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OF THE
LINNEAN SOCIETY
OF
NEW SOUTH WALES

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FOR THE YEAR

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ANNUAL GENERAL MEETING.

26th MARCH, 1952.

The Seventy-seventh Annual General Meeting was held in the Society's Rooms, Science House, Gloucester Street, Sydney, on Wednesday, 26th March, 1952.

Mr. A. N. Colefax, President, occupied the Chair.

The Minutes of the Seventy-sixth Annual General Meeting, 28th March, 1951, were read and confirmed.

PRESIDENTIAL ADDRESS.

In appearing before you tonight to deliver the Annual Presidential Address I am aware what a privilege it is, and am also deeply conscious of the high standard which has been set by past Presidents of the Society.

As is customary, the first part of my address will be concerned with the activities of the Society over the past year. In this regard I consider it of first importance to bring before your notice the sterling services rendered respectively by our Honorary Treasurer, Dr. A. B. Walkom, and our Honorary Secretary, Dr. W. R. Browne.

Scientific societies all over Australia are today feeling the effects of the economic crisis through which we are passing. Rising costs, difficulty of obtaining grants, and falling membership, are only some of the consequences of this, and if the Linnean Society of N.S.W. is in a slightly better position than most, we can ascribe much of this to the untiring efforts of our Honorary Treasurer and our Honorary Secretary.

Dr. Walkom has looked after the financial affairs of the Society in his usual meticulous fashion and has also given us the benefit of his unique experience as an Editor.

Dr. Browne, in his capacity of Honorary Secretary, has given his time unselfishly, and to him is due, in no small measure, the smooth running of our meetings, both Council and General. On him also has fallen a large proportion of the administrative work of the Society. As President I am in a particularly good position to appreciate just how much time and labour this has involved. Towards the end of the evening I will ask some member of the Society to propose a vote of thanks to these gentlemen as a token of our appreciation.

I also cannot let this opportunity pass without mentioning the conscientious and valuable services rendered by our paid Assistant Secretary, Miss Allpress. Miss Allpress has been with us a long time now, and I sometimes think that we rather tend to take for granted the high standard of loyalty and cheerful service that characterize her work at all times. To her I owe a special debt, in that she has provided most of the material for this first part of my Address.

It is now my task to summarize the activities of the Society for the year 1951.

Volume 76, Parts 1-4 of the Society's Proceedings were published in 1951 and Parts 5-6 in January, 1952. Volume 76 consists of 225 + xxxvii pages, 15 plates and 236 text-figures. This is a smaller volume than the previous one owing to an increase of 50% in the cost of printing the Proceedings as from March, 1951. Financial assistance (£28 16s. 10d.) was given by the University of Melbourne towards the publication of the paper by C. G. Elliott.

Exchanges received from scientific societies and institutions totalled 1,667 for the year—an increase on previous years. Loans from the library, particularly interstate inter-library loans, have been requested as in the previous year. New exchanges were commenced with: Instituto de Biologia Aplicada, Barcelona, Spain; Université de Besançon, Besançon, France ("Annales Scientifiques"); Fisheries Research Board of Canada, Pacific Biological Station, Nanaimo, Canada; Shimomseki College of Fisheries,

Shimonoseki, Japan; Institut Océanographique de l'Indochine, Nhatrang, Indochine; Museum G. Frey, München, Germany; Entomological Laboratory, Faculty of Agriculture, Kyushu University, Fukuoka, Japan ("Mushi"); Naturhistoriska Riksmuseet, Stockholm, Sweden; Museu Dr. Alvaro de Castro, Lourenco Marques, Portuguese East Africa.

Interesting programmes were given during the year at the following monthly meetings:

April: Addresses by Professor Emmens (Professor of Veterinary Physiology, University of Sydney) on "Biology and Chemistry of Sex Hormones"; and Dr. Margaret Hardy (McMaster Laboratory, University of Sydney) on "Tissue-culture of Hair Follicles".

June: An address by Dr. L. G. M. Baas-Becking, entitled "A Biologist Looks at the Problem of Waste".

July: Lecturettes, illustrated by lantern slides, by members of the expedition to the Kosciusko area, in regard to the Glaciology, Soils, Vegetation and Land Usage.

September: Addresses by Dr. F. V. Mercer on "Biology, the Poor Relation", and by Dr. R. Catala, a visiting French marine biologist, on his observations in the Gilbert Islands, illustrated by lantern slides and photographs.

