
25	in Cl content.	0	—	—	
26	Dist. water	0*	—	—	} 0
27	plus KCl	0	—	—	
28	equivalent to	0	—	—	
29	NaCl 0.1‰	0	—	—	
30	in Cl content.	0	—	—	
31		0*	—	—	} 0
32	Dist. water	0	—	—	
33	plus	0	—	—	
34	Na <sub>2</sub> SO <sub>4</sub> 0.1‰	0	—	—	
35		0	—	—	
36		0*	—	—	} 0
37	Dist. water	0	—	—	
38	plus	0	—	—	
39	MgSO <sub>4</sub> 0.1‰	0	—	—	
40		0	—	—	
41		0*	—	—	} 0
42	Dist. water	0	—	—	
43	plus	0	—	—	
44	NaNO <sub>3</sub> 0.1‰	0	—	—	
45		0	—	—	

\* All larvae died before the third instar.

TABLE 3.  
Summary of Tables 1 and 2.

Comp. of Water.	Mean per cent. Adults.	Comp. of Water.	Mean per cent. Adults.
Tap-water, S‰ 0.06 .. ..	95	NaCl 0.025‰ .. .. .	36
Dist. water, S‰ 0 .. .. .	0	CaCl <sub>2</sub> equivalent in Cl to NaCl 0.1‰	0
NaCl 0.095‰, CaCl <sub>2</sub> 0.005‰, S‰ 0.1	92	MgCl <sub>2</sub> equivalent in Cl to NaCl 0.1‰	0
NaCl 0.0475‰, CaCl <sub>2</sub> 0.0025‰, S‰ 0.05 .. .. .	94	KCl equivalent in Cl to NaCl 0.1‰	0
NaCl 0.02375‰, CaCl <sub>2</sub> 0.00125‰, S‰ 0.025 .. .. .	29	Na <sub>2</sub> SO <sub>4</sub> 0.1‰ .. .. .	0
NaCl 0.1‰ .. .. .	82	MgSO <sub>4</sub> 0.1‰ .. .. .	0
NaCl 0.05‰ .. .. .	79	NaNO <sub>3</sub> 0.1‰ .. .. .	0

TABLE 4.

The development of A. (P.) concolor in sea-water and tap-water at 70° F. and 80° F. Twenty larvae in each experiment.

No. of Exp.	Water and Temp.	No. of 4th Instar Larvae.	No. of Pupae.	No. of Adults.	Mean per cent. Adults.
1	Tap-water S‰ 0.06 70° F.	16	16	16	88.0
2		20	20	20	
3		20	20	20	
4		20	19	19	
5		20	20	19	
6		20	20	17	
7		20	20	14	
8		20	20	17	
9		20	18	16	
10		20	20	15	
11		20	20	20	
12		20	19	16	
13		20	20	20	
14		19	18	17	
15		19	18	18	
16	Tap-water S‰ 0.06 80° F.	20	16	5	27.0
17		20	4	0	
18		20	16	8	
19		18	4	4	
20		20	16	9	
21		16	15	6	
22		20	18	4	
23		20	13	2	
24		20	16	1	
25		20	18	5	
26		18	17	8	
27		20	15	4	
28		17	16	4	
29		20	11	3	
30		15	5	1	
31		17	12	6	
32		20	18	10	
33		20	14	12	
34		19	15	12	
35		19	16	4	

TABLE 4—Continued.

The development of *A. (P.) concolor* in sea-water and tap-water at 70° F. and 80° F. Twenty larvae in each experiment.

No. of Exp.	Water and Temp.	No. of 4th Instar Larvae.	No. of Pupae.	No. of Adults.	Mean per cent. Adults.
36	Sea-water S‰ 35 70° F.	17	16	16	86.5
37		20	17	14	
38		20	20	17	
39		19	18	18	
40		20	20	20	
41		19	15	15	
42		19	19	19	
43		20	18	16	
44		20	20	20	
45		20	19	18	
46	Sea-water S‰ 35 80° F.	20	19	14	82.5
47		20	20	14	
48		20	20	20	
49		20	18	17	
50		20	20	19	
51		20	20	18	
52		20	17	13	
53		20	18	15	
54		20	19	18	
55		20	18	17	
56	Sea-water S‰ 35 transferred to S‰ 70 in 2nd instar. 80° F.	20	20	19	87.5
57		20	19	18	
58		20	18	18	
59		20	20	17	
60		20	20	17	
61		19	19	19	
62		19	17	16	
63		20	20	16	
64		20	19	19	
65		20	17	16	

TABLE 5.

Summary of Table 4.

Water and Temp.	Mean per cent. Adults.	Water and Temp.	Mean per cent. Adults.
Tap-water, S‰ 0.06, 70° F. ..	88.0	Sea-water, S‰ 35, 80° F. .. ..	82.5
Tap-water, S‰ 0.06, 80° F. ..	27.0	Sea-water, S‰ 70, 80° F. (transferred from S‰ 35 to S‰ 70 in 2nd instar) .. .. .	87.5
Sea-water, S‰ 35, 70° F. .. ..	86.5		

Discussion.

It will be seen from Table 3 that *A. concolor* will not develop in distilled water plus food, but will develop normally from egg to adult in tap-water (S‰ 0.06). When a balanced solution of NaCl and CaCl<sub>2</sub> is prepared, development takes place normally with a concentration as low as S‰ 0.05, but there is a significant mortality at S‰ 0.025. When NaCl alone is used, development is normal at S‰ 0.05, but again there is a high mortality at S‰ 0.025, while none of the other commonly-occurring salts, including KCl, give any development whatever. As Wigglesworth (1938) and Beadle (1939) have shown, the ability of a larva to develop in very dilute solutions depends on its capacity to take up chloride from the surrounding medium, and it is obvious that with *A. concolor* the critical amount of NaCl required is round about 0.025 gm. per thousand. The fact that there is a distinct difference between NaCl and either KCl, CaCl<sub>2</sub> or MgCl<sub>2</sub> agrees with Beadle's results for *A. detritus*, although in other respects the experiments are not

comparable. Beadle, however, states that *A. detritus* (a salt-water species very similar in habits to *A. concolor*) will live and develop in distilled water, but does not indicate whether this species was actually bred through from egg to adult in that medium. The amount of NaCl present in the food is a factor that should not be neglected in breeding experiments, since Beadle concludes that in *A. detritus* the chloride is taken up through the gut wall. *Culex pipiens*, a typical freshwater breeder, is stated by Wigglesworth (1938) to be unable to develop in distilled water, while *A. aegypti* can develop normally in that medium. The fact that *A. concolor* is never found in freshwater pools or swamps may possibly be due to lack of NaCl, but analyses of naturally-occurring freshwater and natural food, as compared with tap-water and artificial food, will be necessary before a definite statement can be made. However, the problem is now somewhat simplified since it has been shown that NaCl is the only salt in the surrounding medium of any significance, mere traces of the other necessary minerals in the food or water being sufficient for development.

From Tables 4 and 5 it will be seen that *A. concolor* will develop normally in tap-water and sea-water at a constant temperature of 70°F., or in sea-water (S‰ 35 or S‰ 70) at 80°F., but that a very high mortality occurs during the 4th instar and pupal periods in tap-water at 80°F. This may possibly be due to either excessive bacterial activity in tap-water at 80°F. as compared with sea-water at 80°F., since the food used forms a very suitable medium for bacterial development, or may be connected with the effect of temperature on the chloride uptake. However, no evidence on these points is yet available.

#### SUMMARY.

1. *A. concolor* will not develop in distilled water plus food.
2. Normal development from egg to adult takes place if NaCl is added to the distilled water at the rate of 0.1 or 0.05 gm. per thousand.
3. No very significant increase in the percentage of adults is obtained by substituting a mixture of NaCl and CaCl<sub>2</sub> in the proportion of 95 to 5, for the pure NaCl.
4. A high mortality occurs during the 4th instar when only 0.025 gm. NaCl per thousand is added.
5. No development takes place when either KCl, CaCl<sub>2</sub>, MgCl<sub>2</sub>, Na<sub>2</sub>SO<sub>4</sub>, MgSO<sub>4</sub> or NaNO<sub>3</sub> is added to distilled water at the rate of 0.1 gm. per thousand.
6. *A. concolor* will develop normally from egg to adult in tap-water (S‰ 0.06) or sea-water (S‰ 35) at a constant temperature of 70°F., or in sea-water (S‰ 35 and S‰ 70) at 80°F., but a very high mortality occurs in tap-water at a constant temperature of 80°F.

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## REVISION OF AUSTRALIAN LEPIDOPTERA. OECOPHORIDAE. X.

By A. JEFFERIS TURNER, M.D., F.R.E.S.

[Read 26th November, 1941.]

Two generic names proposed in Part ix are preoccupied. I propose to replace *Oxybeles* (p. 431) by *Oxypages* (οξυπαγης, sharp-pointed) and *Stenoptera* by *Ischnoptera* (ισχνοπτερος, narrow-winged). There are also some corrections and additions to the species which must be recorded.

763. *EULECHRIA PYCNODA* Low. should be transferred to *Coesyra* and follow *C. apora*.

979. *THALEROTRICHA HEMIPSILIA* Meyr. should be transferred to *Atheropla*.

1118. *TACHYSTOLA THIASOTIS* Meyr. *Philobota pyrsopis* Meyr., *Exot. Micro.*, ii, p. 385 is a synonym.

1159. *OCYSTOLA NIPHOSTEPHANA* Turn. is a synonym of *O. ochroptera* Meyr., which name should be substituted.

1168. *OCYSTOLA TYRIANTHINA* Turn. is a synonym of *O. chrysocolla* Turn., which name should be substituted. (Nambour; Brisbane; Rosewood; Toowoomba; Bunya Mts.; Talwood.)

1245. *COESYRA AMYLODES* Meyr. should be transferred to *Ocystola*. It may follow *O. mesoxantha* Meyr. (Ayr, Qd., to Murrurundi.)

1290. *COESYRA ACROTOPA* Meyr. should be transferred to *Philobota*.

1315. *EULECHRIA PSICHIODES* Meyr., *Exot. Micro.*, i, p. 219. This and the next species were accidentally omitted; they may follow (815) *E. plinthochroa*. The antennal ciliations in a male example (now in the National Museum, Melbourne) are 5. (Mt. Kosciusko; Gisborne.)

1316. *EULECHRIA LIMATA* Meyr., *ibid.*, i, p. 168. (Waroona, W.A.)

1317. *MACHAERITIS GYPSOMERA* Low., *Tr.R.S.S.Aust.*, 1920, p. 62. This may follow *M. neurota*. The type is in the National Museum, Melbourne. (Hobart.)

1318. *MACHAERITIS INNUMERA* Meyr., P.L.S.N.S.W., 1888, p. 1660. In this species vein 5 of the hindwings arises from below the middle and approximated to 4. In *M. hemisema* 5 arises similarly and 3 and 4 are stalked. I do not consider that these differences demand generic separation. (Duaringa; Gladstone; Brisbane.)

1319.† *OPSITYCHA MICROSTICTIS* Meyr., *Tr.R.S.S.Aust.*, 1902, p. 139. (Bathurst.)

1320. *OPSITYCHA DELOTYPA*, n. sp. (δηλοτυπος, distinctly marked.)

♂. 19–20 mm. Head and thorax white. Palpi with second joint just reaching base of antennae; terminal joint one-half; white, base of second joint dark fuscous. Antennae white with dark fuscous annulations; basal joint whitish; ciliations in male 3. Abdomen grey. Legs fuscous with whitish rings; posterior pair whitish. Forewings narrow, costa gently arched, apex pointed, termen very oblique; snow-white with blackish markings; a broad oblique streak from base of costa joining a triangular spot on one-fourth dorsum; a discal dot at one-third just above this; a small triangle on costa beyond middle confluent with a discal dot at two-thirds; an irregular tornal dot; a short line on costa before apex broadly connected with termen about middle; three or four terminal dots between this and tornus; cilia white. Hindwings and cilia grey-whitish.

Queensland: Injune in August; one specimen received from Mr. W. B. Barnard. Victoria: Daytrap; one specimen in National Museum, Melbourne.

114. Gen. *HA PALOMORPHA*, n.g. (ἀπαλομορφος, delicately formed.)

Tongue present. Palpi with second joint exceeding base of antennae, with appressed scales, slightly expanded and with some loose scales towards apex anteriorly; terminal joint shorter than second, slender, acute. Antennae nearly as long as forewings; basal

pecten not present; ciliations in male long. Forewings with 7 to termen. Hindwings lanceolate; neuration normal. The palpi are similar to those of *Opsitycha*, from which it differs in the longer antennae and the absence of an antennal pecten. It should follow that genus and precede *Ocystola*. In my key it falls with *Eulachna*, to which it is not allied, and is separated by its long antennae.

1321. HAPALOMORPHA ESTHLOPIS Turn., *Tr.R.S.S.Aust.*, 1917, p. 62 (Mt. Tamborine).

1322. OCYSTOLA AEOLIAS Meyr., P.L.S.N.S.W., 1888, p. 1612. This may come after *O. monostropha* Meyr. (Tasmania.)

1323. OCYSTOLA CNECOPASTA, n. sp. (*κνηκοπαστος*, sprinkled with pale yellow.)

♂. 18 mm. Head grey; side-tufts pale ochreous. Palpi with second joint exceeding base of antennae, terminal joint three-fourths; fuscous, inner surface and terminal joint whitish. Antennae fuscous; ciliations in male one and one-half. Thorax fuscous. Abdomen grey. Legs fuscous. Forewings narrow, costa gently arched, apex rounded, termen very oblique; grey with sparsely scattered ochreous scales here and there; costal edge dark fuscous towards base; a narrow whitish line on costa from base to three-fourths, edged towards base by ochreous scales; elsewhere these scales are loosely scattered, but more numerous towards termen; cilia grey. Hindwings and cilia pale grey. This should precede *O. lithophanes* Meyr., to which it is allied.

New South Wales: Mt. Kosciusko in January; one specimen.

1324. OCYSTOLA ISOLITHA Meyr., *Exot. Micro.*, i, p. 125. This should follow *O. lithophanes*. (Mt. Kosciusko, 5,000-6,000 ft.)

1325. OCYSTOLA LEUCOSTEMMA, n. sp. (*λευκοστεμμος*, white-crowned.)

♂. 14 mm. Head white. Palpi with second joint exceeding base of antennae, terminal joint one-half; whitish. Antennae whitish, towards apex grey; ciliations in male 1. Thorax ochreous. Abdomen grey. Legs fuscous; posterior pair whitish. Forewings narrow, costa slightly arched, apex pointed, termen very oblique; ochreous-yellow; cilia whitish-ochreous. Hindwings grey; cilia grey-whitish. Similar to *O. ochroptera* Meyr., which it should follow, but the forewings are narrower and without brownish tinge, the head is wholly white, and the thorax yellow.

West Australia: Kalamunda near Perth in December (W. B. Barnard); one specimen.

1326. OCYSTOLA CALLICHRYSA Low., *ibid.*, 1898, p. 53 = *trichroa* Meyr., *Tr.R.S.S.Aust.*, 1902, p. 141. This should precede *O. glycydora* Turn. (Sale; Mt. Gambier; Yale Paddock.)

1327. OCYSTOLA DELOGRAPHA, n. sp. (*δηλογραφος*, clearly marked.)

♀. 16 mm. Head and thorax white. Palpi with terminal joint three-fifths; white. Antennae fuscous. (Abdomen missing.) Legs whitish; anterior pair fuscous. Forewings slightly dilated, costa slightly arched, apex round-pointed, termen moderately oblique; brownish-ochreous partly suffused with fuscous; costal border and terminal area fuscous; markings white, clearly defined; a broad costal bar with rounded apex from base to one-third; another from base of dorsum to beyond middle, where it turns upwards, ending broadly beneath costa beyond middle, narrowly interrupted in mid-disc; an elongate subcostal spot before apex; a rounded spot above tornus, surmounted by a grey suffusion, through which two fuscous lines run to termen; cilia white, on apex greyish-tinged, on dorsum fuscous. Hindwings grey; cilia ochreous-whitish, on apex, tornus, and dorsum grey-whitish. This may be placed after *O. suppressella*.

New South Wales: Uki in October; one specimen received from Mr. W. B. Barnard.

1328. OCYSTOLA CYPHOMOCHLA, n. sp. (*κυφομοχλος*, with bent bar or fascia.)

♀. 18 mm. Head white. Palpi with second joint exceeding base of antennae, terminal joint two-thirds; white. Antennae white. Thorax white with broad post-median transverse fuscous bar. Abdomen grey; apices of segments and tuft whitish. Legs whitish; anterior pair fuscous. Forewings narrow, costa gently arched, apex pointed, termen straight, oblique; white with dark fuscous markings; an erect spot on base of dorsum; an outwardly oblique bar from one-third dorsum to beyond middle; a dot on three-fourths dorsum; a fascia from three-fourths costa to tornus, strongly bent inwards, its middle portion grey-brown; a terminal series of dots; cilia white with some dark fuscous points on tornus. Hindwings broadly lanceolate; whitish; cilia whitish. This should follow *O. clethrosema* Turn.

West Australia: Kalamunda near Perth in December (W. B. Barnard); one specimen.

1329. *OCYSTOLA ACATHARTA*, n. sp. (*ἀκαθαρτος*, impure.)

♀. 13 mm. Head yellow. Palpi with second joint exceeding base of antennae, terminal joint two-thirds; ochreous-whitish, terminal joint and a subapical ring on second joint fuscous. Antennae, thorax and abdomen fuscous. Legs fuscous; posterior pair mostly ochreous-whitish. Forewings narrow, costa almost straight, apex rounded, termen obliquely rounded; a narrow dark fuscous basal fascia prolonged on costa to one-third; basal and median areas yellow heavily sprinkled with grey except anteriorly; terminal area purple-fuscous, its edge from three-fifths costa to two-thirds dorsum; cilia fuscous, apices pale yellow. Hindwings and cilia fuscous. The coloration of the median area of forewings is characteristic. This should follow *O. proselia* Turn.

Queensland: Toowoomba in March (W. B. Barnard); one specimen.

1330. *OCYSTOLA ISOGRAMMA* Meyr., P.L.S.N.S.W., 1884, p. 779 (Sydney). This may precede *O. chrysocolla*.

1331. *OCYSTOLA ELECTRODES* Meyr., P.L.S.N.S.W., 1883, p. 509 = *ochrochoa* Low., *Tr.R.S.S.Aust.*, 1894, p. 101. This should precede *O. amyloides*. Palpi with second joint exceeding base of antennae, terminal joint three-fifths. Antennal ciliations in male 1. Hindwings broadly lanceolate. Its most characteristic feature is a very small pale fuscous mark above tornus of forewings. This is noted in Lower's description, but not in that of Meyrick. It is, however, often very faint and easily overlooked. It may not be constant, but I have found it always present in fourteen examples from seven different localities. (Stanthorpe to Hobart; from higher localities in Queensland and New South Wales, but coastal in Victoria and Tasmania.)

1332. *OCYSTOLA PYRGOPHORA*, n. sp. (*πυργοφορος*, carrying a tower.)

♂, ♀. 18 mm. Head yellow. Palpi with second joint exceeding base of antennae, terminal joint fourth-fifths; yellow. Antennae whitish annulated with fuscous; ciliations in male 2. Thorax yellow with median transverse fuscous bar. Abdomen grey; tuft pale ochreous. Legs pale ochreous; anterior pair partly fuscous. Forewings narrow, posteriorly dilated, costa almost straight, apex pointed, termen nearly straight, oblique; deep yellow; markings fuscous; a broad tornal spot narrowly prolonged to above middle at two-thirds, its apex sometimes detached to form a discal dot; an apical spot variably developed; cilia yellow, on spot fuscous. Hindwings and cilia fuscous. This should follow *O. mesoxantha* Meyr.

Queensland: Toowoomba in October and November (W. B. Barnard); two specimens. Type in Queensland Museum.

1333. *OCYSTOLA AUCHMERA* Turn., *Tr.R.S.S.Aust.*, 1917, p. 67. This and the following species may be placed at the end of the genus. (Cairns; Brisbane; Toowoomba.)

1334. *OCYSTOLA NIGRICINCTA* Meyr., *Exot. Micro.*, ii, p. 336. (Brisbane.)

1335. *OCYSTOLA ABARES*, n. sp. (*ἀβάρης*, light.)

♂. 10 mm. Head and thorax ochreous-whitish. Palpi with second joint just reaching base of antennae, terminal joint three-fifths; ochreous-whitish. Antennae grey-whitish; ciliations in male 4. Abdomen grey. Legs ochreous-whitish. Forewings posteriorly dilated, costa moderately arched, apex rounded, termen obliquely rounded; ochreous-whitish sprinkled with fuscous near base and in dorsal and terminal areas; stigmata fuscous, distinct, first discal at two-fifths, plical slightly beyond it, second discal at four-fifths, indistinctly double; cilia ochreous-whitish with some fuscous scales. Hindwings and cilia grey.

Queensland: Toowoomba in March; one specimen.

1336. *OCYSTOLA MICRASTIS* Low., P.L.S.N.S.W., 1900, p. 412. (Geelong; Adelaide.)

1337. *COESYRA PYROCENTRA* Low., *Tr.R.S.S.Aust.*, 1897, p. 53. This and the next three species belong to the narrow-winged section of the genus, and may be placed at its commencement. (Broken Hill.)

1338.† *COESYRA CENTROTHERMA* Low., *ibid.*, 1901, p. 88. (Broken Hill.)

1339. *COESYRA BASATRA* Low., *ibid.*, 1900, p. 43. (Broken Hill.)

1340. *COESYRA EREMOPOLA*, n. sp. (*ἐρημοπολος*, haunting the desert.)

♂. 23-25 mm. Head and thorax pale reddish. Palpi with terminal joint two-fifths; fuscous-reddish. Antennae fuscous; ciliations in male 1. Abdomen pale grey. Legs fuscous-reddish; posterior pair ochreous-whitish. Forewings narrow, posteriorly dilated, termen straight to near apex; apex rounded, termen very oblique; ochreous-whitish suffused with pale reddish and sometimes sprinkled with fuscous; stigmata usually minute, reddish or fuscous-reddish, first discal at two-fifths, plical before it, second discal at two-thirds; cilia pale reddish, bases sometimes fuscous. Hindwings pale grey; cilia pale grey or ochreous-whitish. This follows *C. basatra*.

South Australia: Ooldea in July (J. A. Kershaw); two specimens. Also one from West Australia.

1341. COESYRA DROSERODES Low., *Tr.R.S.S.Aust.*, 1907, p. 116. This should follow *C. zalias* Low. (Broken Hill; Pinnaroo.)

1342. COESYRA APORA Meyr., P.L.S.N.S.W., 1883, p. 381. This may follow *C. xanthocoma* Low. (Duaranga to Broken Hill and Birchip; Kimberley, Broome.)

1343. COESYRA TORPENS Meyr., *Exot. Micro.*, ii, p. 382. This should follow *C. aclea* Meyr. (Sydney.)

1344. COESYRA MEDIOCRIS, n. sp. (*mediocris*, tolerable.)

♂. 18 mm. Head and thorax brown-whitish. Palpi with terminal joint two-thirds; brown-whitish, external surface of second joint except apex pale fuscous. Antennae whitish with fuscous annulations; ciliations in male one and one-half. (Abdomen missing.) Legs brown-whitish; anterior pair fuscous. Forewings moderate, costa rather strongly arched, apex rounded, termen oblique; brown-whitish lightly sprinkled with small brown scales; extreme base of costal edge fuscous; cilia brown-whitish. Hindwings whitish-grey; cilia whitish. Should be placed after *C. panchrysa*, which it resembles in wing-shape.