October: A short summary by Mr. D. J. Lee of recent observations and the importance of entomological work in connection with outbreaks of myxomatosis and encephalitis in Eastern Australia.

November: Reference by the President to the sixtieth anniversary (on 7th December, 1951) of the death of the Society's benefactor, Sir William Macleay, with the exhibition of historic personal relics; and a lecture by Dr. Anton Bruun, leader of the party of scientists from the Danish research frigate "Galathea", on the aims and achievements of the scientific expedition, concluding with a film produced by the party's information officer which showed the early work in fitting and equipping the ship, its trials and departure from Copenhagen.

We thank all who have contributed to these programmes.

Since the last annual meeting the names of 11 members have been added to the list, three members and one corresponding member have been lost by death, one has been removed from the list under Rule VII, and 12 have resigned. The number of members as at 15th March, 1952, is: Ordinary Members, 199; Life Members, 24; Honorary Member, 1; Corresponding Members, 2; total, 226.

Dr. R. N. Robertson resigned as a member of Council on 20th June, 1951. Members of Council testified to Dr. Robertson's live interest in and outstanding service to the Society as a Councillor.

Dr. F. V. Mercer was elected to fill the vacancy on the Council caused by the resignation of Dr. R. N. Robertson.

Dr. A. R. Woodhill was elected a Vice-President on 22nd August, 1951, for the remainder of the session in place of Dr. R. N. Robertson, who had resigned from the Council.

In July, 1951, an application for exemption from the payment of stamp duty on cheques and receipts was granted by the Commissioner of Stamp Duties.

The total net return from Science House for the year was £577. On the resignation of Mr. J. E. Neary as caretaker of Science House a presentation was made to Mr. and Mrs. Neary on 13th June, 1951. Mr. Frank Daly was appointed caretaker as from 10th March, 1951.

Preservation of Natural Areas. A third Natural History Survey was made, under the leadership of Dr. W. R. Browne, of the Spencer's Creek Dam site and other parts of the Kosciusko region from 30th January to 13th February, 1952, when a party of seven scientists visited the area; transport and accommodation were offered for the party by the Snowy Mountains Hydro-electric Authority.

Council decided that it was willing to be represented on the proposed Muogamarra Trust and nominated Mr. R. H. Anderson as its representative.

The Society sent a number of framed photographs and historical relics for exhibition at the Royal Australian Historical Society's Jubilee Exhibition.

On the evening of 10th November, 1951, the Society's aims and activities were featured by your President in the Australian Broadcasting Commission's "Week-end Magazine" session.

We offer congratulations to: Dr. Joan Beattie on the award of the D.Sc. degree; Miss Judith Fraser on obtaining her M.Sc. degree; Dr. R. J. Noble on receiving the Outstanding Achievement Award of the University of Minnesota, U.S.A.; Miss Hilary Purchase on the award of the Thomas Lawrance Pawlett Research Scholarship of the University of Sydney, this being the first award of the scholarship to a woman; Dr. A. R. Woodhill on obtaining the D.Sc.Agr. degree of the University of Sydney; Dr. Janet Harker, F.R.E.S., on obtaining the Ph.D. degree of the University of Manchester; Dr. G. F. Humphrey on the award of the Ph.D. degree of the University of Sydney; Dr. Alex Fraser on the award of the Ph.D. degree of the University of Edinburgh; and Professor W. N. Benson on the award of the Mueller Medal by the Australian and New Zealand Association for the Advancement of Science.

Linnean Macleay Fellowships.

In November, 1950, the Council reappointed Miss Mary Hindmarsh to a Fellowship in Botany for 1951 and appointed Mr. N. C. Stevens and Mr. T. G. Vallance to Fellowships in Geology for 1951.

During 1951 Miss Hindmarsh made investigations into processes concerned with cell division in plants, continuing the study of the action of metabolites and poisons on various stages of mitosis. The effects of dinitrophenol and mononitrophenols on meristematic cells of onion roots were studied further. It was found that cytological abnormalities induced by nitrophenols and colchicine were not the same. Colchicine affects one stage of the cell division process, the spindle mechanism, while nitrophenols, although upsetting the spindle, have a general toxic action on all meristematic cells. These results were published in the Proceedings of the Society during the year. Since so many different chemicals appear to upset the spindle mechanism and since colchicine has been assumed to act by inhibiting spindle formation, an investigation on the presence and absence of the spindle under various conditions was begun. Preliminary examinations of slides of colchicine-treated and untreated roots showed that spindles were not apparent in cells of treated roots but were clearly seen in control roots and in roots which had been allowed to recover in water after treatment. It seems, then, that colchicine does not simply inactivate the spindle mechanism but either destroys the spindle or prevents its formation.

The main subject for study by Mr. Stevens was the petrology of batholithic intrusions in the Cowra-Gunning area. A large area between Lyndhurst and Boorowa was geologically mapped, and the field relations between the granitic rocks and the rocks they intrude were investigated, as well as the structure in both intrusive and invaded rocks, and the relations between gneissic and massive granites. Work on the Cowra intrusion and its xenoliths was completed, and a paper on this work was submitted to the Society. Laboratory work consisted of chemical analyses of the granites and invaded rocks south-west of Cowra, preparation of microslides and air-photo interpretation. The mapping of Ordovician fossiliferous strata at Cliefden Caves, at the north end of the Wyangala batholith, was also completed.

Mr. Vallance reports that during the past year field and laboratory investigations of the relations between granite and the metamorphic series in the Wagga Wagga-Adelong district, New South Wales, have been continued. Some interesting correlation between the mineralogical and chemical compositions and the field distribution of the two groups has been discovered. This, it is hoped, will throw some light on the problem of the significance of the granite and metamorphism in the region.

In November, 1951, the Council reappointed Miss Mary Hindmarsh and Mr. T. G. Vallance to Fellowships in Botany and Geology respectively for 1952. Mr. Stevens did not apply for reappointment to a Fellowship.

Miss Hindmarsh proposes to continue work on the effects of mitotic poisons on the cell division process as follows:

(1) The reversal of sulphanilamide inhibition by p-aminobenzoic acid can be obtained under certain conditions. Attempts will be made to repeat this work and to ascertain the cause of the variable results obtained in experiments with sulphanilamide and p-aminobenzoic acid.

(2) Work on the cytological action of nitrophenols has shown clearly that the action of all mitotic poisons is not the same, although most of them produce a cytological picture superficially very like that of colchicine-treated cells. Substances which upset the spindle mechanism do not necessarily possess a common mode of action and a critical review of the cytological action of all mitotic poisons is needed. In this connection it is of interest to find out first whether these substances destroy or inactivate the spindle mechanism, and second whether tumours produced in the zone of elongation of roots by many mitotic poisons are all formed in the same way. A comparative anatomical study of tumours produced by colchicine, sulphanilamide and nitrophenols will be made. At the same time, dividing cells in root tips will be carefully examined for presence or absence of spindle fibres after treatment with various substances.

(3) Observations made in 1951 suggest that p-aminobenzoic acid inhibits root growth at concentrations where it has no effect on the cell division process. Apparently, p-aminobenzoic acid does affect cell elongation or cell differentiation. For this reason it is suggested that indole acetic acid, which is known to affect cell elongation, be used in combination with sulphanilamide, colchicine and p-aminobenzoic acid to find out whether p-aminobenzoic acid has any connection with auxins in the cell.

Mr. Vallance wishes to continue his research project entitled "Geological Investigations in the Ordovician Metamorphic Belt of Central-Western New South Wales".

We wish both Fellows success in their year's work.

The Council of the Society decided that an applicant for a Linnean Macleay Fellowship who is or intends to become a candidate for the Ph.D. degree shall first obtain the approval of the Council for this.

Macleay Bacteriologist.

During the year 1951-52 Dr. Yao-tseng Tchan has continued his work on soils and his morpho-cytological and physiological work on the N-fixing bacteria isolated from the Sydney district gave sufficient information to classify them as a new species—"*Azotobacter beijerinckii* var. *acido-tolerans*". This species has the general morpho-cytological characters of *Azotobacter* but differs from the latter in its dimensions, presence of fatty bodies and a remarkable tolerance to acidity of media. After the bush fires some research was done to investigate the effect of fire on the microbiological equilibrium of soils. This work was aimed to show the relationship of bush fire and partial sterilization of soils. A new technique for the estimation of mineral elements in the soil, based on the growth of N-fixing bacteria, was started. The principle was to estimate quantitatively these elements at the natural pH range of soils. Very serious difficulties have to be overcome before any positive results can be expected. Based on the fluorescence of the chlorophylls, a technique for the direct microscopic estimation of soil and water algae was established. It has to be improved to make it quantitative. Two papers have been submitted to the Society for publication.