North Queensland: Kuranda in September; one specimen received from Mr. F. P. Dodd.

1345. COESYRA PERSONATA Meyr., P.L.S.N.S.W., 1884, p. 774. This should be placed after *C. phricomita* Turn. (Brisbane to Melbourne.)

1346. COESYRA PLEUROPHAEA, n. sp. (*πλευροφαιος*, with dusky costa.)

♂. 14 mm. Head pale yellow. Palpi with terminal joint two-thirds; pale yellow, basal half of outer surface of second joint fuscous. Antennae fuscous; ciliations in male 4. Thorax fuscous, anterior edge pale yellow. Abdomen fuscous. Legs fuscous; posterior pair whitish-ochreous. Forewings dilated posteriorly, costa moderately arched, apex round-pointed, termen oblique; pale yellow with fuscous markings; a broad costal streak from base narrowing to a point at three-fourths; a narrow inwardly-curved fascia from four-fifths costa to tornus; cilia fuscous. Hindwings and cilia grey. This should follow *C. triptycha* Meyr.

North Queensland: Gordonvale near Cairns; type in Coll. Lyell.

1347. COESYRA KERSHAWI Low., *Tr.R.S.S.Aust.*, 1893, p. 293. Meyr., 1902, p. 138. (Glen Innes; Scone; Melbourne; Bothwell, Tas.) This, with the next two species, should follow *C. dichroella* Zel.

1348. COESYRA COMOXANTHA Meyr., P.L.S.N.S.W., 1888, p. 1657. (Geraldton.)

1349.† COESYRA CROCINASTIS Meyr., *ibid.*, 1888, p. 1656. (Carnarvon.)

1350.† COESYRA PSILOSTOLA Meyr., *ibid.*, 1888, p. 1661. Unknown to me. I am not sure that it comes under this genus. (Sydney.)

#### Key to Genera.

I have modified the latter part of the key given in Part ix and extended it as far as *Philobota*.

36. Tongue absent .....	<i>Sphaerelictis</i>
Tongue present .....	37
37. Anterior tibiae thickened with scales .....	<i>Aristeis</i>
Anterior tibiae not thickened .....	38
38. Hindwings with 4 absent .....	<i>Periorycta</i>
Hindwings with 4 present .....	39
39. Forewings with 10 absent .....	<i>Syscalma</i>
Forewings with 10 present .....	40
40. Forewings with 2 and 3 stalked .....	41
Forewings with 2 and 3 separate .....	46

41. Forewings with 7, 8, 9 stalked .....	<i>Zatrichodes</i>
Forewings with 9 separate .....	42
42. Antennae without basal pecten .....	<i>Cryptopeges</i>
Antennae with basal pecten .....	43
43. Antennae thickened with scales on dorsum .....	<i>Pycnocera</i>
Antennae not thickened .....	44
44. Palpi with second joint not reaching base of antennae .....	<i>Eudrymopsis</i>
Palpi with second joint reaching base of antennae .....	45
45. Palpi with second joint clothed with rough scales above and beneath .....	<i>Trachyzancla</i>
Palpi not so .....	<i>Chezala</i>
46. Ciliations of male antennae minute .....	47
Antennal ciliations moderate or long .....	48
47. Antennae without basal pecten .....	<i>Machetis</i>
Antennae with basal pecten .....	<i>Sphyrrelata</i>
48. Thorax with posterior crest .....	49
Thorax without crest .....	51
49. Forewings with tufts of raised scales .....	<i>Pyrgoptila</i>
Forewings smooth .....	50
50. Antennae without basal pecten .....	<i>Actenista</i>
Antennae with basal pecten .....	<i>Mesolecta</i>
51. Palpi with second joint not reaching base of antennae .....	52
Palpi with second joint reaching base of antennae .....	57
52. Palpi with terminal joint one-third or less .....	53
Palpi with terminal joint one-half or more .....	54
53. Palpi with terminal joint minute .....	<i>Hemibela</i>
Palpi with terminal joint not less than one-fourth .....	<i>Hippomacha</i>
54. Antennal pecten large and dense, covering front of eye .....	<i>Calypta</i>
Antennal pecten normal .....	55
55. Anterior tibiae and tarsi dilated with dense scales .....	<i>Crepidosecles</i>
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59. Antennae without basal pecten .....	60
Antennae with basal pecten .....	61
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65. Antennae nearly as long as forewings .....	<i>Hapaloteucha</i>
Antennae four-fifths .....	<i>Philobota</i>

115. Gen. ZATRICHODES Meyr. (*Exot. Micro.*, i, p. 247.)

Tongue short. Palpi recurved, ascending; second joint not reaching base of antennae, thickened with dense scales; terminal joint shorter than second. Antennae nearly 1; dilated with dense projecting scales on posterior edge; without basal pecten; ciliations in male moderate. Forewings with 2 and 3 stalked, 7, 8, 9 stalked, 7 to termen. Hindwings elongate-ovate; neuration normal. All tibiae and basal joint of posterior tarsi densely clothed with long spreading hairs. Type *Z. thyrsota* Meyr. from Ceylon. There are only two species known.

1351.† ZATRICHODES HORRIFICA Meyr., *Exot. Micro.*, ii, p. 512. (Darwin.)

116. Gen. PYCNOCERA Turn. (*Tr.R.S.S.Aust.*, 1896, p. 21.)

Tongue present. Palpi smooth-scaled; second joint not reaching base of antennae; terminal joint shorter than second. Antennae with basal pecten; in male obtusely dentate, each dentation ending in a tuft of cilia, thickened with scales on dorsum. Forewings with 2 and 3 stalked, 7 to termen. Hindwings ovate; neuration normal. Monotypical.

This must not be confused with *Cryptopeges* Butl. In the latter the male antennae are neither dentate nor thickened, there is no antennal pecten, and the second joint of the palpi reaches the base of the antennae.

1352. PYCNOGERA HYPOXANTHA Turn., *Tr.R.S.S.Aust.*, 1896, p. 22, and 1917, p. 102. In the latter citation the statement that the antennal pecten is usually absent is erroneous. The disparity in size between the sexes is striking. (Nambour to Lismore.)

117. Gen. CRYPTOPEGES Butl. (*Ann. Mag. Nat. Hist.*, (5) ix, 1882, p. 100.)

Tongue present. Palpi smooth; second joint reaching or exceeding base of antennae; terminal joint shorter than second. Antennae without basal pecten; ciliations in male long. Forewings with 2 and 3 stalked, 7 to termen. Hindwings elongate-ovate; neuration normal. Type *C. fulvia* Butl. *Enchronista* Meyr. is a synonym. Four species.

1353. CRYPTOPEGES FULVIA Butl., *ibid.*, p. 101; Meyr., P.L.S.N.S.W., 1884, p. 732. Antennal ciliations of male extremely long (6) and dense (Victoria).

1354. CRYPTOPEGES ICASTA, n. sp. (*εικαστος*, similar.)

♂. 18–20 mm. Head, thorax, and abdomen fuscous. Palpi with second joint reaching base of antennae, terminal joint one-third; fuscous. Antennae fuscous; in male sparsely ciliated in tufts, ciliations three and one-half. Legs fuscous; posterior pair ochreous. Forewings suboblong, costa moderately arched, apex rounded, termen nearly straight, slightly oblique; fuscous with fine whitish irroration; cilia whitish, bases fuscous, on tornus wholly fuscous. Hindwings ochreous-yellow; a fuscous terminal band, broadest at apex, with some fuscous irroration on its margin; cilia fuscous.

Distinct from the preceding by its antennal structure, but otherwise very similar. Minor differences are the whitish irroration and apices of cilia of forewings, and the blurred outline of the yellow area of the hindwings.

West Australia: Perth; Waroona in September; two specimens.

1355. CRYPTOPEGES PROXIMELLA Wlk., xxviii, p. 490; Meyr., P.L.S.N.S.W., 1884, p. 733. (Lindeman I. to Melbourne and Mt. Lofty.)

1356. CRYPTOPEGES BATHROSTICHA Turn., *P.R.S.Tas.*, 1926, p. 150. (Tasmania.)

118. Gen. EUDRYMOPSIS Low. (*Tr.R.S.S.Aust.*, 1903, p. 228.)

Tongue present. Palpi smooth-scaled; second joint not reaching base of antennae; terminal joint shorter than second. Antennae with basal pecten; ciliations in male moderately long. Palpi with 2 and 3 stalked, 7 to termen. Hindwings elongate-ovate; neuration normal. Type *E. xyloscopa* Low. Meyrick records an additional species from India.

1357.† EUDRYMOPSIS XYLOSCOPIA Low., *ibid.*, 1903, p. 228. (Broken Hill.)

1358. EUDRYMOPSIS ORITES, n. sp. (*ὄρειτης*, a mountaineer.)

♂. 22 mm. Head and thorax fuscous. Palpi with terminal joint one-half; fuscous. Antennae fuscous; ciliations in male 1. Abdomen and legs fuscous. Forewings with costa moderately arched, apex round-pointed, termen obliquely rounded; pale fuscous; discal dots at two-fifths and three-fifths, often obsolete; cilia pale fuscous. Hindwings and cilia dark grey.

New South Wales: Mt. Kosciusko in December; three specimens received from Mr. G. M. Goldfinch, who has the type.

Gen. TRACHYZANCLA Turn. (*Tr.R.S.S.Aust.*, 1917, p. 79.)

This was included in Part viii. I give a revised definition of this genus, which is a derivative of *Chezala* differing in the roughly-coated palpi.

Tongue present. Palpi with second joint more than twice length of face, expanded towards apex, clothed with rough scales above and beneath; terminal joint much shorter than second, slender, acute. Antennae with basal pecten; ciliations in male long. Forewings with 2 and 3 stalked, 7 to termen. Hindwings elongate-ovate; 5 from middle or from nearer 4 than 6. Type, *T. histrica* Turn. (Cunderdin, W.A.)

1359. TRACHYZANCLA OCHROBAPTA Low., *Tr.R.S.S.Aust.*, 1920, p. 64. ♂. 28–34 mm. Head and thorax white. Palpi with second joint more than three times length of face, terminal joint one-half; white, base of second joint grey. Antennae white; in male strongly dentate with fascicles of long cilia. Abdomen whitish-grey. Legs grey; posterior

pair whitish. Forewings sub-oblong, costa strongly arched, apex rectangular, termen rounded, oblique; white; cilia white. Hindwings broadly ovate; pale grey; cilia whitish. ♀. 44 mm. Head, thorax, and palpi grey. Forewing narrower, apex pointed, termen more oblique; pale grey. (Duaringa; Milmerran; Talwood, Injune.)

119. Gen. CHEZALA Wlk. (xxix, p. 787.)

Tongue present. Palpi with second joint smooth; exceeding or much exceeding base of antennae; terminal joint shorter than second. Antennae with basal pecten; ciliations in male sometimes moderate, but usually long. Forewings with 2 and 3 stalked, 7 to termen. Hindwings elongate-ovate or broadly ovate; 5 usually from middle, but sometimes from nearer 4, and less often from nearer 6. Type, *C. privatella* Wlk. A natural genus comprising thirty-two Australian species and one from New Guinea.

*Trachyzancla* Turn. should be removed from the position previously assigned to it and precede *Chezala*, of which it is a derivative, differing in its peculiar palpi.

1360. CHEZALA BRACHYPEPLA MEYR., P.L.S.N.S.W., 1882, p. 524. (Bundaberg to Victoria.)

1361. CHEZALA CARPHALEA MEYR., P.L.S.N.S.W., 1884, p. 731 = *cosmia* Turn., *Tr.R.S.S.Aust.*, 1898, p. 209 = *passalias* MEYR., *Exot. Micro.*, i, p. 122. (Townsville to Tweed Hds.)

1362. CHEZALA ABSONA Turn., *Tr.R.S.S.Aust.*, 1917, p. 80. (Daly R., N.A.)

1363. CHEZALA MACULATA, n. sp. (*maculatus*, spotted.)

♂. 17-20 mm. ♀. 24 mm. Head ochreous-whitish. Palpi with second joint much exceeding base of antennae, terminal joint four-fifths; ochreous-whitish, base of second joint fuscous. Antennae grey; ciliations in male two and one-half. Thorax dark fuscous. Abdomen grey; tuft whitish-ochreous. Legs fuscous with ochreous-whitish rings; posterior pair ochreous-whitish. Forewings broad, costa strongly arched, apex rounded-rectangular, termen straight, slightly oblique; white; markings dark fuscous; a basal fascia; a fascia from one-third costa to two-thirds dorsum sometimes interrupted into a small costal and large dorsal spot; a spot on two-thirds costa connected with a tornal spot to form an oblique fascia; a terminal fascia; cilia ochreous-whitish, on tornus fuscous. Hindwings elongate-ovate; grey; cilia whitish with a grey sub-basal line.

North Queensland: Cape York in November and April; four specimens received from Mr. W. B. Barnard, who has the type.

1364.† CHEZALA ERYTHRASTIS MEYR., P.L.S.N.S.W., 1888, p. 1626. (Sydney.)

1365.† CHEZALA EURYCAPNA MEYR., *Exot. Micro.*, ii, p. 313. (Brisbane.)

1366. CHEZALA ELLENELLA NEWM. *Tr. Ent. Soc.*, iii, (n.s.), p. 295; Pl. 18, f. 3.

♂, ♀. 22-30 mm. Head and thorax brownish-grey. Palpi very long; second joint 5 times length of face; terminal joint two-fifths; fuscous, extreme apex of second joint whitish-ochreous. Antennae ochreous-whitish annulated with fuscous; ciliations in male 6. Abdomen fuscous; tuft whitish-ochreous. Legs fuscous; hairs on posterior tibiae whitish-ochreous. Forewings dilated, costa gently arched, apex rounded, termen slightly rounded, oblique; light brownish-grey; costal edge near base fuscous; sometimes a fuscous discal dot before two-thirds; cilia concolorous. Hindwings with termen gently rounded, slightly sinuate beneath apex; ochreous-yellow; a suffused fuscous terminal band, broad at apex, gradually narrowing and not reaching tornus; cilia pale fuscous. Nearly allied to *C. conjunctella*.

Queensland: Stanthorpe. New South Wales: Ben Lomond; Ebor. Victoria: Mt. Alexander Range; Castlemaine.

1367. CHEZALA CONJUNCTELLA Wlk., xxix, p. 686; MEYR., P.L.S.N.S.W., 1884, p. 736. (Eidsvold to Moruya.)

1368. CHEZALA PRIVATELLA Wlk., xxix, p. 753; MEYR., *ibid.*, 1884, p. 737 = *latiorella* Wlk., xxix, p. 755 = *allatella* Wlk., xxix, p. 788. (Cairns to Melbourne.)

1369. CHEZALA TORPIDA Turn., *Tr.R.S.S.Aust.*, 1917, p. 81. (Stradbroke I.; Tweed Hds.; Mt. Tamborine; Toowoomba.)

1370. CHEZALA MINYRA MEYR., *Exot. Micro.*, i, p. 221 = *nugax* MEYR., *ibid.*, ii, p. 382. (Cairns.)

1371. CHEZALA LEPARGA Turn., *Tr.R.S.S.Aust.*, 1917, p. 108. (Cairns; Atherton.)

1372. *CHEZALA FICTILIS* Meyr., *Exot. Micro.*, i, p. 248. Palpi with second joint exceeding base of antennae, terminal joint two-thirds; white, basal half of external surface of second joint fuscous. Antennal ciliations in male 2. Forewings ochreous-whitish; sometimes slight grey irroration near dorsum and in terminal area; first discal and plical absent, a minute second discal with an additional dot beneath it usually present. (Robertson; Allyn R.; Gosford; Sydney.)

1373. *CHEZALA LUCENS* Meyr., *Exot. Micro.*, i, p. 302. ♂. 20–26 mm. Antennae without dentations, ciliations 4. Forewings with minute fuscous stigmata, first discal at one-third, plical beneath it, second discal before two-thirds; terminal area with faint grey suffusion between veins. ♀. 20–32 mm. (Darwin; Banks I.; Cape York; Dunk I.; Atherton. I have not seen an example from the first locality.)

1374. *CHEZALA FLACCIDA* Meyr., *ibid.*, i, p. 126. (Margaret R.; Waroona; Perth.)

1375. *CHEZALA CARPHODES*, n. sp. (*καρφωδης*, straw-coloured.)

♂. 20–23 mm. Head pale ochreous; sides of face fuscous. Palpi with second joint reaching base of antennae, terminal joint three-fifths; pale ochreous, basal three-fourths of second joint fuscous. Antennae grey becoming pale ochreous towards base; ciliations in male 3. Thorax pale ochreous. Abdomen whitish-ochreous; tuft pale ochreous. Legs fuscous; posterior pair pale ochreous. Forewings moderate, sub-oblong, costa rather strongly arched, apex rounded-rectangular, termen scarcely oblique; rounded beneath; pale ochreous; base of costal edge and dots fuscous; first discal at one-third, plical beyond it, second discal before two-thirds; a curved line of dots, sometimes indistinct or obsolete, from beneath five-sixths costa to tornus; cilia pale ochreous. Hindwings and cilia whitish-ochreous.

Queensland: Macpherson Range (3,000–4,000 ft.) in December and January; abundant but only the one sex taken.

1376. *CHEZALA BUTYRINA*, n. sp. (*βουτυρινος*, butter-coloured.)

♂. 16 mm. Head whitish-ochreous. Palpi with second joint reaching base of antennae, terminal joint two-thirds; whitish, lower part of external surface of second joint fuscous. Antennae fuscous; ciliations in male 1. Thorax fuscous. Abdomen grey; tuft grey-whitish. Legs fuscous; posterior pair whitish. Forewings narrow, costa gently arched, apex rounded, termen straight, oblique; whitish-ochreous; markings fuscous; a narrow basal fascia slightly prolonged on costa; a large quadrangular terminal blotch, edged by a wavy line from two-thirds costa to two-thirds dorsum; cilia fuscous, apices whitish-ochreous, on tornus wholly fuscous. Hindwings and cilia grey-whitish.

Queensland: Macpherson Range (3,500 ft.) in December; one specimen.

1377.† *CHEZALA GLAPHYROPLA* Meyr., *P.L.S.N.S.W.*, 1884, p. 735. (Hobart; Coles Bay.)

1378. *CHEZALA INCONSTANS*, n. sp. (*inconstans*, variable.)

♂. 19–22 mm. Head and thorax whitish-ochreous. Palpi with second joint exceeding base of antennae, terminal joint two-thirds; whitish-ochreous; second joint fuscous except at base and apex. Antennae ochreous-whitish annulated with fuscous; ciliations in male slightly over 1. Abdomen whitish-ochreous, apices of segments whitish; dorsum of first two segments fuscous. Legs fuscous; posterior pair whitish. Forewings narrow, slightly dilated, costa slightly arched, apex pointed, termen slightly rounded, very oblique; ochreous-whitish or pale grey; usually a minute fuscous dot before two-thirds; cilia ochreous-whitish. Hindwings with apex and termen rounded; pale grey; cilia pale grey. In some examples the thorax and basal costal area of forewings are suffused with ochreous or orange. All the stigmata may be absent, or rarely all may be developed with plical beneath first discal.

West Australia: Collie and Albany; abundant in November; a series taken.

1379.† *CHEZALA MARCENS* Meyr., *Exot. Micro.*, i, p. 220. (Hoyleton, S.A.)

1380. *CHEZALA ALEURIAS* Turn., *Tr.R.S.S.Aust.*, 1917, p. 80. (Cairns.)

1381. *CHEZALA OSTEOCHROA* Turn., *ibid.*, 1898, p. 210. (Mt. Tamborine; Tweed Hds.; Macpherson Rge.; Toowoomba; Killarney.)

1382. *CHEZALA LIOPA* Turn., *P.R.S.Tas.*, 1926, p. 150. (Cradle Mt.)

1383. *CHEZALA ANAXIA*, n. sp. (*ἀναξιος*, of little worth.)

♀. 26–28 mm. Head and thorax grey. Palpi with second joint exceeding base of antennae, terminal joint three-fifths; grey, apex of second joint whitish. Antennae grey,

towards base whitish. Abdomen pale grey. Legs grey; posterior pair whitish-ochreous. Forewings sub-oblong, costa rather strongly arched, apex rounded-rectangular, termen rounded, slightly oblique; whitish-grey; stigmata pale fuscous, minute, first discal at one-third, plical beyond it, second discal at three-fifths; cilia whitish with a faint grey basal line. Hindwings with apex and termen rounded; grey-whitish; cilia whitish.

Victoria: Beaconsfield in October; two specimens.

1384. *CHEZALA ATERPNA*, n. sp. (*ἀτερπνος*, unattractive.)

♂. 22 mm. Head and thorax ochreous-grey. Palpi with second joint reaching base of antennae, terminal joint two-thirds; pale ochreous-grey. Antennae pale grey; ciliations in male 5. Abdomen grey. Legs pale grey; posterior pair ochreous-whitish. Forewings sub-oblong, costa arched at base, thence nearly straight, apex sub-rectangular, termen straight, slightly oblique; pale ochreous-grey with fuscous dots; first discal at one-third, plical beneath it, second discal at middle; an outwardly curved series of dots from four-fifths costa to tornus; cilia ochreous-grey. Hindwings ovate; pale grey; cilia pale grey.

North Queensland: Kuranda in September; one specimen received from Mr. W. B. Barnard.

1385. *CHEZALA RHADINA*, n. sp. (*ῥαδινος*, slender.)

♂, ♀. 14-18 mm. Head ochreous-whitish. Palpi with second joint reaching base of antennae, terminal joint three-fourths; ochreous-whitish with a few fuscous scales. Antennae ochreous-whitish; ciliations in male two and one-half. Thorax ochreous-whitish with a few fuscous scales. Abdomen ochreous-whitish. Legs ochreous-whitish; anterior pair dark fuscous on dorsum. Forewings narrow, somewhat dilated posteriorly, costa gently arched, apex acute, termen straight, oblique; ochreous-whitish with a variable amount of fuscous irroration; dots fuscous; first discal before one-third, plical slightly beyond it, second discal before two-thirds; a submarginal series of dots before termen; cilia ochreous-whitish with some fuscous scales. Hindwings and cilia whitish.

Queensland: Mt. Tamborine in November; Macpherson Range (3,000-3,500 ft.) in December and January; eight specimens.

1386.† *CHEZALA ISOCYCLA* Meyr., *Arkiv. f. Zool.*, xiv (15), p. 8. (Cooktown; Atherton.)

1387. *CHEZALA OMOPHAEA*, n. sp. (*ὀμοφαίος*, dark-shouldered.)

♂. 14-15 mm. Head and thorax ochreous-whitish. Palpi with second joint exceeding base of antennae, terminal joint three-fourths; whitish. Antennae grey; ciliations in male one and one-half. Abdomen ochreous-grey; apices of segments and tuft whitish-grey. Legs ochreous-whitish; anterior pair grey. Forewings narrow, suboval, costa moderately arched, apex obtusely pointed, termen oblique; ochreous-whitish posteriorly sprinkled with fuscous; markings fuscous; a broad but short basal costal streak; stigmata small, first discal at one-third, plical slightly beyond, second discal at two-thirds; a suffused terminal series of dots; cilia ochreous-whitish. Hindwings and cilia whitish.