Dr. Tchan gave a short course in bacteriology at the School of Agriculture, University of Sydney, during the year.

A suitable house for Dr. Tchan in Margate Street, Ramsgate, was purchased by the Society from the Bacteriology Fund.

Obituaries.

It is recorded with regret that the following members died during the year: Dr. Robert Broom (Corresponding Member), Mr. Edwin Cheel, Professor T. Harvey Johnston and Mr. Ralph Dudingston Wilson.

Professor T. Harvey Johnston, M.A., D.Sc.

Thomas Harvey Johnston, who had been a member of this Society since 1907, died on 30th August, 1951, at the age of 69 years, just as he was looking forward to the years of retirement following upon a very busy scientific career.

Born in December, 1881, he graduated B.A. of the University of Sydney in 1904, B.Sc. (Hons.) in 1906, M.A. in 1907, and D.Sc. in 1911. This was not, however, the end of his achievement in academic spheres, for in 1908 he became an Associate of Sydney Technical College (in Biology and Agriculture), and a Fellow in 1910.

He lectured in Zoology and Physiology at Sydney Technical College, 1907-8, and during the latter year was also Assistant Director of Bathurst Technical College, N.S.W.

In 1909 he became Assistant Microbiologist in the Government Bureau of Microbiology, Sydney, N.S.W., which position he held for two years. In 1911 he was appointed Lecturer-in-charge, Department of Biology in the University of Queensland, and after seven years was elevated to the Chair in that subject.

He acted in this capacity for three years, and in 1922 successfully applied for the Chair of Zoology at Adelaide University, a post which he held at the time of his death. During this period he was also for a time (1928-34) Honorary Professor of Botany at this university.

This very brief sketch of his academic career gives little idea, however, of the wide and active interest that he had in Australian scientific life. In fact, it would be difficult to cite any other person who gave up so much of his time in furthering the cause of the science he loved so much.

Apart from having been at various times Honorary Zoologist to the Museums at Sydney, Brisbane and Adelaide, he was also President, Royal Society of Queensland, 1915-16; President, Royal Society of South Australia, 1931-32; Editor, Royal Society of South Australia, 1934-35; and also President, Section D, Australian and New Zealand Association for the Advancement of Science, 1923. He was one of the original Fellows of this organization.

He was Chief Biologist to the B.A.N.Z.A.R. Expedition, 1929-30 and 1930-31, and acted as Honorary Editor of the Biological Reports of the Australian Antarctic Expedition (1912-14) since 1930. He fulfilled a similar capacity in connection with the B.A.N.Z.A.R. Expedition, 1931-51, and just as though he felt this weren't enough he also functioned as a member of the Editorial Committee for the Australian Journal for Experimental Biology and Medical Science from 1926 to 1951.

One would have thought that a man who occupied so much of his time with editorial duties would have had little time for research, yet Harvey Johnston's output in this direction was unusually high. He published some 296 papers and reports on a wide variety of subjects, including protozoan parasites, mites, ticks, some marine invertebrates, aboriginal ethnology, and the helminth parasites of Australian reptiles, birds and mammals.

The helminthological work which gained him considerable international renown occupied the closing years of his research career, but what many people of the present generation do not realize is the tremendous debt owed to him by the pastoral industry of Australia. Harvey Johnston was one of the small band of workers who were responsible in the second decade of this century for the introduction of the cochineal insect, and later of the moth *Cactoblastis*, which have proved so spectacularly successful in the eradication of prickly pear.

His work did not go unrecognized among his scientific colleagues, who honoured him in 1939 with the award of the coveted Mueller Medal (Australian and New Zealand Association for the Advancement of Science) for distinguished services to Australian science.

Harvey Johnston was a man of charming personality and one who acted as an inspiration to student and colleague alike. He will be sadly missed, and the sympathies of this Society go out to his family.

Mr. Edwin Cheel.

Edwin Cheel was born in England on 14th January, 1872, coming to Australia as a young man. After working in the Queensland canefields and in private gardens in Sydney he was appointed to the staff of Centennial Park in 1897. Subsequently he was transferred to the gardening staff of the Sydney Botanic Gardens, but soon showed an unusual aptitude for botanical studies. He was appointed to the botanical staff in 1908 and eventually rose to the position of Chief Botanist and Curator of the New South Wales National Herbarium. His botanical interests were wide. His early studies were devoted to the lichens and fungi, but subsequently were extended to most groups of plants.