Victoria: Beaconsfield (Dr. W. E. Drake) in March; two specimens received from the National Museum, which has the type.

1388. *CHEZALA DIMALEA*, n. sp. (*δαιμαλεος*, timid.)

♂. 14-16 mm. Head white. Palpi with second joint reaching base of antennae, terminal joint two-thirds; white, second joint except apex fuscous. Antennae pale grey; ciliations in male 3. Thorax pale fuscous. Abdomen grey; tuft whitish. Legs grey; posterior pair whitish. Forewings suboval, costa gently arched, apex round-pointed, termen oblique; white with fuscous dots; some fuscous suffusion at base of dorsum; first discal at one-third, plical beyond it, second discal before two-thirds, double, connected by fuscous suffusion with costa and tornus; terminal area beyond this grey; a terminal series of minute dots; cilia white, on tornus grey. Hindwings and cilia whitish.

North Queensland: Babinda near Innisfail in September; three specimens.

1389. *CHEZALA ADELOSEMA* Low., *Tr.R.S.S.Aust.*, 1920, p. 65 (Cairns).

1390. CHEZALA TORVA, n. sp. (*torvus*, gloomy.)

♀. 22–23 mm. Head, thorax and antennae pale ochreous-brown. Palpi with second joint much exceeding base of antennae, terminal joint one-half; whitish. Abdomen pale grey. Legs grey; posterior pair ochreous-whitish. Forewings narrow, costa strongly arched, apex pointed, termen oblique; pale ochreous-brown; markings fuscous; first discal at one-third, plical beyond it, second discal before two-thirds; some fuscous irroration in terminal area; an outwardly rounded series of dots from four-fifths costa to tornus; cilia pale ochreous-brown with a fuscous sub-basal line. Hindwings ovate; pale grey; cilia pale grey.

Queensland: Macpherson Range (3,000–3,500 ft.) in October and November; two specimens.

1391.† CHEZALA SPRETA Meyr., *Exot. Micro.*, ii, p. 382. (Busselton, W.A.)

## 120. Gen. PYRGOPTILA Meyr. (P.L.S.N.S.W., 1888, p. 1600.)

Tongue present. Palpi long, smooth, slender; second joint exceeding base of antennae; terminal joint shorter than second. Antennae with basal pecten; in male moderately ciliated. Thorax with a posterior crest. Forewings with tufts of scales; 7 to termen. Hindwings elongate-ovate; neuration normal. A small endemic genus of uncertain affinities. Type, *P. serpentina* Meyr.

1392. PYRGOPTILA PRAECANA Meyr., *Exot. Micro.*, i, p. 128 = *penthistis* Low., *Tr.R.S.S.Aust.*, 1923, p. 54. (Dorrigo; Pt. Macquarie; Gosford.)

1393. PYRGOPTILA CALLIDESMA Low., *ibid.*, 1894, p. 96. (Windermere, Tas.)

1394. PYRGOPTILA PLATYLEUCA, n. sp. (*πλατυλευκος*, broadly white.)

♂. 24–26 mm. Head whitish. Palpi whitish; base of second joint fuscous. Antennae whitish with slender fuscous annulations; ciliations in male one and one-half. Thorax grey; apices of tegulae and a posterior spot whitish. Abdomen brown; tuft and under-side whitish. Legs whitish; anterior pair and middle tarsi fuscous with whitish rings. Forewings elongate, not dilated, costa gently arched, apex pointed, termen obliquely rounded; whitish with patchy brownish suffusion and sparsely scattered fuscous scales; markings fuscous; a short longitudinal streak from base of costa; a costal spot beyond middle; a discal dot at one-third connected with a dorsal dot at one-third forming an oblique bar; a costal spot before apex connected by an oblique brownish suffusion with a dorsal dot at two-thirds; cilia whitish-grey with more or less distinct fuscous bars. Hindwings grey-whitish; cilia whitish.

New South Wales: Maryland near Stanthorpe, Qd.; three specimens received from Mr. W. B. Barnard. Type in Queensland Museum.

1395.† PYRGOPTILA SERPENTINA Meyr., P.L.S.N.S.W., 1888, p. 1600. (Perth.)

1396.† PYRGOPTILA ZELOTIS Meyr., *Tr.R.S.S.Aust.*, 1902, p. 142. (Launceston.)

## 121. Gen. MACHETIS Meyr. (P.L.S.N.S.W., 1883, p. 331.)

Tongue present. Palpi long, smooth, slender; second joint reaching or exceeding base of antennae; terminal joint shorter than second. Antennae without basal pecten; ciliations in male minute. Thorax with a posterior crest. Forewings smooth; 7 to termen. Hindwings elongate-ovate; neuration normal. Type, *M. aphroboia* Meyr. A small endemic genus with nine known species. Its exact relationship is obscure, for I do not attach much weight to the minute male antennal ciliations, but in structure it does not seem remote from *Pyrgoptila*.

1397. MACHETIS DELTOTYPA, n. sp. (*δελτοτυπος*, marked with a triangle.)

♂. 12–16 mm. Head and thorax fuscous. Palpi with second joint reaching base of antennae, terminal joint two-thirds; whitish, outer surface of second joint except a subapical band fuscous. Antennae whitish annulated with dark fuscous; in male somewhat thickened and dentate. Abdomen grey. Legs dark fuscous with white rings; posterior pair whitish. Forewings narrow, costa gently arched, apex obtusely pointed, termen slightly rounded, strongly oblique; white with sharply defined dark fuscous markings; a basal patch, its outer edge concave from one-fourth costa to one-third dorsum; a midcostal triangle with somewhat irregular edge, its apex sometimes reaching mid-disc; a large apical spot giving off a fine line towards tornus; sometimes a spot or some irroration above tornus; terminal edge white; cilia grey-whitish with some fuscous bars. Hindwings and cilia pale grey.

North Queensland: Atherton Tableland in September. Queensland: Macpherson Range (low level) in November. New South Wales: Lismore in October; five specimens.

1398. *MACHETIS LATICINCTA* Turn., *Tr.R.S.S.Aust.*, 1917, p. 115. (Mt. Tamborine.)

1399. *MACHETIS EUDMETA* Turn., *ibid.*, 1917, p. 115. (Mt. Tamborine; Brisbane; Macpherson Rge., 2,500–3,500 ft.; Stanthorpe. N.S.W.: Ebor.)

1400. *MACHETIS DIAMOCHLA*, n. sp. (*διαμοχλος*, with a bar right through.)

♂, ♀. 16–20 mm. Head white sprinkled with blackish. Palpi with second joint exceeding base of antennae, terminal joint three-fifths; white sprinkled with blackish. Antennae white; ciliations in male one-half. Thorax with a moderate posterior crest; white mixed with blackish. Abdomen pale grey. Legs ochreous-whitish; anterior pair fuscous. Forewings narrow, costa gently arched, apex pointed, termen oblique; white; markings and some irroration blackish; a broad streak from base of costa along fold, curved upwards to three-fifths costa, thence curved and ending on costa near apex; some irroration on base of costa and before termen and tornus; cilia white with blackish points. Hindwings and cilia pale grey.

Queensland: Maryborough in September; Toowoomba in October; Bunya Mts. in December; five specimens.

1401. *MACHETIS MESOPLACA*, n. sp. (*μεσοπλακος*, with median blotch.)

♀. 15–18 mm. Head fuscous or fuscous-whitish. Palpi with second joint reaching base of antennae, terminal joint three-fifths; whitish, terminal joint except base and apex, and a subapical ring on second joint, fuscous. Antennae grey. Thorax with a small posterior crest; fuscous. Abdomen grey. Legs ochreous-whitish; anterior pair fuscous. Forewings narrow, costa gently arched, apex pointed, termen very oblique; fuscous with whitish markings; a transverse fascia at one-third broadening in middle into a round ante-median blotch; a small bent fascia from three-fourths costa to tornus; a fuscous discal spot at two-thirds; a pale terminal line; cilia whitish. Hindwings and cilia pale grey.

North Queensland: Atherton Plateau (Millaa-Millaa) in September; Eungella in October. Queensland: Bunya Mts. in November; three specimens.

1402. *MACHETIS APHROBOLA* Meyr., P.L.S.N.S.W., 1883, p. 331. (Brisbane to Hobart.)

1403. *MACHETIS PLAGIOZONA* Turn., *Tr.R.S.S.Aust.*, 1917, p. 114. (Brisbane; Toowoomba.)

1404. *MACHETIS SERPENTIGERA*, n. sp. (*serpentigerus*, carrying a snake.)

♂. 18–22 mm. Head fuscous-brown. Palpi with second joint reaching base of antennae, terminal joint two-thirds; brownish. Antennae pale grey; in male minutely ciliated (one-sixth). Thorax high-crested; anteriorly fuscous-brown, posteriorly fuscous. Abdomen whitish-ochreous. Legs grey; posterior pair whitish-ochreous. Forewings sub-oblong, costa moderately arched, apex round-pointed, termen oblique; grey; a long bisinuate fuscous streak from one-fifth costa, above middle of disc, before termen sharply curved to end above tornus; a white discal spot edged with fuscous before two-thirds; cilia grey. Hindwings and cilia pale grey.

Queensland: Toowoomba in October; two specimens received from Mr. W. B. Barnard. Type in Queensland Museum.

1405.† *MACHETIS VERSATRIX* Meyr., *Exot. Micro.*, i, p. 171. (Gisborne.)

## 122. Gen. SPHYRELATA Meyr. (P.L.S.N.S.W., 1883, p. 360.)

Tongue present. Palpi with second joint reaching base of antennae, much thickened with appressed scales; terminal joint slender, shorter than second. Antennae with basal pecten; ciliations in male minute. Forewings with 7 to termen. Hindwings elongate-ovate; neurulation normal. Type, *S. amotella* Wlk. A small endemic genus of uncertain affinities.

1406. *SPHYRELATA MELANOLEUCA* Meyr., *ibid.*, 1883, p. 363. (Brisbane; Gosford; Sydney; Barrington Tops.)

1407. *SPHYRELATA AMOTELLA* Wlk., xxx, p. 1034 = *indecorella* Meyr., *ibid.*, 1883, p. 362, *nec* Wlk. = *laetifica* Turn., *Tr.R.S.S.Aust.*, 1917, p. 116. (Stanthorpe and Milmerran to Sydney and Melbourne.)

1408. *SPHYRELATA INDECORELLA* Wlk., xxix, p. 764. (Brisbane.)

1409.† *SPHYRELATA ESCHARIAS* Meyr., *Exot. Micro.*, ii, p. 402. (Gisborne.)

## 123. Gen. LEISTOMORPHA Meyr. (P.L.S.N.S.W., 1883, p. 509.)

Tongue present. Palpi with second joint reaching or exceeding base of antennae, slender or only slightly thickened with appressed scales; terminal joint shorter than second. Antennae with weak basal pecten; ciliations in male moderate or rather long. Middle and posterior tibiae with median and posterior whorls of rough hairs. Forewings with 7 to termen. Hindwings elongate-ovate; neuration normal. An Australian genus. In the type species, *L. brontoscopa*, the tibial whorls are dense and composed of very long hairs; in the other species they are moderate or short. In the new species described below the palpi are extremely long.

1410. LEISTOMORPHA MACROZANCLA, n. sp. (*μακροζαγλος*, with long sickles.)

♀. 16-17 mm. Head, thorax, and abdomen fuscous. Palpi slender, second joint five times as long as face, terminal joint one-half; fuscous. Antennae fuscous. Legs fuscous; whorls of hairs on middle and posterior tibiae moderately long; posterior tarsi with whitish rings. Forewings sub-oblong, rather narrow, costa slightly arched, apex rounded, termen obliquely rounded; fuscous sprinkled with whitish; a fuscous dot at one-third; an erect white mark from dorsum before tornus reaching middle of disc, edged with fuscous posteriorly; cilia pale fuscous, on tornus darker. Hindwings fuscous; basal half of costa white; cilia fuscous.

Victoria: Beaconsfield in October; two specimens.

1411. LEISTOMORPHA BRONTOSCOPA Meyr., *ibid.*, 1883, p. 510. (Bathurst and Mt. Kosciusko to Hobart.)

1412. LEISTOMORPHA TRISSOSEMA Turn., *P.R.S.Tas.*, 1938, p. 97. (Derwent Bridge, Tasmania.)

124. Gen. ACTENISTA, n.g. (*ἀκτενιστος*, combless.)

Tongue present. Palpi smooth, slender; second joint reaching base of antennae; terminal joint shorter than second. Antennae without basal pecten; ciliations in male moderate. Thorax with a posterior crest. Forewings with 7 to termen. Hindwings elongate-ovate; neuration normal. Differs from *Mesolecta* only in the absence of an antennal pecten.

1413. ACTENISTA MERIDARCHA Meyr., P.L.S.N.S.W., 1888, p. 1576 = *cyclogramma* Low., *ibid.*, 1897, p. 267. (Nanango and Stanthorpe to Gisborne and Moe.)

125. Gen. MESOLECTA Meyr. (*Ibid.*, 1883, p. 371.)

Tongue present. Palpi smooth, slender; second joint reaching base of antennae; terminal joint shorter than second. Antennae with basal pecten; ciliations in male moderate or long. Thorax with a posterior crest. Forewings with 7 to termen. Hindwings elongate-ovate; neuration normal. An endemic derivative of *Philobota* distinguished by the presence of a thoracic crest. Type, *M. psacasta* Meyr.; nine species.

1414. MESOLECTA EUZONA, n. sp. (*εὐζωνος*, well girdled.)

♂, ♀. 14-18 mm. Head yellow. Palpi with second joint reaching base of antennae, terminal joint four-fifths; whitish, outer surface of second joint sprinkled with dark fuscous, terminal joint with sub-basal and subapical dark fuscous rings. Antennae grey; ciliations in male 3. Thorax dark fuscous. Abdomen grey. Legs fuscous with whitish-ochreous rings; posterior tibiae whitish-ochreous. Forewings with costa strongly arched, apex rounded, termen obliquely rounded; yellow; markings dark fuscous; a broad transverse basal fascia; a moderate fascia from two-thirds costa to tornus; from this proceeds a broad marginal line round apex and termen to tornus; cilia dark fuscous. Hindwings and cilia grey.

North Queensland: Cape York in November, April, May, and June (W. B. Barnard); eight specimens. Type in Queensland Museum.

1415. MESOLECTA CALLISTIS Meyr., *ibid.*, 1888, p. 1602. (Albany.)

1416. MESOLECTA XANTHASTIS Meyr., *ibid.*, 1888, p. 1602. (Albany to Perth.)

1417. MESOLECTA DIAMITA, n. sp. (*διαμυτος*, sewn through.)

♂. 24 mm. Head and thorax ochreous-whitish. Palpi with second joint reaching base of antennae, terminal joint three-fifths; whitish, external surface of second joint sprinkled with fuscous. Antennae ochreous-whitish becoming fuscous towards apex; ciliations in male 3. Abdomen whitish-grey. Legs fuscous; posterior pair whitish.

Forewings elongate, costa arched near base, thence straight to near apex; apex rounded, termen very obliquely rounded; ochreous-whitish; markings and some irroration fuscous; a median streak from base to subterminal line; an interrupted line on fold; a doubly sinuate line from five-sixths costa to tornus; a terminal series of dots; cilia ochreous-whitish with an interrupted fuscous submedian line. Hindwings and cilia whitish-grey.

Queensland: Southport in July; one specimen received from Mr. W. B. Barnard.

1418. *MESOLECTA CHIMERINA* Meyr., *ibid.*, 1888, p. 1601. (Sydney.)

1419. *MESOLECTA ANGUSTELLA* Wlk., *xxix*, p. 694 = *variabilis* Turn., *Tr.R.S.S.Aust.*, 1896, p. 22. (Cairns to Lismore.)

1420. *MESOLECTA PSACASTA* Meyr., *ibid.*, 1883, p. 371. (Melbourne; Mt. Lofty; Pt. Lincoln.)

1421. *MESOLECTA LUTULENTA* Meyr., *Exot. Micro.*, *i*, p. 131. (Cairns.)

1422. *MESOLECTA STENOPHANES*, n. sp. (*στενοφανης*, narrow.)

♂. 26 mm. Head and thorax fuscous. Palpi with second joint reaching base of antennae, terminal joint two-thirds; fuscous, extreme apex of second joint whitish. Antennae fuscous; ciliations in male 1. Abdomen grey. Legs fuscous; posterior pair grey-whitish. Forewings elongate, posteriorly dilated, costa gently arched, apex pointed, termen slightly rounded, strongly oblique; fuscous densely sprinkled with whitish, less so towards margins; markings blackish; a broad oblique mark from base of costa crossing fold; first discal at one-third, plical beneath it, second discal expanded into a long crescent before two-thirds, a dot above and between discals, and a short longitudinal streak above and beyond plical; a suffused costal spot at four-fifths, giving off a slender outwardly curved line to tornus; cilia fuscous. Hindwings pale grey, faintly brownish-tinged, cilia brown-whitish.

South Australia: Adelaide in October; one specimen received from Mr. F. M. Angel.

126. Gen. *LIOCNEMA*, n.g. (*λειοκνημος*, smooth-legged.)

Tongue present. Palpi recurved, ascending, smooth-scaled; second joint slightly exceeding base of antennae; terminal joint much shorter than second. Antennae with basal pecten; ciliations in male moderate. Posterior tibiae smooth-scaled excepting for a few long hairs on base of dorsum; spurs long. Forewings with 7 and 8 stalked, 7 to termen. Hindwings elongate-ovate; neuration normal, 5 from middle of cell.

Distinguished by the smooth posterior tibiae, which might suggest some relationship to the Hyponomeutidae, but all other details of structure are definitely Oecophorid.

1423. *LIOCNEMA CRYPSIRRHODA* Turn., *P.R.S.Tas.*, 1938, p. 96. (Hobart.)

127. Gen. *CORMOTYPA* Meyr. (*Exot. Micro.*, *i*, p. 250.)

Palpi with second joint reaching or somewhat exceeding base of antennae; terminal joint as long or nearly as long as second (three-fourths to one), slender. Antennae with basal pecten; ciliations in male moderate or long. Forewings with 7 to termen. Hindwings elongate-ovate; neuration normal. Type, *C. subpunctella* Wlk. I consider *Chrysonoma* Meyr. a synonym. Distinguished from *Philobota* by the greater length of the terminal joint of the palpi as compared with the second joint. The separation is convenient and, I think, for the most part natural. It is closely allied both to *Philobota* and *Coesyra*. There are thirty-nine Australian species and Meyrick has recorded a few from New Guinea, India, and Africa.

1424. *CORMOTYPA PHAEDROPA* Low., *Tr.R.S.S.Aust.*, 1901, p. 92 = *leucocosma* Turn., *ibid.*, 1917, p. 85. (Perth; Waroona; Mt. Barker.)

1425. *CORMOTYPA SIGMOPHORA* Meyr., *P.L.S.N.S.W.*, 1883, p. 516. (Stanthorpe to Melbourne.)

1426. *CORMOTYPA OPHIODES* Meyr., *ibid.*, 1888, p. 1621. (Glen Innes; Mt. Kosciusko; Gisborne.)

1427. *CORMOTYPA CHALCHOXANTHA* Meyr., *ibid.*, 1888, p. 1622. (Stanthorpe to Victoria.)

1428. *CORMOTYPA EUGRAMMA* Low., *Tr.R.S.S.Aust.*, 1894, p. 98. (Ebor; Barrington Tops; Katoomba; Melbourne.)

1429. *CORMOTYPA PENTAMERA* Low., *ibid.*, 1893, p. 292. (Gisborne.)

1430. CORMOTYPA ATRICOLLIS Meyr., P.L.S.N.S.W., 1884, p. 726 = *leucopsina* Rosen. *Ann. Mag. Nat. Hist.*, (5) xvi, p. 441. (Brisbane to Hobart and Mt. Lofty.)
1431. CORMOTYPA PLATYZOSTRA Turn., *P.R.S.Tas.*, 1938, p. 97. (Tasmania.)
1432. CORMOTYPA MITROCOSMA, n. sp. (*μυτροκοσμος*, prettily girdled.)  
 ♀. 21 mm. Head whitish-ochreous. Palpi white, terminal joint fuscous. Antennae fuscous; basal joint whitish. Thorax white, anterior edge fuscous. Abdomen ochreous-grey-whitish. Legs ochreous-whitish; anterior pale fuscous. Forewings moderate, not dilated, costa moderately arched, apex pointed, termen oblique; shining white with fuscous markings; two moderate transverse fasciae, at one-third and two-thirds, both slightly produced posteriorly on costa; a terminal line from beneath apex to tornus; cilia fuscous, on apex grey. Hindwings and cilia grey.  
 Queensland: Stanthorpe in December (W. B. Barnard); one specimen.
1433. CORMOTYPA FASCIALIS Fab., *Syst. Ent.*, p. 644 = *bimaculana* Don., *Ins. New Hol.*, i; Pl. 40, *Feld. Reis. Nov.*, Pl. 138, f. 48; Meyr., P.L.S.N.S.W., 1883, p. 506. (Darwin; Cape York to Tasmania and South Australia; North-west Australia: Kimberley; New Guinea)
1434. CORMOTYPA EPULARIS Meyr., *Exot. Micro.*, i, p. 127. (Albany; Waroona; Perth.)
1435. CORMOTYPA MEGALOXANTHA Turn., *Tr.R.S.S.Aust.*, 1917, p. 92. (W.A.: Cunderdin.)
1436. CORMOTYPA BULLIFERA Meyr., *Exot. Micro.*, ii, p. 34. (Adelaide; Mt. Lofty; Albany.)
- 1437.† CORMOTYPA MACROPODIAS Meyr., *Exot. Micro.*, i, p. 127. *Gen. Ins. Oecophor.*, Pl. 5, f. 82. (Atherton.)
- 1438.† CORMOTYPA CONSULARIS Meyr., *ibid.*, i, p. 111. (Townsville.)
1439. CORMOTYPA TRIGONOCOSMA, n. sp. (*τριγωνοκοσμος*, with triangular decoration.)  
 ♂, ♀. 22–24 mm. Head and palpi yellow. Antennae grey; ciliations in male 1. Thorax fuscous with a small yellow posterior spot. Abdomen ochreous. Legs grey; posterior pair ochreous. Forewings moderate, not dilated, costa gently arched, apex pointed, termen oblique; pale yellow; a fuscous triangle resting on tornus, its apex reaching middle, acute, sometimes slightly produced and bent outwards; rarely a few fuscous scales before termen; cilia yellow. Hindwings grey; cilia pale yellow. Very like *C. gilvella* Turn., but without dark terminal line on forewings and with much darker hindwings.  
 West Australia: Busselton in February (W. B. Barnard); five specimens. Type in Queensland Museum.
1440. CORMOTYPA GILVELLA Turn., *Tr.R.S.S.Aust.*, 1917, p. 73. (Adavale, Qd.)
1441. CORMOTYPA DELTOSEMA Meyr., P.L.S.N.S.W., 1884, p. 782 = *isosceliphora* Low., *Tr.R.S.S.Aust.*, 1894, p. 97. (Duarina; Gisborne; Adelaide.)
1442. CORMOTYPA ZANCLOTYPA Turn., *ibid.*, 1917, p. 73. (Adavale, Qd.; Cunderdin, W.A.)
- 1443.† CORMOTYPA PANXANTHA Low., *ibid.*, 1894, p. 98. (Duarina.)
1444. CORMOTYPA PROTOPHAES Meyr., P.L.S.N.S.W., 1882, p. 457. (Atherton to Tasmania, South Australia and West Australia.)
1445. CORMOTYPA RHOECOSEMA, n. sp. (*ῥοικοσημος*, crookedly marked.)  
 ♀. 17 mm. Head and palpi yellow. Antennae whitish with blackish annulations. Thorax yellow; apices of tegulae and a postmedian transverse bar blackish. Abdomen dark fuscous. Forewings narrow, posteriorly dilated, costa moderately arched, apex pointed, termen straight, oblique; deep yellow with blackish markings; a narrow basal fascia; a narrow mark on one-third costa continued on costal edge to base; an oblique mark on one-third dorsum; a wavy line from three-fourths costa at first transverse, in middle bent longitudinally to one-half, there acutely angled outwards to two-thirds dorsum; an interrupted terminal line; cilia yellow, on tornus fuscous. Hindwings and cilia dark grey.  
 West Australia: Denmark in April (W. B. Barnard); one specimen.
1446. CORMOTYPA SUBPUNCTELLA Wlk., xxix, p. 693; Meyr., *ibid.*, 1883, p. 516. (Gosford; Sydney.)

1447. *CORMOTYPA AUREOLA* Turn., *Tr.R.S.S.Aust.*, 1898, p. 211. (Mt. Tamborine; Macpherson Range; Bunya Mts.)

1448. *CORMOTYPA CROCIAS*, n. sp. (*κροκίας*, saffron-yellow.)

♂, ♀. 24–26 mm. Head and thorax deep yellow. Palpi with terminal joint three-fourths; yellowish, external surface of second joint except apex fuscous. Antennae grey; ciliations in male 4. Abdomen brownish-yellow. Legs yellowish. Forewings sub-oblong, costa slightly arched, apex pointed, termen slightly sinuate, oblique; deep yellow; base of costa fuscous; stigmata blackish, first discal at one-fourth, plical well beyond it, second discal at one-half; a fine fuscous line from beneath five-sixths costa, curved outwards till near termen, then parallel to it to tornus, where it meets a similar oblique line from second discal; cilia yellow. Hindwings and cilia grey-whitish.

Near *C. subpunctella* and *C. aureola*, but with much less curved costa of forewing and differing in colour of hindwings and palpi.

Queensland: National Park (3,000 ft.) in November; two specimens received from Mr. W. B. Barnard. Type in Queensland Museum.

1449. *CORMOTYPA EOCROSSA* Meyr., *P.L.S.N.S.W.*, 1887, p. 949. (Injune; Bathurst; Horsham; Mt. Lofty.)

1450. *CORMOTYPA DOLOPIS*, n. sp. (*δολωπίς*, deceitful.)

♂. 24 mm. Head and thorax orange. Palpi with second joint reaching base of antennae; terminal joint three-fourths; pale brownish-yellow, terminal joint fuscous anteriorly. Antennae grey; ciliations in male 1. Abdomen grey; tuft whitish-ochreous. Legs fuscous; posterior pair pale ochreous. Forewings sub-oblong, costa strongly arched, apex subrectangular, termen obliquely rounded; yellow; base of costal edge dark fuscous; a small transversely elongate fuscous spot at two-thirds; cilia yellow. Hindwings and cilia grey. Extremely like *Tanyzancla euxantha* Meyr., but the palpi are much shorter. They are also differently coloured, and the antennae are not distinctly annulated.

West Australia: Kalamunda, near Perth, in December (W. B. Barnard); one specimen.

1451. *CORMOTYPA HAPLOGRAMMA* Turn., *Tr.R.S.S.Aust.*, 1917, p. 72. (Ebor.)

1452. *CORMOTYPA CNECOPIS* Turn., *ibid.*, 1917, p. 92. (Darwin.)

1453. *CORMOTYPA MIMOPA* Meyr., *ibid.*, 1902, p. 139. (S.A.: Halbury; Hoyleton.)

1454. *CORMOTYPA SPHODRA*, n. sp. (*σφοδρος*, intense.)

♂. 21 mm. Head blackish. Palpi yellow, terminal joint, base of outer surface, and a subapical ring on second joint, fuscous. Antennae ochreous-whitish with blackish annulations; ciliations in male 2. Thorax blackish; apices of tegulae and a posterior spot yellow. Abdomen blackish; bases of middle segments pale brown. Legs yellow; anterior and middle pairs partly fuscous. Forewings moderate, costa rather strongly arched, apex rounded, termen obliquely rounded; deep yellow; markings blackish; a narrow costal line to middle, at base prolonged to dorsum; a large apical blotch, its edge incurved from two-thirds costa to three-fourths dorsum; cilia blackish. Hindwings and cilia blackish.

Queensland: Macpherson Range (2,500 ft.) in December; one specimen.

1455. *CORMOTYPA CATACHRYSA* Meyr., *P.L.S.N.S.W.*, 1888, p. 1625. (Stanthorpe to Melbourne.)

1456. *CORMOTYPA AUTOMIMA* Meyr., *ibid.*, 1888, p. 1625. (Macpherson Range to Mittagong.)

1457. *CORMOTYPA SELENIACA* Meyr., *ibid.*, 1884, p. 778. (Townsville; Duinga; Eidsvold.)

1458. *CORMOTYPA FUSCA*, n. sp. (*fuscus*, dark.)

♂. 18–20 mm. Head and thorax brownish-fuscous. Palpi fuscous, external surface of second joint whitish towards apex except a subapical bar. Antennae grey; ciliations in male one and one-half. Abdomen fuscous; tuft ochreous. Legs fuscous; posterior pair ochreous. Forewings sub-oblong, costa gently arched, apex rounded, termen slightly rounded, slightly oblique; uniform brownish-fuscous; cilia fuscous. Hindwings and cilia grey.

Queensland: Rockhampton in August; two specimens.

1459.† *CORMOTYPA HOMOTONA* Meyr., P.L.S.N.S.W., 1883, p. 508. (Bulli.)

1460. *CORMOTYPA MACULIFERA* Low., *Tr.R.S.S.Aust.*, 1916, p. 542. (Cairns.)

1461. *CORMOTYPA XANTHOPOLIA*, n. sp. (*ξανθοπολιος*, yellow and grey.)

♂. 27–29 mm. ♀. 32 mm. Head whitish-ochreous. Palpi fuscous, apex of second joint white. Antennae fuscous; ciliations in male three-fourths. Thorax fuscous; apices of tegulae and posterior margin grey-whitish. Abdomen ochreous-grey; apices of segments and tuft yellowish. Legs fuscous; posterior pair pale ochreous. Forewings moderate, costa rather strongly arched, apex round-pointed, termen obliquely rounded; whitish-grey with fuscous markings; a narrow basal fascia; first discal at one-third, plical beneath it, second discal at two-thirds, crescentic, a dot above and between discals, and another beyond and beneath first discal; a strong inwardly oblique streak from costa slightly beyond middle; a line from three-fourths costa, at first inwardly oblique, soon curved outwards and again inwards to tornus, its extremities united by a fuscous suffusion; cilia grey. Hindwings pale yellow; extreme apex grey; cilia pale yellow, on apex grey.

New South Wales: Ben Lomond (4,500 ft.) in January; Ebor (4,500 ft.) in December; four specimens.

1462. *CORMOTYPA METAXANTHA*, n. sp. (*μεταξανθος*, yellow posteriorly.)

♂, ♀. 22–26 mm. Head whitish-ochreous. Palpi fuscous, apex of second and outer surface of terminal joint white. Antennae grey with fuscous annulations; ciliations in male three-fourths. Thorax white, anterior margin and tegulae fuscous. Abdomen ochreous-grey; apices of segments and tuft yellow. Legs fuscous; posterior pair pale ochreous. Forewings narrow, costa gently arched, apex round-pointed, termen very obliquely rounded; white; markings and some irroration fuscous; a small basal fascia; a narrow costal triangle from one-fifth to three-fifths; usually some dorsal suffusion; first discal at one-third, sometimes touching costal triangle, plical beneath it, second discal at two-thirds, crescentic, a dot above and between discals touching costal triangle, and another beneath and beyond first discal; a broadly suffused line from four-fifths costa to tornus touching second discal, inwardly curved, with a short outwardly curved line between its extremities; an apical spot and some terminal dots; cilia white, on apex fuscous. Hindwings yellow; cilia pale yellow.

New South Wales: Murrurundi in October and November; seven specimens received from Dr. B. L. Middleton.

128. Gen. *STHENOZANCLA*, n. g. (*σθενοζαγλος*, with strong sickles.)

Tongue present. Palpi long, recurved, ascending; second joint exceeding base of antennae, much thickened with appressed scales, slightly rough anteriorly; terminal joint nearly as long as second, slender, acute. Antennae with basal pecten; ciliations in male moderately long. Forewings with tufts of raised scales; 2 from well before angle, 3 and 4 closely approximated from angle, 7 to termen. Hindwings elongate-ovate; 2 from middle of cell.

1463. *STHENOZANCLA PLAGIOTYPA*, n. sp. (*πλαγιωτυπος*, obliquely marked.)

♂. 25 mm. Head and thorax brown-whitish; apices of tegulae whitish. Palpi whitish; base of outer surface of second joint and all inner surface of terminal joint fuscous. Antennae whitish with fuscous annulations; ciliations in male one and one-half. Abdomen whitish-ochreous. Legs whitish-ochreous; anterior pair fuscous. Forewings rather narrow, posteriorly dilated, costa moderately arched, apex pointed, termen very oblique; whitish with sparsely scattered blackish scales and small patches of pale brown suffusion; base of costa dark fuscous, markings composed of pale brown spots sprinkled with blackish scales, those in basal area with raised scales; a sub-basal spot beneath costa; costal spots at three-fourths and before apex; a dorsal spot at two-thirds; an oblique suffused line connecting posterior costal with dorsal spot; stigmata blackish, first discal at one-third, plical before it, larger and nearly touching one-third dorsum, a dot beneath and between discals; cilia brown-whitish with slight bars of blackish scales. Hindwings grey-whitish; cilia whitish.

Maryland, N.S.W. (near Stanthorpe, Qd.) in May; one specimen received from Mr. W. B. Barnard.

129. Gen ZAPHANAULA Meyr. (*Exot. Micro.*, ii, 313.)

Palpi long, recurved, ascending, second joint reaching base of antennae, smooth; terminal joint nearly as long as second, slender, acute. Antennae without basal pecten; ciliations in male moderately long. Forewings with 7 to termen, 9 and 10 somewhat approximated at origin. Hindwings elongate-ovate; 2 from middle of cell.

1464. ZAPHANAULA XENOPHILA Meyr., *Exot. Micro.*, ii, 313. (Brisbane, Lismore.)

130. Gen. HALALOTEUCHA Meyr. (*Exot. Micro.*, i, p. 251.)

Tongue present. Palpi long recurved, ascending; second joint exceeding base of antennae, smooth; terminal joint shorter than second, rather stout, rather obtusely pointed. Antennae almost as long as forewings; basal pecten present; ciliations in male moderate. Forewings with 7 to termen. Hindwings elongate-ovate; neuration normal. Monotypical.

1465. HALALOTEUCHA PARAGRAMMA Meyr., P.L.S.N.S.W., 1884, p. 766. (Sydney.)

131. Gen. LOPHOCEROS, n.g. (*λοφοκερος*, with tufted horns.)

Tongue absent. Palpi long, ascending, recurved; second joint exceeding base of antennae, loosely haired towards apex anteriorly; terminal joint shorter than second, slender, acute. Antennae with basal pecten; in male with a double row of fascicles of long cilia. Forewings with 2, 3 and 4 nearly equidistant, 7 to termen. Hindwings elongate-ovate; neuration normal.

1466. LOPHOCEROS ONCERA, n. sp. (*ὄγκερος*, large.)

♂. 28-30 mm. Head and thorax pale grey. Palpi with terminal joint two-thirds; whitish sprinkled with fuscous. Antennae pale grey; ciliations in male 4. Abdomen pale grey. Legs grey; posterior pair whitish. Forewings elongate, costa almost straight, apex round-pointed, termen obliquely rounded; pale grey; costal edge near base fuscous; stigmata fuscous, first discal at two-fifths, minute, plical beneath it, also minute, second discal at three-fifths, larger and double; a series of terminal dots; cilia pale grey. Hindwings and cilia whitish-grey.

North Queensland: Charters Towers in June; three specimens.

132. Gen. TANYZANCLA Meyr. (*Exot. Micro.*, ii, p. 218.)

Palpi with second joint more than twice length of face, smooth; terminal joint variable in length, smooth, slender, acute. Antennae four-fifths; ciliations in male moderate or long. Forewings with 7 to termen. Hindwings elongate-ovate; neuration normal. Type, *T. marionella* Newm. Differs from *Philobota* in the greater length of the second joint of the palpi; the terminal joint varies from one-fourth to one. No advantage would be gained by using these differences for further subdivision. There are eight Australian species, and Meyrick has recorded one from New Guinea, seven from South Africa, and one from Asia Minor.

1467. TANYZANCLA IDIOPHANES, n. sp. (*ιδιοφανης*, peculiar.)

♂. 15 mm. Head blackish; face orange. Palpi with terminal joint two-thirds; fuscous. Antennae fuscous; ciliations in male 3. Thorax fuscous; tegulae except bases orange. Abdomen fuscous. Legs fuscous; posterior tibiae ochreous-whitish. Forewings narrow, costa straight except at base and apex; apex round-pointed, termen very obliquely rounded; blackish; costal and terminal edge orange; a short dorsal orange streak from base, another subcostal, a third in mid-dise from one-third to two-thirds; cilia fuscous. Hindwings orange; apex broadly fuscous; cilia fuscous.

New South Wales: Barrington Tops in February; one specimen in Coll. Goldfinch.

1468. TANYZANCLA TRIMERIS Low., *Tr.R.S.S.Aust.*, 1902, p. 241. Unfortunately the palpi of the type, which I have examined, are broken so that its generic position is uncertain. (S.A.: Port Victor.)

1469. TANYZANCLA CALLIOPHTHALMA Meyr., P.L.S.N.S.W., 1888, p. 1639. (Albany; Waroona; Perth; Geraldton.)

1470. TANYZANCLA CREMANTIS Meyr., *ibid.*, 1888, p. 1638. (Cunderdin; Geraldton.)

1471. TANYZANCLA MELANOCROSSA Meyr., *ibid.*, 1888, p. 1640. (Denmark to Geraldton.)

1472. TANYZANCLA ARGUTELLA, *Zel., Hor.. Ross.*, 1877, p. 391; *Meyr., ibid.*, 1884, p. 726. (Herberton; Stradbroke I. to Melbourne; South Australia; W.A.: Mt. Barker.)

1473. TANYZANCLA MARIONELLA *Newm., Tr.Ent.Soc.*, 1855, p. 294; *Meyr., ibid.*, 1884, p. 728 = *gloriosella* *Wlk.*, xxix, p. 697. (Stradbroke I. to Victoria; Tas.: Epping; South-west Australia.)

1474. TANYZANCLA CHRYSODETA, n. sp. (*χρυσοδέτος*, inlaid with gold.)

♀. 15 mm. Head white; side-tufts brown. Palpi with second joint four times length of face, terminal joint two-thirds; white, base and a subapical ring on second joint pale fuscous. Antennae grey. Thorax white. Abdomen whitish-ochreous. Legs pale fuscous; posterior pair ochreous-whitish. Forewings suboval, costa strongly arched, apex pointed, termen oblique; white; markings golden-yellow; a broad basal fascia, its posterior edge from one-third costa to one-fifth dorsum; a narrow fascia from midcosta to mid-dorsum, broader on dorsum; a fascia confluent with preceding on costa, thence to tornus; a terminal fascia; cilia white. Hindwings pale ochreous; some grey suffusion at apex; cilia pale ochreous.

Queensland: Yeppoon in November; one specimen in Coll. Goldfinch.

1475. TANYZANCLA HELIAS *Meyr., P.L.S.N.S.W.*, 1884, p. 733. (Nambour to Sydney.)

1476. TANYZANCLA BASIPLAGA *Wlk.*, xxviii, p. 490; *Meyr., ibid.*, 1884, p. 735 = *quadratella* *Wlk.*, xxx, p. 1029. (Cairns to Sydney.)

1477. TANYZANCLA MIMETIS *Turn., Tr.R.S.S.Aust.*, 1917, p. 86. (Nambour; Macpherson Range.)

1478. TANYZANCLA HOMOPHYES, n. sp. (*ὁμοφυης*, closely related.)

♀. 18 mm. Head yellow. Palpi with terminal joint two-thirds; yellow, base of second joint fuscous. Antennae fuscous with whitish annulations. Thorax fuscous. Abdomen grey. Legs fuscous with pale ochreous rings; posterior pair pale ochreous. Forewings narrow, costa gently arched, apex pointed, termen oblique; fuscous with a few whitish scales; a small yellow sub-basal dorsal blotch, its irregular upper edge reaching mid-disc, posterior edge inwardly curved; a small whitish-ochreous triangle on midcosta; another at five-sixths giving off a fine curved line to tornus; cilia yellow, on apex and tornus fuscous. Hindwings and cilia dark grey. Very similar to *T. mimetis*, but differs in the annulated antennae, dorsal blotch of forewing widely separated from costa, midcostal triangle, and curved subterminal line.

Queensland: Tweed Hds. (Southport) in October; one specimen.

1479. TANYZANCLA XENOMIMA *Meyr., Exot. Micro.*, i, p. 122. (Cairns.)

1480. TANYZANCLA MARMORATA *Meyr., P.L.S.N.S.W.*, 1888, p. 1611. (Queensland.)

1481. TANYZANCLA HILDA *Turn., Tr.R.S.S.Aust.*, 1917, p. 91. (Mt. Tamborine; Toowoomba.)

1482. TANYZANCLA MALACOSTOLA, n. sp. (*μαλακοστολος*, softly robed.)

♂. 16-18 mm. Head yellow. Palpi with terminal joint four-fifths; whitish-ochreous, outer side of base and a subapical ring on second joint and terminal joint fuscous. Antennae fuscous; ciliations in male 1. Thorax fuscous; middle of anterior edge yellow. Abdomen grey. Legs fuscous with ochreous-whitish rings; posterior pair mostly ochreous-whitish. Forewings moderate, costa gently arched, apex round-pointed, termen oblique; whitish sprinkled with fuscous; a fuscous basal fascia extending to one-fifth costa; a yellow triangle on dorsum from near base to one-third, its apex approaching one-fifth costa, partly edged with fuscous posteriorly; stigmata fuscous, first discal at one-third, plical beneath it, second discal well before two-thirds with an additional dot beneath it; terminal area fuscous with whitish patches, edged by a curved yellow line from three-fourths costa to tornus, where it is expanded; cilia fuscous, on midtermen and tornus yellow. Hindwings and cilia grey.

North Queensland: Atherton Tableland (Lake Barrine) in September and January; two specimens.

1483. TANYZANCLA CLYTOPHANES, n. sp. (*κλυτοφανης*, illustrious.)

♂, ♀. 20-26 mm. Head white; back of crown fuscous. Palpi with terminal joint three-fourths; whitish, base and a subapical ring on second joint and all terminal joint fuscous. Antennae whitish with dark fuscous annulations; ciliations in male one and one-fourth. Thorax bright yellow. Abdomen brownish-grey. Legs ochreous; anterior

pair fuscous. Forewings sub-oblong, costa moderately arched, apex rounded-rectangular, termen straight, slightly oblique; bright yellow; a thick fuscous costal streak to one-fourth; terminal area bounded by a strongly sinuate line from midcosta to one-fourth dorsum, fuscous irregularly suffused with whitish except on margins, at apex, and a discal spot at two-thirds confluent with a larger tornal spot; cilia grey, on apex and tornus fuscous. Hindwings and cilia grey.

Queensland: Yeppoon in October; Toowoomba in October, November, and December; seven specimens.

1484. *TANYZANCLA LUNATA* Turn., *Tr.R.S.S.Aust.*, 1896, p. 25 = *leucoplaca* Low., *ibid.*, 1897, p. 53. (Duarina to Pt. Macquarie.)

1485. *TANYZANCLA ACUTELLA* Wlk., xxx, p. 1031; Meyr., P.L.S.N.S.W., 1883, p. 503 = *idae* Low., *Tr.R.S.S.Aust.*, 1893, p. 180. (Healesville; Adelaide; Albany.)

1486. *TANYZANCLA INCOMPOSITA* Meyr., *ibid.*, 1884, p. 728. (Glen Innes to Gisborne.)

1487. *TANYZANCLA ALYA* Turn., *ibid.*, 1914, p. 560. (Ebor.)

1488. *TANYZANCLA CHIONOSPILA*, n. sp. (*χιονοσπίλος*, snow-spotted.)

♂, ♀. 18–20 mm. Head fuscous; face white. Palpi with terminal joint three-fifths; white, a subterminal ring on second joint and anterior edge of terminal joint fuscous. Antennae white with fuscous annulations; ciliations in male one and one-fourth. Thorax white; anterior border fuscous. Abdomen pale ochreous-grey. Legs ochreous-whitish; anterior pair except tarsi fuscous. Forewings with costa gently arched, apex round-pointed, termen moderately oblique, fuscous-brown with sharply defined white markings; a narrow fascia from one-third costa to one-third dorsum; a roundish spot on dorsum beyond middle; an inwardly oblique spot on three-fourths costa, variable in size; middle third of termen narrowly white; cilia fuscous, on midtermen white. Hindwings pale ochreous suffused with fuscous towards apex; cilia pale ochreous, on apex fuscous.

Queensland: Bunya Mts. in November (W. B. Barnard); four specimens. Type in Queensland Museum.

1489. *TANYZANCLA ISOZONA* Low., *Tr.R.S.S.Aust.*, 1902, p. 93 = *thermophanes* Turn., *ibid.*, 1917, p. 86. (Cape York; Atherton; Townsville.)

1490.† *TANYZANCLA MELODORA* Meyr., *ibid.*, 1888, p. 1623. (Fernshaw.)

1491. *TANYZANCLA THEORICA* Meyr., *ibid.*, 1883, p. 729 = *chrysozona* Turn., *Tr.R.S.S.Aust.*, 1896, p. 27. (Brisbane to Gisborne.)

1492. *TANYZANCLA THERMOCHROA* Meyr., *ibid.*, 1884, p. 730. (Sydney; Gisborne; Melbourne; Mt. Lofty.)

1493. *TANYZANCLA PENTATYPA*, n. sp. (*πεντατυπος*, five-marked.)

♀. 17–19 mm. Head blackish; face white. Palpi with terminal joint three-fifths; white, base and a subapical ring on second joint and all terminal joint blackish. Antennae whitish-grey annulated with blackish. Thorax white. Abdomen grey; apices of segments whitish. Legs fuscous; coxae white; posterior pair pale ochreous. Forewings slightly dilated, costa moderately arched, apex pointed, termen straight, oblique; fuscous with five white spots; first basal, second on one-third costa, third on dorsum beyond middle, fourth on two-thirds costa, fifth on midtermen; cilia fuscous, on terminal spot white. Hindwings pale ochreous; a small apical fuscous blotch; cilia pale ochreous, on apex fuscous.