He published many papers on Australian plant life and became a recognized authority in this field. He took an active part in the work of scientific societies and was a member of this Society from 1899, a member of Council from 1925 to 1940, President, 1930-31, and Honorary Treasurer for 1928 and 1929. He was a frequent attendant at monthly meetings of the Linnean Society, bringing exhibits of botanical specimens and adding greatly to the interest of the meetings. In addition he occupied the position of President of the Royal Society of New South Wales and President of the Naturalists' Society of New South Wales. In his public life he was a keen supporter of the Friendly Society Movement, rising to the highest position in the Manchester Unity Independent Order of Oddfellows.

Although without the benefit of an early training in science, he made valuable contributions to our knowledge of Australian plants and was untiring in his enthusiasm for science.

Advancement in our knowledge of both plant and animal life in Australia owe much to the energy and devotion of self-trained naturalists, and amongst these Edwin Cheel has a secure and honoured place. Mr. Cheel died on 19th September, 1951.

Mr. Ralph Dudingston Wilson.

Ralph Dudingston Wilson, M.Sc.Agr. (Syd.), M.S. (Wis.), died on 13th March, 1952, aged 41 years. He joined the Public Service as an Agricultural Cadet in 1928 and after a brilliant career at the University of Sydney was appointed to the Biological Branch of the New South Wales Department of Agriculture in 1932. At the time of his death he held the position of Plant Pathologist, Grade III, and was in charge of investigations of diseases of vegetable crops. In 1938 he was awarded a Walter and Eliza Hall Fellowship and undertook post-graduate studies at the University of Wisconsin, U.S.A., and took his M.S. degree there.

Before returning to Australia Mr. Wilson travelled extensively, visiting agricultural research institutions in U.S.A., Canada, Great Britain and Europe. Mr. Wilson's professional work was devoted to the study and investigation of diseases of vegetable crops, in which he made important contributions to knowledge. His investigation of bacterial diseases of beans won for him world recognition. It was due to his energy that the New South Wales Bean Seed Certification Scheme was established, and in recent years Mr. Wilson turned his attention to a group of disorders caused by deficiency of soil in available molybdenum. As a result, much more is now known concerning whiptail disease of crucifers, bean scald, and a number of scald and chlorosis diseases of lettuce, tomatoes, rockmelons and other crops.

Mr. Wilson had been a member of the Society from 1938 to 1943 and again from 1949.

Dr. Robert Broom, F.R.S.

Dr. Robert Broom, F.R.S., who died on 6th April, 1951, at the age of 84, had been an Ordinary Member of this Society from 1895 to 1902 and a Corresponding Member since 1902.

He was born in 1866 and studied medicine at the University of Glasgow. He also served an apprenticeship in the Department of Chemistry of that university as junior assistant, and graduated in 1889.

The title of his first paper, "On the Volume of Mixed Liquids", appeared in the Proceedings of the Royal Society of Edinburgh during this early period of training

and gave little hint of the direction in which his researches were to take him in future years.

In a sense Broom was fortunate to be on the threshold of his scientific career at a time when interest in the problems of evolution was almost at fever pitch, and he seems quickly to have made up his mind that his real life's work lay in the biological field. He found himself particularly attracted to the problem of the evolution of the mammals, and it was this preoccupation that was partly responsible for his coming to Australia in 1892. He, no doubt, felt that the Australian monotreme and marsupial fauna would provide him with first-hand information in this field.

Over the next few years he contributed a number of papers on morphological and embryological subjects, the main object of which was to establish the phylogenetic relationships between mammals and reptiles.

A turning-point in his career came when he visited London in 1897 and became deeply interested in a collection of cynodont skulls which had been made in South Africa by Dr. H. G. Seeley. He was inspired to go to South Africa in order to make further studies of the group, and as the demands of his medical practice were not very great he was able to go on periodical collecting expeditions to the Karoo.

For a time he held the Chair of Geology and Zoology at Victoria College, Stellenbosch, and was about to enter on a particularly productive part of his career. Over a period of two decades, he published a number of paper on mammal-like reptiles, and also on the anatomy and classification of the Chrysochloridea and other groups of recent mammals.

In 1920 he was elected a Fellow of the Royal Society, and in 1928 had the honour of being awarded one of the Royal Medals. Honorary degrees were also conferred upon him by several universities.

His great monograph, "The Mammal-like Reptiles of South Africa", was published in 1932 and fully justified the outstanding reputation he had created for himself as one of the leading figures in mammal phylogeny.