Queensland: Toowoomba in November; two specimens received from Mr. W. B. Barnard. Type in Queensland Museum.

1494. *TANYZANCLA EUDMETA*, n. sp. (*ευδημος*, well fashioned.)

♀. 20 mm. Head blackish; face white. Palpi with terminal joint two-thirds; white, base and a broad subapical ring on second joint blackish, terminal joint fuscous. Antennae white with blackish annulations, towards base wholly blackish. Thorax pale ochreous with a small blackish posterior spot. Abdomen blackish; tuft ochreous. Legs pale ochreous; anterior pair partly fuscous. Forewings with costa moderately arched, apex obtusely pointed, termen straight, oblique; blackish; markings whitish-ochreous; a broad straight-edged transverse basal fascia; a triangular erect mark on tornus; a large triangular subapical spot from costa to above tornus; cilia fuscous, apices pale ochreous except on apex and tornus. Hindwings ochreous; apical blotch; cilia fuscous.

Near *T. theorica*. The blackish rings on palpi are a good distinction, and there are minor differences in fore and hindwings.

New South Wales: Rivertree in October; type in Coll. Goldfinch.

1495. TANYZANCLA DIACRITA Turn., *Tr.R.S.S.Aust.*, 1917, p. 85. Palpi with terminal joint two-thirds. Antennal ciliations of male one and one-half. (Ebor; Murrurundi.)

1496. TANYZANCLA SYNGENES, n. sp. (*συγγενης*, of the same stock.)

♂. 16 mm. Head yellow. Palpi with terminal joint two-thirds; whitish-ochreous, outer surface of second joint near base and just before apex fuscous. Antennae fuscous; ciliations in male one and one-half. Thorax fuscous with a whitish-ochreous posterior spot. (Abdomen missing.) Legs fuscous with whitish-ochreous rings; posterior pair whitish-ochreous. Forewings moderate, posteriorly dilated, costa gently arched, apex pointed, termen oblique; fuscous with some whitish sprinkling and markings; a rounded spot above dorsum near base extending slightly above fold, yellow; an irregular median fuscous spot at one-third representing conjoined first discal and plical; second discal before two-thirds with a dot beneath; a whitish suffused spot between second discal and costa; an inwardly directed whitish triangle from costa before apex, giving off a suffused curved line to tornus; cilia fuscous, on midtermen yellowish with two fuscous bars, on tornus yellowish. Hindwings grey; cilia whitish-grey. It is possible that fresh examples may show more yellow colouring. This species appears to be akin to both *T. diaereta* and *T. malacostola*.

Queensland: Bunya Mts. (3,000 ft.) in January; one specimen.

1497. TANYZANCLA ERYTHROTAENIA Wlgrn., *Res. Eugen. Ins.*, p. 386; Meyr., *Gen. Ins. Oecoph.*; Pl. 4, f. 76 = *pretiosella* Wlk., xxviii, p. 518; Meyr., P.L.S.N.S.W., 1883, p. 499. (Stradbroke I. to Tasmania and Mt. Lofty.)

1498. TANYZANCLA ADAPTATELLA Wlk., xxix, p. 689; Meyr., *ibid.*, 1883, p. 500 = *propiella* Wlk., xxix, p. 691. (Atherton; Brisbane to Jervis Bay.)

1499. TANYZANCLA IOSEMA Meyr., *ibid.*, 1888, p. 1618. (Milmerran; Bathurst.)

1500. TANYZANCLA ANACHORDA Meyr., *ibid.*, 1883, p. 499. (Katoomba; Bathurst; Gisborne; Beaconsfield, Vict.; Zeehan.)

1501. TANYZANCLA CAMPYLA Meyr., *ibid.*, 1888, p. 1617. (Beechworth.)

1502. TANYZANCLA BROCHOSEMA Meyr., *ibid.*, 1883, p. 500. (Victoria; Mt. Lofty.)

1503. TANYZANCLA ANAZANCLA Meyr., *ibid.*, 1888, p. 1617. (Waroona; Perth; Yancheop.)

1504. TANYZANCLA ENCHALCHA Turn., *Tr.R.S.S.Aust.*, 1917, p. 90. (Glen Innes; Ben Lomond, N.S.W.)

1505. TANYZANCLA GLAUOPTERA Meyr., *ibid.*, 1883, p. 490. (Sydney to Gisborne.)

1506. TANYZANCLA DICHOTOMA, n. sp. (*διχοτομος*, bisected.)

♂. 28-32 mm. Head white. Palpi with terminal joint two-thirds; fuscous, internal surface white. Antennae grey; ciliations in male 1. Thorax fuscous; apices of tegulae and a posterior spot white. Abdomen grey; apices of segments and tuft grey-whitish. Forewings elongate, narrow, costa only slightly arched, apex rounded, termen strongly oblique; white with fuscous markings; a moderate costal streak from one-fourth to three-fourths, attenuated towards extremities; a broad median streak from base to near termen, where it is bent upwards to apex; stigmata darker fuscous, first discal at one-third, plical beneath it, second discal at two-thirds, sometimes a dot above and between discals; traces of a fine subterminal line; a terminal series of dots or fine short streaks on veins; cilia grey, tips grey-whitish. Hindwings and cilia grey.

Victoria: Beaconsfield in March (Dr. W. E. Drake); five specimens. Type in National Museum, Melbourne. Another example in Coll. Goldfinch with darker forewings and ochreous-tinged cilia of hindwings, from Katoomba, N.S.W., appears to be a form of the same species.

1507. TANYZANCLA DIACHORDA, n. sp. (*διαχορδος*, streaked right through.)

♀. 25-28 mm. Head whitish-ochreous. Palpi with terminal joint three-fourths; grey, internal surface and terminal joint whitish. Antennae grey, towards base whitish. Thorax pale grey. Abdomen whitish-grey. Legs fuscous; posterior pair grey. Forewings elongate, costa gently arched, apex rounded, termen oblique; whitish; costal edge near base dark fuscous; a broad subcostal fuscous streak from base to apex; stigmata

fuscous, first discal at two-fifths, plical before it, second discal at three-fifths, both discals touching subcostal streak and sometimes not distinguishable from it; sometimes a few submarginal fuscous dots opposite lower half of termen and a small suffusion between second discal and tornus; cilia whitish. Hindwings and cilia pale grey.

West Australia: Waroona in February (Mr. G. F. Berthoud); two specimens received from Mr. Geo. Lyell. Type in National Museum, Melbourne.

1508. TANYZANCLA MELANOTYPA Turn., *P.R.S.Tas.*, 1926, p. 151. (Cradle Mt.)

1509.† TANYZANCLA ZITELLA Newm., *Tr.Ent.Soc.*, 1855, p. 296.

1510. TANYZANCLA OCHROCAUSTA Meyr., *P.L.S.N.S.W.*, 1883, p. 511. (Stanthorpe to Melbourne.)

1511. TANYZANCLA TOLMERA, n. sp. (τολμηρος, bold.)

♂, ♀. 24–28 mm. Head blackish; face whitish-ochreous. Palpi with terminal joint three-fourths; whitish-ochreous, base of second and all terminal joint fuscous. Antennae blackish; ciliations in male 1. Thorax ochreous-yellow. Abdomen fuscous; apices of segments and tuft ochreous. Legs ochreous; posterior pair partly fuscous. Forewings oval, costa strongly arched, apex rounded-rectangular, termen obliquely rounded; ochreous-yellow with blackish markings; a moderate fascia from two-fifths costa to mid-dorsum; a subterminal fascia, broad on costa, narrowing to tornus, from which it emits a narrow oblique process not reaching middle; cilia ochreous-yellow, on tornus fuscous. Hindwings fuscous, base ochreous, line of junction irregular; cilia fuscous, above middle with apices pale ochreous.

Queensland: Toowoomba in October and November; seven specimens received from Mr. W. B. Barnard. Type in Queensland Museum.

1512. TANYZANCLA ZONOSTOLA Meyr., 1883, p. 772. (Scone; Sydney; Gisborne; Melbourne; Mt. Lofty.)

1513. TANYZANCLA OCULARIS Turn., *Tr.R.S.S.Aust.*, 1896, p. 26. (Charters Towers.)

1514. TANYZANCLA ACROBAPHES Meyr., *ibid.*, 1884, p. 1074 = *monadelta* Low., *Tr.R.S.S.Aust.*, 1897, p. 53. (Sydney; Katoomba.)

1515. TANYZANCLA EUXANTHA Meyr., 1883, p. 505. (Toowoomba to Tasmania and Mt. Lofty.)

1516. TANYZANCLA GUMMOSA Meyr., *Exot. Micro.*, i, p. 127. (Darwin.)

1517. TANYZANCLA LEUCOPHLEBIA, n. sp. (λευκοφλεβιος, white-veined.)

♀. 20 mm. Head grey; side-tufts white. Palpi with terminal joint two-thirds; whitish, external surface of second joint sprinkled with fuscous. Antennae grey; basal third whitish. Thorax grey. Abdomen grey; bases of second to sixth segments broadly ferruginous on dorsum. Legs grey; posterior pair grey-whitish. Forewings moderate, somewhat dilated, costa moderately arched, apex rounded, termen obliquely rounded; grey; costal edge and all veins outlined with whitish; some dark fuscous irroration forming slender broken streaks between veins; cilia grey with whitish bars opposite veins. Hindwings and cilia pale grey.

Queensland: Mundubbera in October; one specimen.

1518. TANYZANCLA SCIOSTICHA, n. sp. (σκιοστιχος, with shaded streaks.)

♂. 19 mm. Head and thorax dark grey. Palpi with terminal joint two-thirds; whitish sprinkled with fuscous. Antennae whitish; basal joint dark grey; ciliations in male 5. Abdomen pale grey. Legs grey; posterior pair whitish. Forewings with costa moderately arched, apex obtusely pointed, termen oblique; grey-whitish slightly sprinkled with fuscous; stigmata fuscous, minute, first discal at two-fifths, plical obsolete, second discal at three-fifths; upper edge of cell and between costal veins slenderly fuscous; cilia grey-whitish. Hindwings and cilia whitish.

West Australia: Denmark in March; one specimen received from Mr. W. B. Barnard.

1519. TANYZANCLA CERATINA Meyr., *P.L.S.N.S.W.*, 1884, p. 737. (Lorne; Mt. Wellington.)

1520. TANYZANCLA OCHROLITHA Low., *Tr.R.S.S.Aust.*, 1903, p. 223. (Duaringa.)

1521. TANYZANCLA CATAXERA Meyr., *P.L.S.N.S.W.*, 1884, p. 736. (Tasmania.)

1522. TANYZANCLA CAMPTOSEMA, n. sp. (καμπτοσημος, with curved markings.)

♂. 22 mm. Head pale brownish. Palpi with terminal joint one-fourth; fuscous-brown, inner surface and anterior edge of second joint ochreous-whitish. Antennae pale

ochreous; ciliations in male 6. Thorax pale ochreous; anteriorly brownish. Abdomen ochreous-whitish; tuft pale ochreous. Legs ochreous; anterior pair fuscous. Forewings sub-oblong, costa strongly curved in basal half, thence straight, apex rounded, termen rounded, slightly oblique; pale ochreous; two obscure ochreous lines first from base through middle of disc to tornus; second from beneath midcosta to termen beneath apex; cilia pale ochreous. Hindwings and cilia whitish.

Exceptional in its palpi.

New South Wales: Rous near Lismore in March; one specimen received from Mr. V. J. Robinson.

1523. *TANYZANCLA SERICODES*, n. sp. (*σερικωδης*, silken.)

♂. 20–22 mm. Head and thorax pale ochreous. Palpi with terminal joint three-fifths; ochreous-whitish. Antennae grey; ciliations in male three-fourths. Abdomen ochreous-grey. Legs ochreous-whitish; anterior pair fuscous. Forewings with costa gently arched, apex pointed, termen oblique; pale ochreous; cilia whitish-ochreous. Hindwings and cilia pale grey.

New South Wales: Tabulam in December; three specimens.

1524. *TANYZANCLA HYPERCHYTA*, n. sp. (*υπερχυτος*, suffused.)

♂. 20 mm. Head white. Palpi with terminal joint two-fifths; white. Antennae pale grey; ciliations in male three-fourths. Thorax and abdomen grey. Legs whitish; anterior pair grey. Forewings narrow, oval, costa gently arched, apex pointed, termen obliquely rounded; white; basal and dorsal areas broadly suffused with grey; cilia white. Hindwings pale grey; cilia whitish.

South Australia: Henley Bay near Adelaide in March (Lower); one specimen.

1525. *TANYZANCLA NOTIA*, n. sp. (*νοτιος*, damp.)

♂. 20 mm. Head white. Palpi with terminal joint one-half; white, anterior surface fuscous. Antennae fuscous with white annulations; ciliations in male two-thirds. Thorax grey. Abdomen grey; apices of segments and tuft whitish. Legs fuscous; posterior pair ochreous-whitish. Forewings rather narrow, somewhat dilated, costa slightly arched, apex rounded, termen oblique; pale glossy ochreous-grey; a white costal streak from near base to three-fourths; attenuated towards extremities; extreme base of costa dark fuscous; cilia pale grey. Hindwings pale grey; cilia whitish.

Queensland: Milmerran in October; one specimen received from Mr. J. Macqueen.

1526. *TANYZANCLA ORTHOTOMA* Turn., *Tr.R.S.S.Aust.*, 1917, p. 88. (Brisbane; Toowoomba; Warwick; Stanthorpe.)

1527. *TANYZANCLA DIAERETA* Turn., *ibid.*, 1917, p. 89. (Toowoomba; Warwick.)

1528. *TANYZANCLA AGNESELLA* Newm., *Tr.Ent.Soc.*, (2) iii, p. 297; Turn., *ibid.*, 1917, p. 493, *nec* Meyr., P.L.S.N.S.W., 1883, p. 493. (Bundaberg and Injune to Melbourne and Adelaide.)

1529. *TANYZANCLA PHYSAULA* Meyr., *Exot. Micro.*, i, p. 273 = *eremosema* Low., P.L.S.N.S.W., 1915, p. 480 = *agnesella* Meyr., *ibid.*, 1883, p. 493, *nec* Newm. (Rosewood and Toowoomba to Melbourne and Adelaide.)

1530. *TANYZANCLA CHIONOPTERA* Meyr., *ibid.*, 1883, p. 494. (Bundaberg to Sydney; Adelaide.)

1531. *TANYZANCLA POLITA*, n. sp. (*politus*, polished.)

♂. 23–24 mm. Head and thorax white. Palpi with terminal joint three-fourths; white, base of outer surface of second joint fuscous. Antennae white; ciliations in male 1. Abdomen whitish-grey. Legs whitish; anterior pair grey. Forewings slightly dilated posteriorly, costa moderately arched, apex obtusely pointed, termen sinuate, oblique; white; extreme base of costa fuscous; stigmata fuscous, minute; first discal at one-third, plical beneath it, second discal at three-fifths; an interrupted fuscous terminal line; cilia white. Hindwings and cilia white.

New South Wales: Jervis Bay in October. Victoria: Beaconsfield in November and December; five specimens.

1532. *TANYZANCLA ATAUROTA*, n. sp. (*αταυρωτος*, virginal.)

♂, ♀. 20–22 mm. Head and thorax white. Palpi with terminal joint three-fifths; grey, terminal joint and apex of second joint white. Antennae dark grey; ciliations in male two-thirds. Abdomen grey. Legs grey; posterior pair whitish. Forewings narrow,

costa slightly arched, apex pointed, termen obliquely rounded; shining white; costal edge near base dark fuscous; cilia white. Hindwings and cilia pale grey. Forewings narrower and more pointed than in *T. polita* and hindwings not white.

Queensland: Stanthorpe in January (W. B. Barnard); two specimens. Type in Queensland Museum.

1533. *TANYZANCLA APARTHENA* Meyr., P.L.S.N.S.W., 1884, p. 722. (Katoomba; Mt. Buffalo; Gisborne.)

1534.† *TANYZANCLA PURA* Meyr., *ibid.*, 1884, p. 723. (Deloraine; Hobart.)

1535. *TANYZANCLA EURYPTILA*, n. sp. (εὐρυπτεῖλος, broad-winged.)

♂. 27-30 mm. Head pale yellow. Palpi with terminal joint two-thirds; fuscous, internal surface whitish-ochreous. Antennae grey; ciliations in male 1. Thorax grey; apices of tegulae and posterior margin pale yellow. Abdomen grey; apices of terminal segments and tuft whitish-ochreous. Legs fuscous; posterior pair whitish-ochreous. Forewings moderately broad, posteriorly dilated, costa slightly arched, apex rounded, termen obliquely rounded; pale yellow; costal edge near base fuscous; cilia whitish-grey. Hindwings and cilia grey. Broader-winged than the two following species.

New South Wales: Capertee in December; two specimens received from Mr. G. M. Goldfinch, who has the type.

1536. *TANYZANCLA PHAEOPLEURA*, n. sp. (φαειπλευρος, with dusky costa.)

♂. 28 mm. Head pale yellow. Palpi with second joint three-fifths; whitish, external surface of second joint fuscous. Antennae grey; ciliations in male 1. Thorax fuscous; apices of tegulae and a posterior spot pale yellow. Abdomen pale ochreous; basal segments grey. Legs fuscous; posterior pair whitish-ochreous. Forewings narrow, posteriorly dilated, costa slightly arched, apex pointed, termen slightly sinuate, strongly oblique; pale yellow; a fuscous line on costa from base nearly to apex; a dark fuscous discal dot at two-thirds; cilia ochreous-whitish. Hindwings and cilia grey. Easily distinguished from *T. germinalis* by the different shape of the forewings and the fuscous costal line.

South Australia. Pinnaroo (Lower). Type in South Australian Museum.

1537. *TANYZANCLA GERMINALIS* Meyr., *Exot. Micro.*, i, p. 126 = *apricata* Meyr., *ibid.*, i, p. 127 = *solaris* Meyr., *ibid.*, i, p. 126. (Waroona; Perth.)

1538. *TANYZANCLA CARINARIA* Meyr., *ibid.*, i, p. 125. (Perth.)

1439. *TANYZANCLA CROCOBAPTA* Meyr., P.L.S.N.S.W., 1883, p. 498. Kingscote, Kangaroo I.; Pt. Lincoln.)

1540. *TANYZANCLA MELIRRHOA* Meyr., *ibid.*, 1883, p. 498. (Murrurundi; Bathurst.)

1541. *TANYZANCLA MEDIOCRIS*, n. sp. (*mediocris*, tolerable.)

♂, ♀. 18 mm. Head ochreous-whitish. Palpi with terminal joint one-half; ochreous-whitish, external surface of second joint except apex fuscous. Antennae whitish with fuscous annulations; ciliations in male two-thirds. Thorax grey anteriorly, whitish posteriorly. Abdomen grey; apices of segments and tuft ochreous-whitish. Legs fuscous; posterior pair ochreous-whitish. Forewings suboval, rather narrow, costa moderately arched, apex round-pointed, termen very oblique; ochreous-whitish; stigmata and a few scattered scales fuscous; stigmata minute or absent, first discal at one-third, second at two-thirds with a dot beneath it; cilia whitish-ochreous. Hindwings pale grey; cilia whitish.

Queensland: Eumundi near Nambour in December; Rosewood in September; two specimens.

1542. *TANYZANCLA CINETICA* Meyr., P.L.S.N.S.W., 1884, p. 738. (Glen Innes to Gisborne; Hobart; Mt. Lofty.)

1543. *TANYZANCLA TYROXANTHA* Meyr., *ibid.*, 1883, p. 497. (Murrurundi; Castlemaine; Melbourne.)

1544. *TANYZANCLA ATARACTA*, n. sp. (ἀταρακτος, untroubled.)

♀. 20 mm. Head and thorax pale grey. Palpi with terminal joint two-thirds; whitish, external surface of second joint except apex grey. Antennae grey. Abdomen grey; apices of segments and tuft whitish. Legs grey; posterior pair grey-whitish. Forewings sub-oblong, costa slightly arched, apex rounded, termen obliquely rounded;

grey-whitish; cilia whitish. Hindwings whitish; apical area suffused with grey; cilia whitish.

West Australia: Perth in January; one specimen received from Mr. W. B. Barnard.

1545. *TANYZANCLA MONOXYLA*, n. sp. (*μονοξύλος*, wooden.)

♀. 28 mm. Head and thorax brown. Palpi with terminal joint three-fifths; pale brown. Antennae whitish with fuscous annulations. Abdomen grey. Legs grey; posterior pair ochreous-whitish. Forewings elongate, slightly dilated, costa moderately arched, apex pointed, termen moderately oblique; brown; stigmata minute, fuscous, first discal at one-third, plical slightly beyond it, second discal at three-fifths; a series of minute fuscous dots from three-fourths costa obliquely outwards, angled in disc towards tornus; cilia brown. Hindwings and cilia pale grey.

Tasmania: Cradle Mt. (3,000 ft.) in January; one specimen received from Mr. W. B. Barnard.

1546. *TANYZANCLA MICROSTICTIS* Meyr., *Tr.R.S.S.Aust.*, 1902, p. 139. (Bathurst.)

1547. *TANYZANCLA SUCCENSA* Meyr., *Exot. Micro.*, ii, p. 383. (Cairns.)

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THE RELATION OF TEMPERATURE AND SOIL MOISTURE TO THE  
DEVELOPMENT OF SEEDLING BLIGHT OF MAIZE DUE TO  
*GIBBERELLA FUJIKUROI* AND *GIBBERELLA FUJIKUROI* VAR.  
*SUBGLUTINANS*.

By E. T. EDWARDS, Ph.D., M.Sc.Agr., Plant Pathologist, Department of  
Agriculture, Sydney.

(Plates xiii-xiv.)

[Read 26th November, 1941.]

INTRODUCTION.

*Gibberella zeae* (Schw.) Petch and *Gibberella fujikuroi* (Saw.) Wr. are common pathogens of maize in all parts of the world. *Gibberella fujikuroi* (Saw.) Wr. var. *subglutinans* Edwards is also widely distributed on maize, but appears to be more important in Australia and South Africa than in America or elsewhere.

*G. fujikuroi* and *G. fujikuroi* var. *subglutinans* are prevalent as internal seed-borne organisms in maize grown in New South Wales, and the sowing of infected grain is responsible commonly for defective germination and the development of seedling-blight diseases. *G. zeae* is also a common cause of seedling blight, but it rarely occurs internally in the grain, and seedling infection usually arises from perithecial material or soil-borne inoculum. The importance of the *Gibberella* seedling diseases varies considerably from year to year, and it has been assumed generally that these fluctuations were correlated with variations in environmental conditions.

Dickson (1923) studied the relation of environment to the causation of seedling-blight diseases of both maize and wheat by *G. zeae*, and concluded that soil temperature was the most important factor governing infection. The most favourable temperatures for seedling blight development ranged in maize from 8°-20°C. and in wheat from 12°-28°C. There was no infection in maize above 24°C. and none in wheat below 12°C. The seedling development of maize is favoured by high temperature and that of wheat by low temperature, and in each case the most severe seeding blight occurred at temperatures unfavourable for optimum host development. It was shown also in the case of wheat seedlings that there was an important interaction between soil temperature and soil moisture, since low soil moisture induced blighting even at low soil temperatures. Koehler (1920) also studied the relation of soil moisture to the pathogenicity of *G. zeae* on wheat seedlings, and found that infection occurred at all moistures suitable for the growth of the host, although the maximum infection occurred at medium soil moistures.