In 1934 he joined the staff of the Transvaal Museum, Pretoria, and this was to be the beginning of an epoch-making series of studies on the Taung's skull (*Australopithecus*). These studies were to be based on rich discoveries of new *Australopithecus* material that he himself made at Sterkfontein, Kromdraai and Swartkrans, all of which places were very close to Pretoria.

As a result of this work Broom received two great honours—the Wollaston Medal of the Geological Society of London and the Elliot Gold Medal of the United States National Academy of Sciences.

He was actively engaged in research right up till the time of his death, and even though he was over 80 years old his energies appeared to be undiminished. On his eightieth birthday the Royal Society of South Africa did him the signal honour of publishing a special Robert Broom Commemorative Volume entitled "Robert Broom: Naturalist". This contained papers by a number of scientists on fossil reptiles, fossil men and man-like apes, the human races that have inhabited Africa in the past, and appropriately papers of an embryological nature. Broom, himself, contributed a paper on Theriodonts. The volume has a Broom bibliography at the end which reveals that at the time of publication of the Commemorative Volume he had produced 402 papers, the first of which, already mentioned, appeared in 1885. He published further papers between then and the time of his death.

This Society is honoured by its association with so great a man, and in conclusion I would like to quote D. M. S. Watson, who gives this fine appraisal of his worth: "Broom's life-work is unparalleled by that of anyone now living. In its range, in its mere mass, it recalls the great Victorians, Owen, Huxley and Lankester; in its quality, in the extent to which modern work in many fields can be traced back to it, and in the verve and vigour it shows, it is indeed worthy to be compared with that of the great men of the past."

VARIATIONS ON A THEME.

SOME ASPECTS OF SCALE STRUCTURE IN FISHES.

I am aware that in view of the wide scientific interests of this Society, the subject I have chosen is a rather specialized one; however, I hope that the inherent interest of the problems I propose to deal with will sustain your attention.

I must also confess to another object in selecting this topic. Information on fish scales is widely scattered through the literature, much of which is hard to come by. There is no single book or small group of books to which the student of this aspect of fish structure can go for information, and it is my hope that this Address will at least partly fill that deficiency. It has long been my opinion that the value of a published scientific paper, and especially of an address such as this, can be enhanced if the writer bears in mind the needs of the student as well as those of the research worker. I can refer you to a number of Presidential Addresses delivered to this Society which are particularly outstanding in this regard.

The study of the structure and development of fish scales can be approached from a number of different angles. The main title I have selected would suggest that my sole object was to present to you an account of the amazingly varied types of scale structure that arise, all as an expression of the developmental potency of a single organ—the skin. That indeed is one of my aims, but stemming from this there are matters of wider biological significance touching upon the fascinating subject of early vertebrate evolution. I will also have occasion to discuss the use of scales in the practical field of fisheries biology.

The first part of the Address will be concerned with a formal account of the structure and development of scales and related structures in the principal fish groups, both living and extinct. Purely as a matter of convenience, I will commence with the placoid scale so typical of elasmobranchs (sharks and rays). Such scales, like all others, are developed from the skin, and it will therefore be convenient to describe skin structure first.

The dogfish *Scyllium* may be taken as an example. The skin is primarily two-layered and consists of an outer *epidermis* and an inner *dermis*. The epidermis, of ectodermal origin, is many cells in thickness. In the outermost layers the cells tend to be flattened, but at the base of these there is a definite layer of cells of columnar or polyhedral form. These are sometimes termed the Malpighian cells, and are important in that they are constantly dividing to provide replacement for those cells of the outer strata of the epidermis which are lost through wear and tear. This Malpighian layer also plays a visible but not always understood role in the genesis of scales, and of related structures such as teeth.

Scattered among the ordinary epidermal cells will be found gland cells, the function of which is to secrete the slippery mucus which covers the surface of the fish. That is their normal function, although as will appear later (p. xxx) at least one author has claimed that they secrete calcium salts for the formation of scales in teleosts. The epidermis very seldom contains a nerve or vascular supply.

Immediately beneath the epidermis lies the dermis, cutis or corium, of mesodermal origin. In fishes it consists of two layers—an outer, rather loosely aggregated one with numerous cells, and a deeper fibrous one with comparatively few cells.

The cells of the more superficial layer have plentiful cytoplasm and lie within a meshwork of loosely-arranged fibres. This part of the dermis, which has a rich network of nerves and blood vessels, has aptly been termed by Hertwig "the germinal layer of the integument" because it plays such an important part in the formation of tegumentary structures such as scales, spines, fin rays and teeth.

The deeper part of the dermis consists of a number of parallel fibrous lamellae. In any given lamella the fibres run parallel, but the fibres in adjacent lamellae tend to run at right angles to one another, and all are disposed diagonally with respect to the long axis of the body. The rows of scales are also disposed in this diagonal fashion (Klaatsch, 1890, Pl. VII, fig. 7).

There are also vertical fibres which run straight up into the outermost layer of the dermis (Schneider, 1902, fig. 586, p. 762).

In the higher vertebrates the dermis consists largely of a densely-felted mass of connective tissue fibres. This part of the skin, when tanned, becomes leather, as implied by the alternative name "corium", which is sometimes applied to the dermis.

The skin in fishes, as in other vertebrates, performs a number of important functions, but the one that concerns us at the moment is its ability to produce skeletal structures in the form of scales, denticles, bony plates, and so on, which primarily have a protective function. Such structures in fish present an almost bewildering array of variations, some of which are exceedingly complicated. It is thus convenient to start with a comparatively simple example—the placoid scale.

Structure of Placoid Scales (Fig. 1).

While the arrangement of these on the surface of the body and the sculpturing of the individual scales may vary a good deal from group to group, the most common form is that of a sharp backwardly-directed denticle (with, occasionally, secondary spines) projecting above the epidermis. The denticle or main spine is continuous with

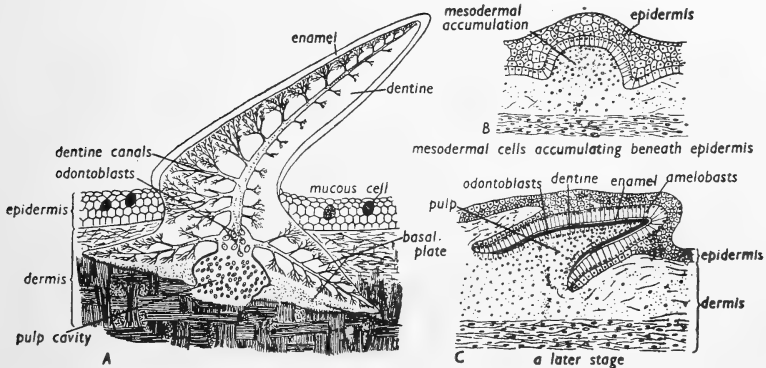


Fig. 1.—A vertical section through the skin of a dogfish showing the epidermis, the dermis divisible into superficial loose, and deeper densely fibrous zones, and a placoid scale.

B-C. Early and late stages in the development of a placoid scale. (From Murray, "Biology". Macmillan & Co., London, 1950. By kind permission of the author.)

a basal plate which anchors the scale in the dermis. The spine is capped with a hard tissue variously called enamel or vitrodentine. "Enamel" implies that it is identical with the enamel of the teeth of higher vertebrates, and is therefore of ectodermal origin. "Vitrodentine" allies it with ordinary dentine (a tissue closely related to bone) which makes up the bulk of the spine, and which is mostly a mesodermal product (see, however, p. xxxviii). The precise nature of its origin is obscure. According to some authors the enamel is invested superficially by a delicate membrane ("Oberhäutchen", Schneider, 1902, p. 761).

Internally the spine has a comparatively wide branched space continuous with a still wider one towards the basal plate. This is the pulp cavity and is filled with a loose vascular tissue, the pulp. Cells (odontoblasts) at the periphery of the pulp send long cytoplasmic processes into a series of branching dentinal canals which penetrate radially into the substance of the spine and extend (as still finer canals) into the enamel cap.

The spine merges into the calcified substance of the basal plate. The latter has no cells, and its undersurface is perforated by an aperture for the passage of the vascular, lymphatic and nervous supply of the pulp.

This external armament of placoid denticles with their basal plates placed edge to edge and joined by connective tissues constitutes the so-called "shagreen" of the shark.

It will be judged from the foregoing that the placoid scale, although superficially simple in appearance, has in reality a very complicated structure. For further understanding of this and of its close relationship to the skin, a study of the development is necessary.

The Development of the Placoid Scale (Fig. 1).