Prior to the investigations reported herein, little critical work had been done on the relation of environmental factors to the causation of maize seedling blight by either *G. fujikuroi* or *G. fujikuroi* var. *subglutinans*, and widely divergent views had been expressed concerning the relation of temperature to infection with *G. fujikuroi*.

Stover (1921) studied the relation of soil temperature to the development of seedling blight of maize caused by *G. zeae*, *G. fujikuroi* and *Helminthosporium* sp. The results with *G. zeae* were in substantial agreement with those later obtained by Dickson (1923). The most severe blighting occurred at 12°-16°C., although infection occurred at all temperatures up to 24°C., with an abrupt decrease above 20°C. Soil temperatures of 24°-32°C. were stated to be the most favourable for the production of seedling blight

by *G. fujikuroi*, with the maximum injury occurring at 28°C. Infection with this organism was reported at all temperatures from 8°–36°C., but at the lower temperatures up to 16° or 20°C. the lesions were stated to be small and inconspicuous.

Limber (1927) also concluded that high soil temperature favoured the development of seedling blight in maize following inoculation with *G. fujikuroi*, and stated that infection mainly occurred above 20°C., while serious injury was restricted to the higher temperature of 28°–30°C.

Peterson (1929) studied the seedling reaction of selfed lines of maize to *G. zea* and *G. fujikuroi* and found that the former organism was a much more vigorous pathogen than the latter. Seedling blight was found to be most severe at temperatures of 12°–17°C., but it always occurred first at 24°C., which was the highest temperature at which blighting occurred.

Leonian (1932) tested the pathogenicity of a considerable number of isolates of *G. fujikuroi* and found that at 25°C. or above, little or no infection occurred under greenhouse conditions. In field inoculation experiments where successive plantings were made from the middle of April until the middle of July, it was found that inoculations made in June or July were ineffective, while those made in early May commonly produced diseased seedlings. In general, temperatures lower than 24°C. were favourable for blight development, while higher temperatures kept the pathogen in check and aided the host plant. Wet, cool springs were stated to be ideal for the production of seedling blight by this organism, and seedlings growing in low moist spots were found to be particularly susceptible.

The writer (1935) reported that soil inoculation, or the direct inoculation of maize seedlings, with *G. fujikuroi* var. *subglutinans* was ineffective under summer conditions when temperatures were relatively high. The same inoculation techniques, however, produced severe seedling blight when carried out during the late winter or early spring. Surveys in New South Wales showed that defective germination and the development of seedling-blight diseases due to *G. fujikuroi* and *G. fujikuroi* var. *subglutinans*, were of common occurrence in the early-sown crops and were particularly severe when cool moist weather conditions prevailed during the early stages of seedling growth.

Ullstrup (1936) as a result of soil inoculations with *G. fujikuroi* var. *subglutinans* obtained over 80% infection in maize seedlings grown in the greenhouse at a soil temperature of about 22°C.

De Haan (1937) conducted seedling infection experiments with *G. fujikuroi* and found in the case of two varieties of maize that the maximum infection occurred at temperatures between 19°–26°C.

#### INVESTIGATIONAL WORK.

The investigations reported herein were carried out at the University of Wisconsin, Madison, Wisconsin, U.S.A., during the tenure of a Commonwealth Fund Service Fellowship. The work was designed to furnish more specific information on the relation of various environmental factors to the development of seedling blight in maize, as a result of infection with *G. fujikuroi* or *G. fujikuroi* var. *subglutinans*. The present paper is concerned with the effects of temperature and soil moisture only.

#### *Materials and Methods.*

The soil temperature experiments were carried out in Wisconsin soil temperature tanks, four tanks being maintained in each of four temperature-controlled greenhouses. The air temperatures of the greenhouses were maintained, with slight variations, at 16°, 20°, 24° and 28°C. respectively. Soil temperatures ranging from 12° to 32°C. were maintained at various times at each of these air temperatures. The low soil temperatures were maintained by adjusting the flow of lake water through the tanks, and the higher temperatures were maintained by thermostatically-controlled heating units. In some instances the lower temperatures were maintained by a combination of running lake water and thermostatically-controlled heating units, as the lake water throughout the winter commonly entered the tanks at 6°–8°C. Thermometers were placed in each tank

and temperatures were checked twice daily throughout the course of each experiment. Thermographs were maintained in each temperature house, and the temperature of each house was controlled thermostatically.

Seedlings were grown in sterilized and unsterilized field soil that had never grown maize previously, in soil and sand mixtures and in sand alone. In all temperature experiments the seedlings were watered regularly and supplied with whatever amount of water was necessary to maintain good conditions for growth.

Soil temperatures of 12° and 32°C. were not utilized after the preliminary experiments as it is unlikely that such temperatures are of common occurrence at the normal time of sowing maize under field conditions. Moreover both temperatures proved to be unsatisfactory for the purpose of the investigation. At 12°C. emergence and seedling growth were often very unsatisfactory in both control and inoculated lots of material, and at a constant soil temperature of 32°C. considerable seedling injury occurred quite independently of inoculation.

The soil moisture experiments, with the exception of those conducted in Australia, were all carried out in a mixture of equal parts of unsterilized field soil and sand. The Australian series was sown in sterilized sandy loam soil in six-inch earthenware pots. All other moisture experiments were conducted in eight-inch earthenware pots, adjusted to uniform weight by the addition of broken crocks. The pots were then partly filled to a uniform height with the soil and sand mixture which was compacted slightly before sowing. All seeds were sown at a uniform depth of three inches from the top of the pot, and were covered with two inches of soil. After sowing, the pots were compacted uniformly and brought to constant weight by the addition of a small amount of soil. In the earlier moisture experiments a perforated aluminium tube was placed in the centre of each pot to give a uniform distribution of water throughout the soil, but in later experiments the tubes were abandoned and all water was applied directly to the surface of the soil. Immediately after planting, the appropriate amount of water was added to each pot to bring the soil to the desired state of saturation, and thereafter the pots were weighed and watered three times each week.

The water-holding capacity of the soil and sand medium was determined for each experiment, and was expressed as the amount of water which the oven-dry mixture retained at saturation. In all cases four two-hundred gram samples were used to determine the oven-dry weight (110°C. for 24-30 hours), and an additional four samples served to determine the water-retaining capacity of the soil. The soil moistures maintained in the Australian experiments are not directly comparable to those used later, as the water-holding capacity of the soil in the former experiments was determined on the basis of air-dry soil.

With the exception of the Australian series, the soil moisture experiments were always carried out in the temperature-controlled greenhouses and maintained at several air temperatures in order to study possible interactions between soil moisture and temperature.

In both the temperature and moisture experiments seedling-blight infection was established by soil inoculation, external grain inoculation and by the use of seed heavily infected internally with either *G. fujikuroi* or *G. fujikuroi* var. *subglutinans*. The internally-infected seed was obtained from the open-pollinated variety Golden Glow. This variety as well as open-pollinated Funk's Yellow Dent and an inbred line known as R4 was used in the other infection experiments.

With the exception of the soil-moisture experiment carried out in Australia, only one isolate of each fungus was used throughout the investigations. These isolates (*G. fujikuroi* 46 and *G. fujikuroi* var. *subglutinans* 99) had been used in previous infection experiments (Edwards, 1935) and were known to be capable of causing seedling blight.

In all experiments where soil inoculation was used, the inoculum consisted of pure cultures growing on sterilized oats. External grain inoculation was effected by soaking the seed in an aqueous conidial suspension for 20-30 minutes, and then germinating the grain in incubators maintained at the same temperature as the temperature of the soil

in which it was proposed to make the sowings in the greenhouse. Rectangular, covered enamel dishes were used as germination chambers, and the kernels were placed on sterilized cheese-cloth overlying a pad of cotton-wool saturated with sterilized water. During the process of germination the kernels were sprayed daily with a fresh conidial suspension, and transplanting was done when the coleoptiles were about one-half to three-quarters of an inch in length. In this way only viable grain was transferred to the pots or cans in the greenhouses. The control seed received similar treatment, being sprayed with sterile water instead of a conidial suspension. In some experiments the kernels were surface-sterilized and washed in sterilized water prior to inoculation, but this treatment had no effect on the ultimate results.

The internally-infected grain was derived from Golden Glow maize that had been inoculated during the summer of 1938 with either *G. fujikuroi* 46 or *G. fujikuroi* var. *subglutinans* 99. As reported previously (Edwards, 1941), ear inoculations prior to the dent stage of development were successful in establishing a very high degree of internal seed-borne infection, and 20-30 ears heavily infected internally with each organism were thus available as a seed source for seedling infection experiments. The grain from a similar number of ears which were almost entirely free from internal fungous infection was available for use in control sowings for each experiment.

As a result of some preliminary infection experiments, it was apparent that in order to obtain a reliable index of the infection occurring under any particular conditions, it was necessary to make a detailed examination of the basal portion of every seedling. It was established also that any accurate measurement of the amount of seedling blight must take into account both the incidence and severity of infection. Ullstrup (1935) in determining the relative pathogenicity of various isolates of *G. zea* utilized a system of indexing infection which took account of both these factors, and with minor modifications this system proved satisfactory in the present investigations. In order to determine the infection index all seedlings were removed from the medium in which they were growing, and after being thoroughly washed in running water, were examined and classified according to the severity of infection.

Six infection classes were recognized and an arbitrary value was assigned to each class as follows:

1. No evidence of lesions .. .. .	0
2. Restricted lesions .. .. .	2
3. Cortical rot involving more than one-third of the subcrown internode .. .. .	4
4. Seedlings obviously stunted or wilted .. .. .	6
5. Seedlings killed after emergence .. .. .	8
6. Seedlings killed before emergence or grain which failed to germinate .. .. .	10

Maize seedlings showing infections characteristic of each class are shown in Plate xiii, fig. 1.

In calculating the infection index, the number of seedlings in each class was multiplied by the class value, and the sum of these products was then divided by the number of kernels sown. The quotient represents the infection index. The infection index was used also to define the extent and severity of a type of non-parasitic seedling injury that often occurred at high temperatures.

In the majority of the experiments, dry-weight determinations of tops were made as an additional aid in determining the effects of the two organisms on the growth of seedlings under different environmental conditions. All seedlings were severed at the second or crown node, and the top portions were then dried to constant weight in a forced air drier at 60°-70°C. The total dry weight of each lot of material was then divided by the number of seedlings which emerged, to give the mean dry weight of the emerged seedlings.

## RELATION OF TEMPERATURE TO SEEDLING-BLIGHT DEVELOPMENT.

*Soil Inoculation Experiments.*

Soil inoculation experiments at controlled temperatures were commenced in December, 1937. Quadruplicate cans of sterilized soil uninoculated or inoculated with *G. fujikuroi* or *G. fujikuroi* var. *subglutinans*, and each sown with 10 grains of inbred R4, were maintained for 6 weeks at soil temperatures of 12°, 16° and 20°C. at an air temperature of 20°C. More extensive experiments with inbred R4 were conducted in February–March, 1938, when soil temperatures of 12°, 16° and 20°C. were each maintained for 32 days at air temperatures of 16° and 20°C., and soil temperatures of 24°, 28° and 32°C. were each maintained at air temperatures of 24° and 28°C. for a similar period.

A third series of soil inoculation experiments was carried out in December, 1938–January, 1939, using the open-pollinated variety Golden Glow. Soil temperatures of 16°, 20°, 24° and 28°C. were maintained in each of the temperature-controlled greenhouses with air temperatures of 16°, 20°, 24° and 28°C. respectively. Infection records for the seedlings grown at soil temperatures of 24° and 28°C. were taken 17 days after sowing, and those for the seedlings grown at the lower soil temperatures were taken a week later.

Additional experiments with open-pollinated varieties were carried out in February, 1939, Funk's Yellow Dent and a white variety from Florida being grown for 26 days in sterilized sand in the presence and absence of inoculum at identical soil and air temperatures of 16°, 20°, 24° or 28°C. in each case.

*Experiment Results.*

The soil and sand inoculation experiments involved 1,200 seedlings of inbred R4 and 1,680 seedlings of the open-pollinated varieties. The same type of infection phenomena occurred in each experiment. The results, therefore, have been grouped together and the mean infection indices for all seedlings at each combination of soil and air temperature are given in Table 1.

TABLE 1.

*Infection indices showing the effect of various combinations of soil and air temperatures on the development of seedling blight in several types of maize as a result of soil inoculation with Gibberella fujikuroi 46 or G. fujikuroi var. subglutinans 99.*

Air Temperature.	Soil Temperature and Treatment.																				
	12° C.			16° C.			20° C.			24° C.			28° C.			32° C.					
	C	46	99	C	46	99	C	46	99	C	46	99	C	46	99	C	46	99			
16° C.	..	..	..	3.0	6.0	8.7	0.7	3.0	3.1	0.4	4.9	4.5	1.9	2.1	2.1	3.6	3.6	2.9	—	—	—
20° C.	..	..	..	2.9	5.7	7.2	0.9	3.7	3.7	0.5	4.1	3.7	1.7	3.1	1.7	3.3	3.5	3.4	—	—	—
24° C.	..	..	..	—	—	—	1.4	1.9	1.4	3.0	3.4	4.2	2.3	3.3	3.0	4.0	3.8	4.4	6.5	7.1	8.0
28° C.	..	..	..	—	—	—	1.5	1.6	2.0	2.2	2.7	4.2	2.5	3.8	2.9	4.2	4.4	4.9	7.6	8.1	8.7

C=uninoculated control.

The type of result obtained by growing seedlings in inoculated soil or sand at temperatures favourable for seedling-blight development is shown in Plate xiv, fig. 3.

Satisfactory results were obtained only at soil temperatures of 16° and 20°C. when maintained at air temperatures of either 16° or 20°C. The best differential reaction between control and inoculated seedlings usually occurred at a soil temperature of 20°C. provided the air temperature did not exceed 20°C. At a soil temperature of 12°C. germination and growth were very slow and the seedlings were usually chlorotic. Severe blighting occurred at this temperature, but the controls likewise always showed a certain amount of faulty germination and post-emergence death of seedlings. Con-

sequently the differences between the inoculated and control series were never as clearly defined as they were at 20°C.

Satisfactory differential results were not obtained at soil temperatures above 20°C. At 24°C. the control and inoculated series usually showed about the same degree of seedling injury, although in some experiments the data indicated that inoculation with *G. fujikuroi* was responsible for a slight increase in the injury which occurred at this temperature. At the higher soil temperatures of 28° and 32°C. the seedlings always showed a considerable amount of injury to the subcrown internode and coronal roots. This injury, which is discussed in a later section of this paper, occurred in both the inoculated and control seedlings, and although it was considered to be distinct from seedling-blight infection, it was, nevertheless, classified on the same basis for the purpose of recording its incidence and severity as an infection index.

Consideration of the interaction between soil and air temperatures shows that soil temperatures of 16° and 20°C. favoured the development of seedling blight at equivalent air temperatures, but failed to give differential results at either 24° or 28°C. Soil temperatures of 24°C. and above were unfavourable for seedling-blight development irrespective of air temperature.

#### *Experiments with Externally-inoculated Seed.*

During the period December, 1938-February, 1939, two series of experiments were carried out in which externally-inoculated and germinated grains of inbred R4 were sown both in unsterilized soil and sand, and maintained at soil temperatures of 16°, 20°, 24° and 28°C. in each of the four temperature-controlled greenhouses. The first series was terminated after 16 days and the second series after 18 days.

#### *Experiment Results.*

Detailed examination of the seedlings showed that similar infections occurred in both the sand and the soil, and accordingly the results have been combined. In these experiments 1920 seedlings were used, and the infection indices for all seedlings grown at the various temperature combinations are given in Table 2.

TABLE 2.

*Infection indices showing the effect of various combinations of soil and air temperatures on the development of seedling blight in inbred R4 maize as a result of external seed-inoculation with Gibberella fujikuroi 46 or G. fujikuroi var. subglutinans 99.*

Air Temperature.	Soil Temperature and Treatment.											
	16° C.			20° C.			24° C.			28° C.		
	C	46	99	C	46	99	C	46	99	C	46	99
16° C. . . . .	0.6	3.3	4.6	0.8	2.3	2.4	2.2	3.5	1.4	5.8	4.6	4.2
20° C. . . . .	0.7	3.0	2.4	0.5	3.2	3.4	2.9	3.5	3.8	4.8	4.0	2.6
24° C. . . . .	1.0	2.4	3.2	1.7	3.3	1.4	3.6	2.3	2.6	5.2	3.9	3.2
28° C. . . . .	1.2	2.6	3.3	2.8	1.8	2.6	6.4	7.8	5.5	5.1	3.8	2.9

It was again apparent that soil temperatures of 16° and 20°C. at air temperatures of 16° or 20°C. were the most favourable for seedling-blight development, as the greatest differences between the inoculated and control seedlings occurred at these temperatures. Infection differences due to inoculation also occurred when a soil temperature of 16°C. was maintained at both 24° and 28°C. A soil temperature of 20°C. under the latter conditions, however, gave less satisfying results.

Little, if any, seedling-blight infection occurred at soil temperatures of 24°C. and none occurred at 28°C., although at the latter soil temperature considerable seedling injury was recorded in both the inoculated and control series at each of the four air

temperatures. The uninoculated control seedlings of the 28°C. soil series were often more severely injured than were either lot of the inoculated seedlings. This was particularly so at the higher air temperatures. Investigations which have been reported elsewhere (Edwards, 1940) showed that abnormally severe injury to the control seedlings at high temperatures was due largely to the action of *Trichoderma viride* (Pers. ex Fries) Bisby. Both *G. fujikuroi* and *G. fujikuroi* var. *subglutinans* inhibited the development of *Trichoderma* and consequently its pathological effects were restricted to seedlings free from *Gibberella* inoculum.

*Experiments with Internally-infected Seed.*

Duplicate experiments with internally-infected grain of Golden Glow were carried out during February and March, 1939. Infection had been established in this material by artificial ear inoculation during the preceding summer. The infected grain was taken only from ears which showed 95% or more internal infection with either *G. fujikuroi* 46 or *G. fujikuroi* var. *subglutinans* 99. The control seed was obtained from ears which had less than 5% of the grain infected internally with any organism. Sowings were made in sterilized sand and maintained at 16°, 20°, 24° and 28°C., the sand and air temperatures in each case being identical. The two experiments were terminated at the end of 21 and 23 days respectively.

*Experiment Results.*

The data from these two experiments involving 840 seedlings have been combined and are given in Table 3. The typical effect of sowing grain heavily infected internally with *G. fujikuroi* or *G. fujikuroi* var. *subglutinans* and maintaining the seedlings at temperatures favourable for seedling-blight infection is shown in Plate xiv, figs. 4 and 5.

TABLE 3.

*The effect of temperature on seedling-blight development in Golden Glow maize arising from internal seed-borne infection with G. fujikuroi 46 or G. fujikuroi var. subglutinans 99.*

Soil and Air Temperature.	Treatment.	Seed Sown. No.	Killed before Emergence. No.	Emerged Seedlings Killed or Lesioned. No.	Emerged Seedlings Free from Injury. No.	Infection Index.	Mean Dry Weight of Seedlings in Mgm.
16° C.	Control .. ..	70	0	8	62	0.2	82
	<i>G. fujikuroi</i> .. ..	70	1	41	28	1.4	62
	<i>G. fujikuroi</i> var. <i>subglutinans</i> .. ..	70	1	54	15	2.2	46
20° C.	Control .. ..	70	0	9	61	0.2	106
	<i>G. fujikuroi</i> .. ..	70	4	58	8	3.1	78
	<i>G. fujikuroi</i> var. <i>subglutinans</i> .. ..	70	2	60	8	2.9	72
24° C.	Control .. ..	70	1	40	29	1.3	186
	<i>G. fujikuroi</i> .. ..	70	0	54	16	1.8	143
	<i>G. fujikuroi</i> var. <i>subglutinans</i> .. ..	70	4	51	15	1.9	127
28° C.	Control .. ..	70	0	69	1	2.2	201
	<i>G. fujikuroi</i> .. ..	70	1	66	3	2.3	167
	<i>G. fujikuroi</i> var. <i>subglutinans</i> .. ..	70	0	67	3	2.0	168

The optimum temperature for seedling-blight development was 20°C., although quite satisfactory infection also occurred at 16°C. Little, if any, infection occurred at 24°C. and none occurred at 28°C., although at both the latter temperatures some seedling injury resulted from constant high temperature. The dry-weight determinations, however, indicate that even at temperatures not favourable for infection, the presence of either *G. fujikuroi* or *G. fujikuroi* var. *subglutinans* had a depressing effect on seedling growth.

Additional data concerning the temperature relations of seedling-blight development arising from internally-infected Golden Glow seed were obtained from other experiments concerning the relation of soil moisture, kernel size and seed treatment to seedling-blight development at different temperatures. The pertinent data from these experiments, together with those already given in Table 3, have been summarized in Table 4. This grouping of data is permissible as neither soil moisture nor kernel size modified disease reaction at any temperature, and the data taken from the seed treatment experiments were restricted to the untreated series which had not received any fungicidal dust.

TABLE 4.

Summary of data from several experiments showing the effect of temperature on seedling-blight development in Golden Glow maize arising from internal seed-borne infection with *G. fujikuroi* 46 or *G. fujikuroi* var. *subglutinans* 99.

Soil and Air Temperature.	Treatment.	Seed Sown. No.	Killed before Emergence. No.	Emerged Seedlings Killed or Lesioned. No.	Emerged Seedlings Free from Injury. No.	Infection Index.	Mean Dry Weight of Seedlings in Mgm.
16° C.	Control .. ..	350	11	59	280	0.7	82
	<i>G. fujikuroi</i> .. ..	350	31	223	96	2.4	69
	<i>G. fujikuroi</i> var. <i>subglutinans</i> .. ..	350	61	253	36	3.7	55
20° C.	Control .. ..	150	1	29	120	0.4	105
	<i>G. fujikuroi</i> .. ..	150	11	116	23	2.9	73
	<i>G. fujikuroi</i> var. <i>subglutinans</i> .. ..	150	11	115	24	3.0	72
24° C.	Control .. ..	150	5	84	61	1.5	150
	<i>G. fujikuroi</i> .. ..	150	6	98	46	1.9	121
	<i>G. fujikuroi</i> var. <i>subglutinans</i> .. ..	150	9	85	56	1.9	114
28° C.	Control .. ..	350	9	195	146	1.4	232
	<i>G. fujikuroi</i> .. ..	350	20	209	121	1.9	200
	<i>G. fujikuroi</i> var. <i>subglutinans</i> .. ..	350	17	190	143	1.4	202

The data in Table 4 were derived from 3,000 seedlings and show clearly that 16° and 20°C. were the optimum temperatures for the development of seedling blight from internally-infected grain. At higher temperatures little, if any, infection occurred, although the type of seedling injury usually associated with constant high temperature occurred in each seedling lot. At all temperatures the seedlings derived from infected seed had a lower mean dry weight than did the corresponding controls raised from nearly-infection-free seed.

#### Discussion of Temperature Experiments.

The infection experiments have shown that soil temperatures of 16° or 20°C. were the optima for the production of seedling blight in maize by *Gibberella fujikuroi* and *Gibberella fujikuroi* var. *subglutinans*. Defective germination and pre-emergence killing were always more prevalent at 16° than at 20°C., but at the latter temperature the emerged seedlings usually showed considerably more lesioning. The greatest differences between the infection indices of the control and inoculated seedlings were also often recorded at 20° C. In most cases soil temperatures of 16° and 20°C. were favourable to the development of seedling blight only when the air temperature did not exceed 20°C., although in experiments with externally-inoculated grain satisfactory infection occurred at soil temperatures of 16°C. when maintained at air temperatures of 24° and 28° C.

Isolations were made from the control and inoculated seedlings in each experiment, and at low temperatures favourable for seedling-blight development pure cultures of the isolate used as inoculum were obtained readily. The uninoculated control seedlings

killed or lesioned at these temperatures, likewise, were infected with either *G. fujikuroi* or *G. fujikuroi* var. *subglutinans*, but the isolates nearly always differed from those recovered from the inoculated series.

Soil temperatures of 24° and 28°C. were unfavourable for seedling-blight infection at all air temperatures, although in a few instances the infection indices showed that slight infection had occurred, particularly at the lower air temperatures.

Considerable seedling injury occurred at soil temperatures in excess of 24°C. This injury was essentially independent of either type of *Gibberella* and in most instances the inoculated and control seedlings were injured to the same extent. Seedling injury at high soil temperature mainly affected the cortical tissues of the subcrown internode, but the coronal roots were likewise affected in some instances. In many cases the cortical tissue of the entire subcrown internode collapsed and disintegrated. The decorticated internode became dark brown in colour, reduced in diameter and showed a typical "wire-stem" effect. In less severe cases the cortical collapse was restricted to localized regions of the internode, sometimes involving only the basal portion in proximity to the seed, and in other cases occurring about the middle of the internode, while the tissues above and below were unaffected.

Seedlings showing the characteristic type of basal injury that occurred at constant high soil temperatures are shown in Plate xiii, fig. 2.

The precise cause of this injury is unknown, but it appeared to be mainly a response to constant high temperature. Infection experiments at various combinations of soil and air temperatures clearly demonstrated that high soil temperature and not air temperature was the main factor influencing injury. The injury was restricted invariably to tissues in contact with the soil, and even at 28°C. seedlings with elongated subcrown internodes showed no cortical collapse above soil level. Growth of seedlings in sterilized soil did not reduce the amount of injury, but seedlings grown in sand often showed considerably less injury than those grown in soil. Repeated isolations from injured seedlings failed to show that any organism was associated consistently with the condition. Isolations from the inoculated and injured plants at high temperatures generally yielded the isolate used as inoculum as well as bacteria and other fungi. Similar isolations from the corresponding injured controls yielded bacteria and a variety of fungi including *Gibberella fujikuroi*, *Trichoderma viride*, *Penicillium* spp. and *Chaetomium* sp.

The occurrence of more or less severe seedling injury in maize grown at constant high temperatures is of considerable interest and undoubtedly explains why Stover (1921) and Limber (1927) both reported that the development of severe seedling blight due to *Gibberella fujikuroi* only occurred at soil temperatures of 24°-32°C. The writer has carefully studied Stover's unpublished paper filed in the library of the University of Wisconsin and it is apparent that he failed to differentiate seedling-blight infection from seedling injury at high temperature. His paper contains a very accurate and detailed description of the typical seedling reaction at high temperature and is illustrated by several excellent photographs, which show conclusively that the injury which he ascribed to seedling-blight infection at temperatures above 24°C. is identical with the injury recorded by the writer for the same temperature range. Stover's failure to obtain satisfactory seedling blight at the temperatures most favourable for infection (16°-20°C.) was probably due to the fact that the isolate used for inoculum was only weakly pathogenic, as it is well known that isolates of *Gibberella fujikuroi* vary considerably in parasitic capabilities. It is considered that Limber (1927) likewise failed to interpret his results correctly. His paper clearly shows that at temperatures of 28° and 32°C. there was considerable injury to the control seedlings. Moreover, in one experiment the most severe root injury was not associated with the presence of *G. fujikuroi*, and Limber suggests that it was mainly a temperature effect. Limber's work was carried out at the Ohio State University where Stover was a member of staff.

## RELATION OF SOIL MOISTURE TO SEEDLING-BLIGHT DEVELOPMENT.

*Soil Inoculation Experiments.*

Preliminary soil inoculation experiments with two isolates of *G. fujikuroi* (46 and 106) and three isolates of *G. fujikuroi* var. *subglutinans* (98, 99 and 101) at three levels of soil saturation were carried out at the Botanic Gardens, Sydney, during the winter of 1937. Triplicate pots of each treatment and of the uninoculated control were each sown with 10 seeds of Funk's Yellow Dent maize and maintained at soil moisture levels of 25, 50 and 75% water-holding capacity. All pots were held for 5 weeks at a mean air temperature of 13°C. (minimum and maximum readings of 10° and 18°C. respectively) and thereafter for 2 weeks at a mean temperature of 16°–18°C.

During January and February, 1939, further soil inoculation experiments with *G. fujikuroi* 46 and *G. fujikuroi* var. *subglutinans* 99 at three levels of soil saturation were carried out in the temperature-controlled greenhouses at the University of Wisconsin. Quadruplicate pots of a mixture of unsterilized field soil and sand, uninoculated or inoculated with either isolate, were sown with Golden Glow maize and maintained at soil moisture levels of 45, 65 and 85% water-holding capacity at air temperatures of 16°, 20°, 24° and 28°C. Infection records were taken at the end of 20 and 28 days respectively for the seedlings grown at 24° or 28°C. and 16° or 20°C.

*Experiment Results.*

The infection indices for the Australian experiment are given in Table 5. These indices are based on the recognition of only three infection classes: (1) killed before emergence, (2) killed after emergence, (3) severely stunted or wilted; and consequently they are not directly comparable to those given elsewhere, as they did not take account of lesioning that did not seriously affect seedling growth. The soil-moisture levels are likewise not comparable to those in other experiments as air-dried and not oven-dried soil was used to determine water-holding capacity.

TABLE 5.

*Infection indices showing the effect of three levels of soil moisture on the development of seedling blight in Funk's Yellow Dent maize following soil inoculation with two isolates of G. fujikuroi (46 and 106) and three isolates of G. fujikuroi var. subglutinans (98, 99 and 101).*

Degree of Soil Saturation.	Control.	<i>G. fujikuroi.</i>		<i>G. fujikuroi</i> var. <i>subglutinans.</i>		
		46	106	98	99	101
25%	0.7	5.1	2.9	3.7	8.6	1.3
50%	0.3	6.0	2.5	6.2	8.4	4.7
75%	0.3	8.5	3.9	7.1	9.1	5.2

It is apparent that the five isolates differed considerably in pathogenicity. *G. fujikuroi* var. *subglutinans* 99 and *G. fujikuroi* 46 were the most vigorous pathogens at each moisture level. Isolate 99 was equally virulent at each soil moisture, but in general the other isolates showed progressive increases in virulence with increase of soil moisture. This increase was due principally to the larger number of seedlings which failed to emerge at the higher soil moistures.

The second experiment involved 1,440 seedlings, and examination of the data given in Table 6 shows that at both 16° and 20°C. inoculation caused a considerable amount of seedling blight with well-defined differences between the inoculated and control series. At 24° and 28°C. many of the seedlings showed the characteristic type of injury associated with constant high temperature, but true seedling blight did not occur.

The degree of soil saturation had no material effect on the development of seedling blight or seedling injury at any of the four temperatures. It likewise had very little effect on seedling growth except at 28°C. where the seedlings in the highest moisture series appeared to be more vigorous and proved to have a higher mean dry weight than those receiving less water.

TABLE 6.

The pathogenicity of *G. fujikuroi* 46 and *G. fujikuroi* var. *subglutinans* 99 on Golden Glow maize seedlings as a result of soil inoculation and subsequent growth at three levels of soil saturation at four different temperatures.

Temperature.	Degree of Soil Saturation.	Control.		<i>G. fujikuroi</i> .		<i>G. fujikuroi</i> var. <i>subglutinans</i> .	
		Infection Index.	Mean Dry Weight. Mgm.	Infection Index.	Mean Dry Weight. Mgm.	Infection Index.	Mean Dry Weight. Mgm.
16° C.	45%	1.0	47	2.3	45	2.6	48
	65%	0.8	62	2.7	69	3.0	51
	85%	0.7	41	3.2	41	2.4	34
20° C.	45%	0.4	86	2.3	82	2.0	89
	65%	0.5	88	2.2	96	1.8	87
	85%	0.6	98	2.6	88	2.2	95
24° C.	45%	1.9	85	1.8	97	2.2	99
	65%	1.7	95	2.1	99	2.1	107
	85%	1.6	94	2.1	100	1.9	109
28° C.	45%	2.2	100	2.6	99	2.3	105
	65%	1.8	111	2.6	109	2.0	114
	85%	2.1	124	2.3	123	3.3	129

*Experiment with Externally-inoculated Seed.*

In November–December, 1938, a soil moisture experiment, using a mixture of unsterilized field soil and sand, was carried out with seed of inbred R4 that had been inoculated externally with *G. fujikuroi* 46 or *G. fujikuroi* var. *subglutinans* 99. Quadruplicate pots of inoculated and control seedlings were maintained at 45, 65 and 85% water-holding capacity at air temperatures of 16°, 20°, 24° and 28°C. Infection records were taken at the end of 18 and 28 days respectively, for the seedlings grown at 24° or 28°C. and 16° or 20°C.

*Experiment Results.*

The results of this experiment which involved 1,440 seedlings are given in Table 7.

TABLE 7.

The pathogenicity of *G. fujikuroi* 46 and *G. fujikuroi* var. *subglutinans* 99 on inbred R4 maize seedlings as a result of external grain-inoculation and subsequent growth at three levels of soil saturation at four different temperatures.

Temperature.	Degree of Soil Saturation.	Control.		<i>G. fujikuroi</i> .		<i>G. fujikuroi</i> var. <i>subglutinans</i> .	
		Infection Index.	Mean Dry Weight. Mgm.	Infection Index.	Mean Dry Weight. Mgm.	Infection Index.	Mean Dry Weight. Mgm.
16° C.	45%	1.8	25	6.2	23	8.3	14
	65%	1.9	26	7.0	22	8.1	15
	85%	2.1	29	7.6	17	9.9	—
20° C.	45%	1.8	68	3.8	63	6.4	55
	65%	2.1	69	4.6	66	6.7	43
	85%	2.2	61	5.8	58	7.4	39
24° C.	45%	1.6	93	1.8	90	2.5	77
	65%	1.7	102	2.7	111	1.9	95
	85%	1.6	91	2.5	107	3.4	100
28° C.	45%	7.6	54	7.8	71	6.0	63
	65%	6.1	66	6.9	58	4.2	88
	85%	6.8	56	5.6	86	3.0	111

As in previous experiments temperature was the principal factor governing infection, and at both 16° and 20°C. considerable seedling blight occurred. At both these temperatures increases in soil moisture from 45 to 85% saturation invariably resulted in a higher infection index, and with one exception increases from 45 to 65% saturation also resulted in slight increases. These increases occurred in both the inoculated and control series, but the latter increases were much smaller than those in the inoculated seedlings, indicating a definite increase in pathogenicity at the higher levels of soil moisture.

The relatively high infection indices obtained in all series at the lower temperatures were due mainly to the fact that seedling emergence in this experiment was somewhat less than usual. The most satisfactory emergence, the maximum growth as determined by dry weight and the minimum seedling injury occurred at 24°C. At 28°C. there was again considerable pre-emergence killing and severe injury to the cortical tissues of the subcrown internode and coronal roots of both the inoculated and control seedlings.

At the higher temperatures the control seedlings were often more severely injured and had a lower mean dry weight than did the corresponding inoculated seedlings. As stated previously, these differences were due to the deleterious effect of *Trichoderma viride* on seedlings grown in the absence of *Gibberella inoculum*.

*Experiments with Internally-infected Seed.*

Quadruplicate pots of mixed unsterilized soil and sand, sown with grain either free from infection or heavily infected internally with either *G. fujikuroi* or *G. fujikuroi* var. *subglutinans*, were maintained at soil moisture levels of 45 and 90% water-holding capacity at air temperatures of both 16° and 28°C. Infection records were taken after 28 and 45 days respectively for the two temperature series and are shown in Table 8.

TABLE 8.

*The effect of soil moisture on the development of seedling blight in Golden Glow maize seedlings derived from grain heavily infected internally with G. fujikuroi 46 or G. fujikuroi var. subglutinans 99.*

Air Temperature.	Degree of Soil Saturation.	Treatment.	Seed Sown. No.	Killed Before Emergence. No.	Emerged Seedlings Killed or Lesioned. No.	Emerged Seedlings Free from Injury. No.	Infection Index.	Mean Dry Weight of Seedlings. Mgm.
16° C.	45%	Control .. ..	40	1	8	31	0.8	119
		<i>G. fujikuroi</i> ..	40	4	18	18	2.1	118
		<i>G. fujikuroi</i> var. <i>subglutinans</i> ..	40	14	24	2	5.2	67
	90%	Control .. ..	40	4	10	26	1.8	81
		<i>G. fujikuroi</i> ..	40	10	23	7	4.0	69
		<i>G. fujikuroi</i> var. <i>subglutinans</i> ..	40	26	14	0	7.5	45
28° C.	45%	Control .. ..	40	0	5	35	0.3	232
		<i>G. fujikuroi</i> ..	40	1	9	30	0.8	219
		<i>G. fujikuroi</i> var. <i>subglutinans</i> ..	40	1	4	35	0.5	215
	90%	Control .. ..	40	2	18	20	1.9	385
		<i>G. fujikuroi</i> ..	40	0	20	20	1.4	287
		<i>G. fujikuroi</i> var. <i>subglutinans</i> ..	40	1	18	21	1.4	306

At 16°C. a considerable amount of infection occurred at each soil moisture level and there were well-defined differences in the infection indices of the control and inoculated series. The higher soil moisture increased the infection indices of both the inoculated and control seedlings. This increase was mainly due to a reduction in

the number of seedlings which emerged. The decrease in seedling emergence from the uninfected grain was considerably less than from the infected seed, thus indicating that a substantial part of the latter reduction was due to the increased pathogenicity of *Gibberella* at the higher moisture levels.

Very little seedling injury occurred in any series at 28° C., although it was a little more common at the higher level of soil moisture. The seedlings derived from infected seed usually had a mean dry weight substantially lower than the controls. These differences occurred even at the higher temperatures unfavourable for seedling-blight infection, although in such cases no visible growth differences were apparent.

Additional data concerning the effect of soil moisture levels of 45 and 90% water-holding capacity on the development of seedling blight from internally-infected seed sown at 16° and 28°C. were obtained from other experiments in which the relation of grain size to blight development was investigated. A summary of these data and of those given in Table 8 is shown in Table 9, which incorporates the mean infection indices and dry-weight determinations for 1,200 seedlings.

TABLE 9.

*Mean infection indices and dry weights of seedlings of Golden Glow maize derived from seed free from infection or heavily infected internally with G. fujikuroi 46 or G. fujikuroi var. subglutinans 99 and maintained at two levels of soil saturation at different temperatures.*

Air Temperature.	Degree of Soil Saturation.	Control.		<i>G. fujikuroi</i> .		<i>G. fujikuroi</i> var. <i>subglutinans</i> .	
		Infection Index.	Mean Dry Weight. Mgm.	Infection Index.	Mean Dry Weight. Mgm.	Infection Index.	Mean Dry Weight. Mgm.
16° C.	45%	0.6	142	2.0	137	4.1	92
	90%	1.2	139	3.2	110	5.1	121
28° C.	45%	0.8	225	1.2	213	1.3	208
	90%	1.5	349	1.9	287	1.9	311

The data in Table 9 again indicate that the higher soil moisture favoured infection with each organism at 16°C., and also increased slightly the amount of seedling injury that occurred at 28°C. The mean dry-weight determinations show that at each moisture level at both temperatures, the control seedlings had a higher dry weight than did those derived from infected seed.

#### *Discussion of Soil Moisture Experiments.*

The infection experiments conducted at different levels of soil saturation have shown that soil moisture is not a very important factor in the production of maize seedling blight by either *G. fujikuroi* or *G. fujikuroi* var. *subglutinans*. At temperatures favourable for infection, relatively severe seedling blight occurred at both high and low moisture levels, but variation in soil moisture never induced seedling blight at unfavourable temperatures.

At favourable temperatures, however, infection was usually somewhat more severe at the higher soil moistures of 85 or 90% saturation than at 45% saturation. This infection increase was due principally to reduced germination and seedling emergence. Data obtained from seed treatment experiments with internally-infected grain, which are to be published later, support this finding and show that high soil moisture results in a statistically significant increase in faulty germination and pre-emergence killing, but has no significant effect on the subsequent lesioning of seedlings. The Australian soil inoculation experiments suggested that high soil moisture had a greater effect on the pathogenicity of weakly parasitic strains of each organism than it did on the more virulent isolates, but this matter has not been investigated further.

## SUMMARY.

1. Studies were made of the relation of temperature and soil moisture to the development of seedling blight in maize due to *Gibberella fujikuroi* and *Gibberella fujikuroi* var. *subglutinans*.
2. The temperature effects were studied in Wisconsin soil temperature tanks in temperature-controlled glasshouses, and infection experiments were conducted at various combinations of soil and air temperatures.
3. The soil moisture effects were studied in temperature-controlled greenhouses and infection experiments at different moisture levels were conducted at several temperatures.
4. Seedling-blight infection with each organism was established in both temperature and moisture experiments by soil inoculation, external seed inoculation, and the sowing of seed that was heavily infected internally. Several open-pollinated varieties and one inbred line of maize were used in the infection experiments.
5. An infection index based on the recognition of six infection classes was used to record the incidence and severity of both seedling blight and a type of non-parasitic injury that occurred at high soil temperatures.
6. The optimum soil temperatures for infection with each organism were 16° and 20°C. The lower temperature favoured defective germination and pre-emergence death of seedlings, while lesioning of emerged seedlings was more prevalent at the higher temperature than at 16°C. Satisfactory infection at these soil temperatures occurred only when the air temperature did not exceed 20°C.
7. Seedling-blight development was not satisfactory at soil temperature of 24°C., although in some cases slight infection occurred.
8. Seedling blight due to *Gibberella fujikuroi* or *Gibberella fujikuroi* var. *subglutinans* did not occur at soil temperatures of 28° or 32°C. Seedlings grown at these temperatures, however, showed severe basal injury that was independent of inoculation or the chance presence of any organism.
9. Infection did not occur when seedlings were grown at favourable air temperatures (16°–20°C.) and unfavourable soil temperatures (above 24°C.).
10. Soil moisture was not an important factor in the production of seedling blight by either organism. At favourable temperatures satisfactory infection occurred at both high and low soil moisture levels, and variation of soil moisture never induced seedling blight at unfavourable temperatures.
11. At temperatures favourable for blight development increase of soil moisture from 45 to 85 or 90% water-holding capacity usually caused a slight infection increase by depressing germination and seedling emergence.
12. Seedlings derived from grain internally infected with either *Gibberella fujikuroi* or *Gibberella fujikuroi* var. *subglutinans* commonly produced less dry matter than seedlings derived from non-infected grain. This reduction in mean dry weight occurred even at temperatures unfavourable for seedling-blight development.

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## EXPLANATION OF PLATES XIII-XIV.

## Plate xiii.

Fig. 1.—Maize seedlings showing injury characteristic of the six infection classes used in determining the infection indices in studies on the relation of temperature and soil moisture to seedling-blight development.

Left to right: 1, Free from infection; 2, Restricted lesions; 3, Cortical rot; 4, Wilted or stunted; 5, Killed after emergence; 6, Killed before emergence.

Fig. 2.—Maize seedlings showing injury to subcrown internode and coronal roots as a result of growth at constant soil temperature of 28°C.

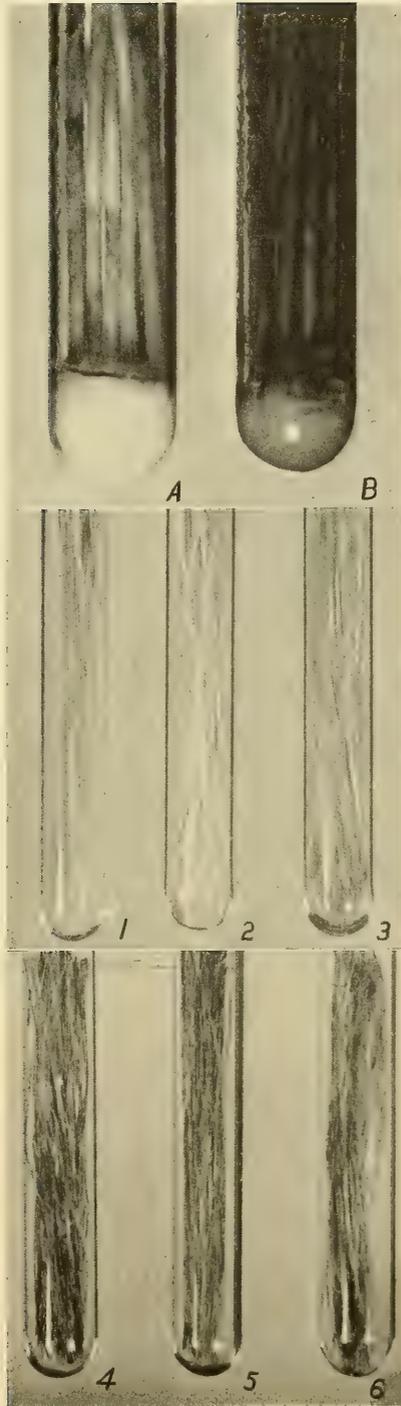
## Plate xiv.

Fig. 3.—Seedlings of Funk's Yellow Dent maize grown for 24 days at 16°C. in uninoculated sand, and in sand inoculated with *Gibberella fujikuroi* or *Gibberella fujikuroi* var. *subglutinans*. Left: Uninoculated control; Centre: Inoculated with *G. fujikuroi* 46; Right: Inoculated with *G. fujikuroi* var. *subglutinans* 99.

Fig. 4.—Seedlings of Golden Glow maize derived from non-infected and infected seed and grown for 21 days at 16°C. Left: Non-infected seed; Centre: Seed infected internally with *Gibberella fujikuroi* 46; Right: Seed infected internally with *Gibberella fujikuroi* var. *subglutinans* 99.

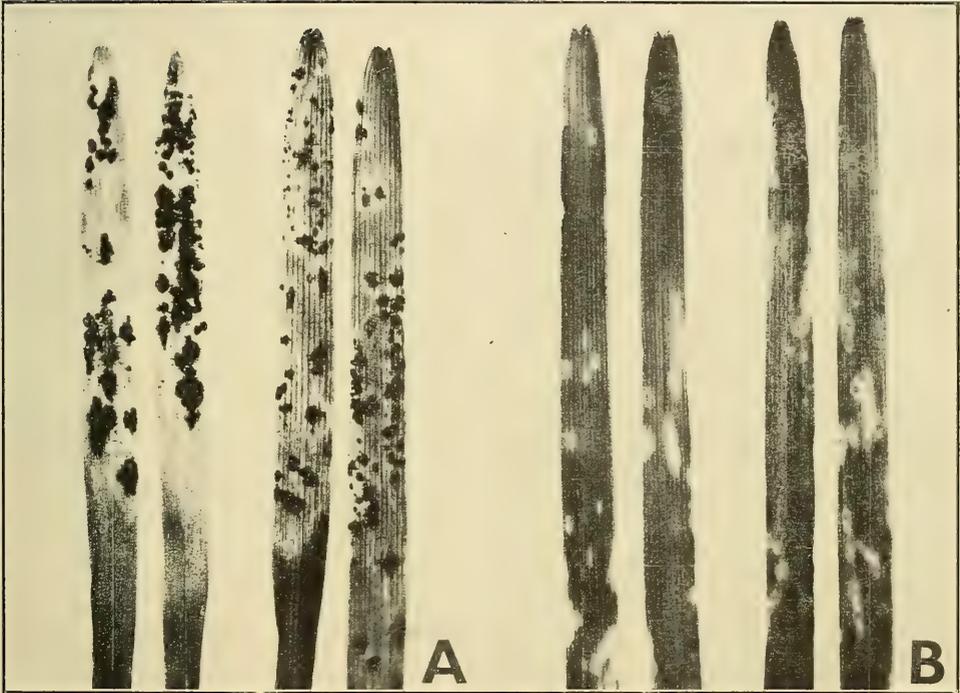
Fig. 5.—Seedlings of Golden Glow maize derived from non-infected and infected seed and grown for 21 days at 20°C. Left: Non-infected seed; Centre: Seed infected internally with *Gibberella fujikuroi* 46; Right: Seed infected internally with *Gibberella fujikuroi* var. *subglutinans* 99.





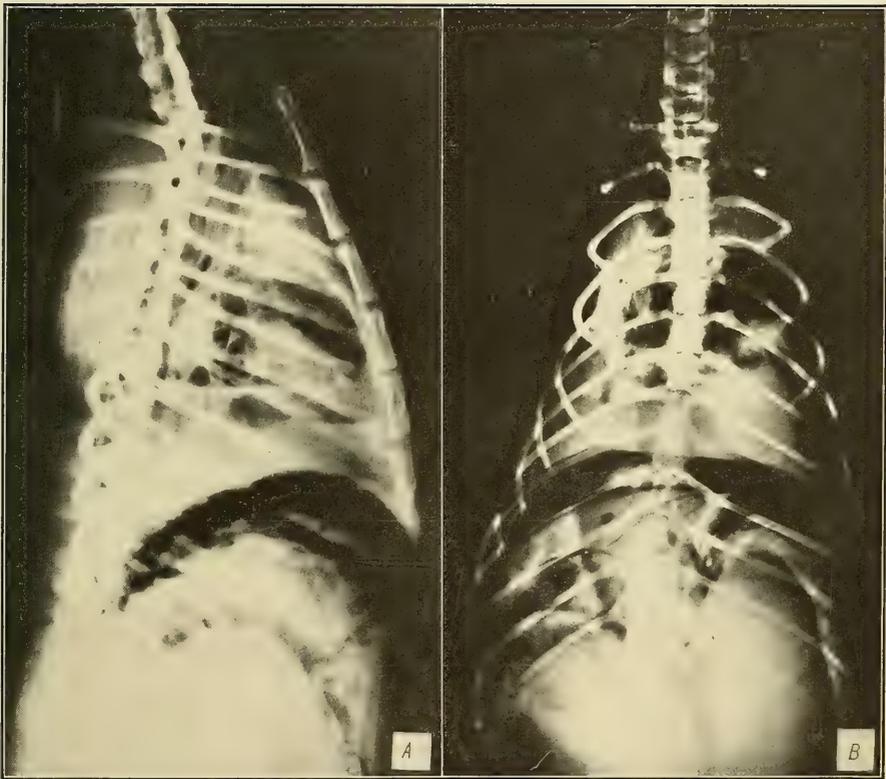
Microbiology of Flax Retting.





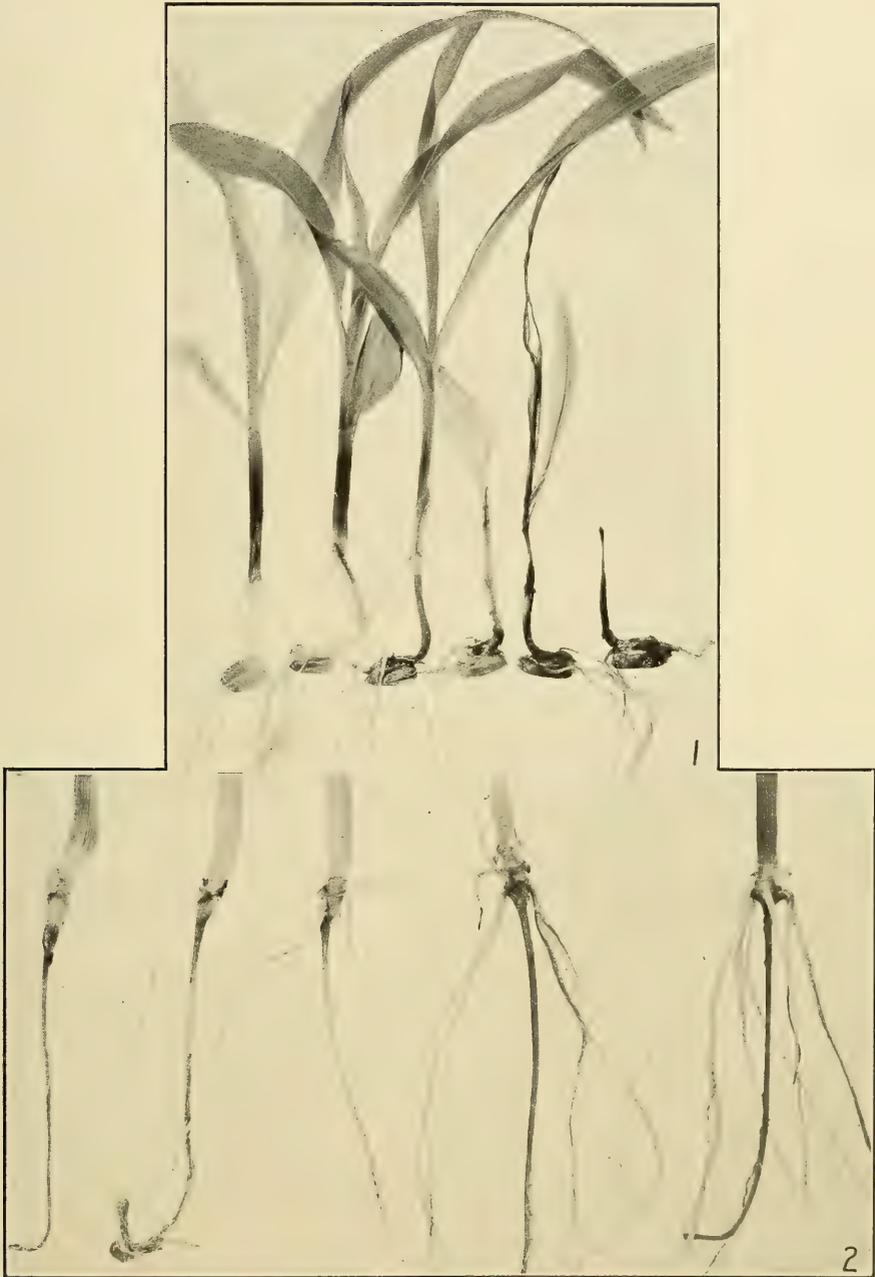
Australian Rust Studies.





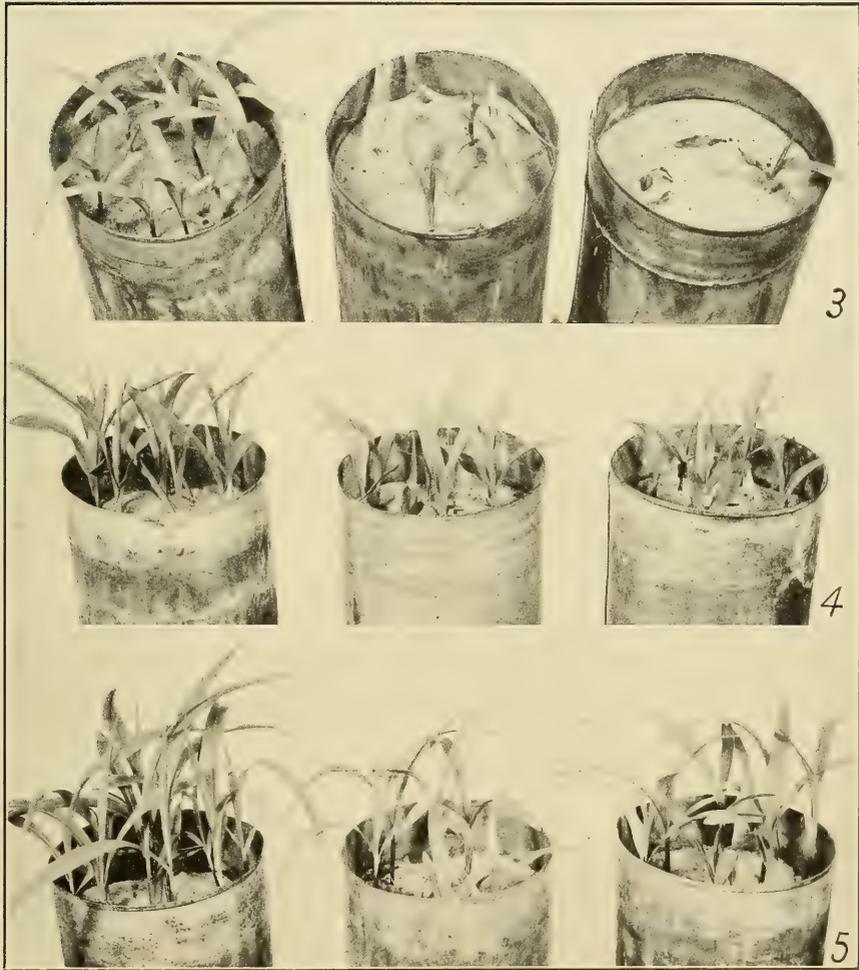
Thorax of the Wallaroo (*Macropus robustus*).





Seedling Blight of Maize.





Seedling Blight of Maize.



## ABSTRACT OF PROCEEDINGS.

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### ORDINARY MONTHLY MEETING.

28th MAY, 1941.

Dr. A. B. Walkom, President, in the Chair.

The President announced that an appeal to all interested in natural history had been received from the Zoological Society of London, which, owing to the war, is in urgent need of financial assistance. Those desiring to contribute are asked to send their donations to The Treasurer, Zoological Society, Regent's Park, London, N.W. 8.

The Donations and Exchanges received since the previous Monthly Meeting (30th April, 1941), amounting to 9 Volumes, 69 Parts or Numbers, 6 Bulletins, 1 Report and 6 Pamphlets, received from 46 Societies and Institutions and 1 private donor, were laid upon the table.

#### PAPERS READ.

1. Physiological Studies in Drought Resistance. i. Technique. By Professor E. Ashby, D.Sc., and Valerie May, M.Sc.

2. The Synonymy, Hosts, and Type Material of *Guntheria bipygalis* (Gunther) (Acarina: Trombidiidae). By Carl E. M. Gunther, M.D., B.S., D.T.M.

3. An Erythraeid Mite from New Guinea (Acarina: Erythraeidae). By Carl E. M. Gunther, M.D., B.S., D.T.M.

4. Nitrogen Fixation and Cellulose Decomposition by Soil Micro-organisms. ii. The Association between *Azotobacter* and Facultative-aerobic Cellulose-decomposers. By H. L. Jensen and R. J. Swaby.

### ORDINARY MONTHLY MEETING.

25th JUNE, 1941.

Dr. A. B. Walkom, President, in the Chair.

Miss Helen R. Browne and Dr. I. A. Watson were elected Ordinary Members of the Society.

The President informed members that the Royal Society of New South Wales will make the fifth award of the Walter Burfitt Prize, in November, 1941, to the worker in pure or applied science whose published contributions during the three years ending 31st December, 1940, are considered to be of the highest scientific merit. Nominations and publications should be submitted to the Royal Society not later than 31st August, 1941.

The Donations and Exchanges received since the previous Monthly Meeting (28th May, 1941), amounting to 15 Volumes, 97 Parts or Numbers, 4 Bulletins, 1 Report and 10 Pamphlets, received from 52 Societies and Institutions, were laid upon the table.

#### PAPERS READ.

1. Two New Trombidiid Larvae from New Guinea (Acarina: Trombidiidae). By Carl E. M. Gunther, M.D., B.S., D.T.M.

2. Studies in Silurian Brachiopoda. i. Description of a New Genus and Species. By Joan Johnston, B.Sc.

3. The Diptera of the Territory of New Guinea. xii. Family Tipulidae. Part iv. By Charles P. Alexander. (*Communicated by F. H. Taylor, F.R.E.S., F.Z.S.*)

4. The Ecology of the Central Coastal Area of New South Wales. iv. Forest Types on Soils from Hawkesbury Sandstone and Wianamatta Shale. By Ilma M. Pidgeon, M.Sc., Linnean Macleay Fellow of the Society in Botany.

5. Serological Studies of the Root-nodule Bacteria. i. Strains of *Rhizobium meliloti*. By J. M. Vincent.

## NOTES AND EXHIBITS.

Mr. E. Cheel exhibited seedlings raised from seed of cultivated plants of *Leptospermum*, formerly classed under the species *L. flavescens* by Bentham, Mueller, Bailey, and Maiden. The seedling plants show all the characteristics of their parents in cultivation and of the original plants in the wild state from which the seed was collected. The following are typical representatives of the more recent classification: (1) *L. flavescens* Sm. (*L. flavescens* var. a. *commune* of Bentham excluding *L. amboinense* DC., an Indian species); (2) *L. citratum* Challinor, Cheel and Penfold (*L. flavescens* var. *citratum* C.T.W.); (3) *L. emarginatum* Wendl. (*L. flavescens* var. b. *obovatum* Benth.); (4) *L. flavescens* var. c. *grandiflorum* Benth. See Cheel (*Proc. Roy. Soc. N.S.W.*, 1920, p. 233) for remarks on this variety; (5) *L. flavescens* var. d. *microphyllum* Benth.; (6) *L. Petersoni* Bail.; seems to be identical with *L. flavescens* var. *grandiflorum* Benth.; (7) *L. flavescens* var. e. *minutifolium* Benth.; (8) *L. flavescens* var. *leptophyllum* Cheel; (9) *L. Liversidgei* R.T.B. (*L. flavescens* var. *citriodora* Bailey); (10) *L. odoratum* Cheel.

Dr. H. L. Jensen exhibited samples of fibre from flax straw retted by various fungi isolated from dew-retted flax. The fungi included *Dematium pullulans*, *Alternaria* spp., and yeasts, not previously recognized as active in the process of dew-retting. Some of the fungi cause a dark colour of the fibre, similar to that of natural dew-retted flax, while others show a tendency to destruction of the fibre.

## ORDINARY MONTHLY MEETING.

30th JULY, 1941.

Mr. C. A. Sussmilch in the Chair.

Mr. Stanley T. Blake was elected an Ordinary Member of the Society.

The Chairman announced that the proclamation protecting certain wildflowers and native plants had been renewed for a further period of three years from 1st July, 1941.

The Donations and Exchanges received since the previous Monthly Meeting (25th June, 1941), amounting to 9 Volumes, 94 Parts or Numbers, 8 Bulletins, 1 Report and 1 Pamphlet, received from 52 Societies and Institutions and 1 private donor, were laid upon the table.

## PAPERS READ.

1. *Trichilogaster maideni* (Froggatt) (Hymenopt., Chalcidoidea), a Wasp causing Galls on *Acacia implexa* Benth., and *A. Maideni* F.v.M. With Observations on Australian Chalcidoid Galls. By N. S. Noble, D.Sc.Agr., M.Sc., D.I.C.

2. Notes on the Measurement of some Physical and Optical Properties of the New South Wales Torbanites. By J. A. Dulhunty, B.Sc., Linnean Macleay Fellow of the Society in Geology.

3. Some Nematode Parasites of Australian Birds. By T. Harvey Johnston and Patricia Mawson.

4. Notes on the Aphididae in Australia. i. Two Aphids new to New South Wales (Hemiptera). By E. H. Zeck.

5. Miscellaneous Notes on Australian Diptera. viii. Subfamily Lomatiinae. By G. H. Hardy.

## ORDINARY MONTHLY MEETING.

27th AUGUST, 1941.

Dr. A. B. Walkom, President, in the Chair.

Dr. E. T. Edwards was elected an Ordinary Member of the Society.

The President referred to the sudden death, on 14th July, 1941, of Mr. R. T. Baker, who had been a member of the Society since 1888 and a member of Council from 1897 to 1922.

The President also, on behalf of members, offered congratulations to Dr. M. F. Day on attaining the degree of Doctor of Philosophy of the University of Harvard.

The Donations and Exchanges received since the previous Monthly Meeting (30th July, 1941), amounting to 9 Volumes, 55 Parts or Numbers, 3 Bulletins, 4 Reports and 24 Pamphlets, received from 45 Societies and Institutions, were laid upon the table.

## PAPERS READ.

1. An Illustrated Key to some Common Australian Culicine Mosquito Larvae with Notes on the Morphology and Breeding Places. By A. R. Woodhill and G. Pasfield.
2. Notes on the Kamilaroi Stratigraphy in the Western Coalfield of New South Wales. By J. A. Dulhunty, B.Sc., Linnean Macleay Fellow of the Society in Geology.
3. Australian Hesperidae. x. On *Hesperilla donnysa* Hewitson, 1868. By G. A. Waterhouse, D.Sc., B.E., F.R.E.S.
4. Notes on Australian Lycaenidae. Part viii. On *Ogyris zosine* Hew., and *O. genoveva* Hew. By G. A. Waterhouse, D.Sc., B.E., F.R.E.S.
5. Nitrogen Fixation and Cellulose Decomposition by Soil Micro-organisms. iii. *Clostridium butyricum* in association with Aerobic Cellulose-decomposers. By H. L. Jensen, Macleay Bacteriologist to the Society.

## ORDINARY MONTHLY MEETING.

24th SEPTEMBER, 1941.

Dr. A. B. Walkom, President, in the Chair.

The President referred to the sudden death, on 1st September, 1941, of Mr. W. F. Blakely, who had been a member of the Society since 1920.

The President announced that the Council is prepared to receive applications for four Linnean Macleay Fellowships tenable for one year from 1st March, 1942, from qualified candidates. Applications should be lodged with the Secretary, who will afford all necessary information to intending candidates, not later than Wednesday, 5th November, 1941.

The Donations and Exchanges received since the previous Monthly Meeting (27th August, 1941), amounting to 5 Volumes, 60 Parts or Numbers, 3 Bulletins, 1 Report and 12 Pamphlets, received from 38 Societies and Institutions, were laid upon the table.

## PAPERS READ.

1. The Genus *Pelecorhynchus* (Diptera, Tabanoidea). 1. Morphology, Relationships and Phylogeny, and Biology. By I. M. Mackerras, M.B., Ch.M., B.Sc., and the late Mary E. Fuller, B.Sc.

This paper has been held over for publication with Part 2, as one paper, in These PROCEEDINGS, Vol. lxxvii, Pts. 1-2, 1942.

2. The Oviposition Responses of Three Species of Mosquitoes, *Aedes* (*Stegomyia*) *aegypti* Linnaeus, *Culex* (*Culex*) *fatigans* Wiedemann and *Aedes* (*Pseudoskusea*) *concolor* Taylor, in relation to the Salinity of the Water. By A. R. Woodhill.

3. Microbiological Investigations on the Dew-retting of Flax. By H. L. Jensen, Macleay Bacteriologist to the Society.

4. On Australian Dermestidae. Part 1. Descriptions of a New Genus and Two New Species; also a Note on the Genus *Anthrenus*. By J. W. T. Armstrong.

## ORDINARY MONTHLY MEETING.

29th OCTOBER, 1941.

Dr. W. R. Browne in the Chair.

The Chairman referred to the death, on 21st October, 1941, of Mr. A. G. Hamilton, who had been a member of the Society since 1885 and a member of Council from 1906 to 1939.

The Chairman reminded candidates for Linnean Macleay Fellowships, 1942-43, that Wednesday, 5th November, 1941, is the last day for receiving applications.

The Donations and Exchanges received since the previous Monthly Meeting (24th September, 1941), amounting to 2 Volumes, 54 Parts or Numbers, 1 Bulletin, 1 Report and 51 Pamphlets, received from 37 Societies and Institutions, were laid upon the table.

## PAPERS READ.

1. On Certain Debatable Questions in Cranioskeletal Homologies. By H. Leighton Kesteven, D.Sc., M.D.
2. Studies in Trombidiidae (Acarina: Trombidiidae). By Carl E. M. Gunther, M.D., B.S., D.T.M.
3. Australian Rust Studies. vi. Comparative Studies of Biotypes of Race 34 of *Puccinia graminis Tritici*. By W. L. Waterhouse and I. A. Watson.
4. The Physical Effects of Heat on the Torbanites of New South Wales. By J. A. Dulhunty, B.Sc., Linnean Macleay Fellow of the Society in Geology.

## ORDINARY MONTHLY MEETING.

26th NOVEMBER, 1941.

Dr. A. B. Walkom, President, in the Chair.

The President announced that the Council had reappointed Mr. J. A. Dulhunty, B.Sc., Mr. M. E. Griffiths, B.Sc., and Dr. Germaine A. Joplin, B.Sc., to Linnean Macleay Fellowships in Geology, Physiology and Geology respectively, for one year from 1st March, 1942, and had appointed Miss Frances M. V. Hackney, M.Sc., to a Linnean Macleay Fellowship in Plant Physiology for one year from 1st March, 1942.

The Donations and Exchanges received since the previous Monthly Meeting (29th October, 1941), amounting to 2 Volumes, 48 Parts or Numbers, 2 Bulletins, 2 Reports and 6 Pamphlets, received from 40 Societies and Institutions, were laid upon the table.

## PAPERS READ.

1. Revision of Australian Lepidoptera. Oecophoridae. x. By A. Jefferis Turner, M.D., F.R.E.S.  
Descriptions of five new genera and sixty-eight new species are included.
2. The Development of *Aedes (Pseudoskusea) concolor* Taylor in relation to Small Quantities of Salts in Solution and to the Temperature of the Water. By A. R. Woodhill.
3. The Relation of Temperature and Soil Moisture to the Development of Seedling Blight of Maize due to *Gibberella fujikuroi* and *Gibberella fujikuroi* var. *subglutinans*. By E. T. Edwards, Ph.D., M.Sc.Agr.
4. On the Anatomy and Functional Adaptation of the Thorax and Pectoral Girdle of the Wallaroo (*Macropus robustus*). By W. Boardman.

## NOTES AND EXHIBITS.

Mr. E. Cheel exhibited specimens of (1) *Psyllium*, *Plantago psyllium* (family Plantaginaceae), the seed of which is used in Medicine as a mucilage; (2) *Agastache rugosa* (family Labiateae), said to be used as a remedy for diabetes.

Dr. H. L. Jensen exhibited a photograph of white clover plants in aseptic agar culture, showing normal growth and root nodule formation after inoculation with two strains of nodule-bacteria, isolated from *Medicago hispida* var. *denticulata*, but unable to produce nodules on this plant and actually identical with the clover-type (*Rhizobium trifolii*) of nodule-bacteria.

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1941.

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