In the Selachian embryo each point in the skin where a placoid scale destined to develop is marked by an accumulation of cells derived from the outer layer of the dermis and lying directly beneath the epidermis. As the mass of dermal cells (the "scale papilla", or "mesodermal accumulation", Fig. 1) becomes compact, it pushes the epidermis upwards as a definite bulge. The epidermal cells (ameloblasts) embracing the tip of the papilla become more columnar and organized into a layer which, by analogy with tooth development in higher vertebrates, is called the "enamel organ". The dermal cells immediately beneath this arrange themselves as a layer of odontoblasts which will ultimately form the dentine.

According to Hertwig (1874), the enamel is the first of the hard substances of the scale to make its appearance. The nuclei of the enamel organ cells, the ameloblasts, at this stage lie towards their outer ends, while the inner ends of the cells develop a longitudinal striation. As the enamel is laid down over the tip of the scale papilla the enamel cells shorten, suggesting that they are being directly converted into enamel from within outwards.

Tomes (1898) disagrees with this and claims that the dermal cells of the scale papilla form the (non-collagenous) matrix of the enamel, and the role of the enamel organ may be to provide the lime salts which harden this.

Beneath the thin enamel cap the odontoblasts have begun dentine formation. They send out cytoplasmic processes along the course of which collagenous ground substance is deposited. The process takes place from without inwards, i.e., centripetally, and as the dentine covering thickens it does so at the expense of the dermal papilla.

As the branching cytoplasmic extensions of the odontoblasts become enclosed in the centripetally-growing mass of ground substance, there are brought into existence the dentine tubules mentioned above. Each tubule is in effect an excavation in the ground substance, housing a cytoplasmic process. The tubules actually penetrate well into the enamel layer. The basal plate develops in continuity with the spine, and is derived wholly from dermal elements. Actually it has a double origin. The more superficial part, in direct continuity with the dentine cone, is derived from the same cells that formed the scale papilla but, unlike the cone, it is homogeneous and lacks both cell processes and cells. The basal part of the plate, on the other hand, is derived from the lower, fibrillar layers of the dermis and partakes of their fibrillar nature. Basal plate, dentine and enamel eventually become calcified, but the details of this process have not yet been fully worked out.

During the formation of the basal plate the denticle has already broken through the epidermis. Denticle and basal plate surround a central pulp cavity occupied by some of the original cells of the scale papilla, which constitute the pulp. As already mentioned, the pulp cavity remains narrowly open below for the entrance of blood vessels, lymphatics and nerve fibres. By reason of its intimate relationship with the fibrous layer of the dermis, the scale is firmly anchored in the skin, this fixing being further assisted by the vertical dermal fibres already referred to.

Such, then, is the structure and development of the placoid scale. It is primarily a protective skeletal unit, yet we find the same basic plan in a number of other skeletal structures of differing functions. Such are the ordinary teeth located on the jaws, the rostral teeth of sawsharks and sawfishes, and the fin spines, as well as the poison spines on the tails of rays. In the next section I propose showing you how close this correspondence is.

The Jaw Teeth of Selachians.

In many Selachians there is an almost imperceptible transition between the placoid scales in the skin of the outer part of the jaw and the teeth on the jaw itself. This fact led Williamson (1849) to term placoid scales "dermal teeth". In a classical paper, Hertwig (1874) describes this relationship in great detail.

In other Selachians the relationship between placoid scales and teeth is not so obvious, because the teeth have in such forms undergone considerable modification, this in turn resulting in characteristic feeding habits.

Thus, whereas more primitive types may retain the simple conical kind of tooth, in the rays the teeth are broad, flat plates suited for the crushing of the molluscs and other organisms on which they feed, while in the predaceous sharks each tooth is in the form of a sharp triangular plate with serrated cutting edges. Compound structures may arise by the fusion of separate tooth germs, and in the shark *Heterodontus*, species of which are common in Australian seas, the teeth are of two kinds. The anterior teeth are slender, pointed and recurved, and admirably adapted for the seizing of prey, while the posterior teeth are flattened and used for crushing.

In spite of their great differences in external form, however, these teeth show the same basic plan of construction (Fig. 2). There is the usual enamel cap, dentine and basal plate, the latter anchoring the tooth in the jaw.

An examination of Figure 3 will show that the jaw teeth originate from a deeply-situated dental lamina and are in successive stages of development from behind forwards. As each tooth matures it pushes forward and assumes the upright working position. Older teeth, further to the front, which have outlived their usefulness are pushed still further forward and eventually drop off. This successional plan is particularly useful to the research worker, because sections through the jaw of one individual will show all stages in tooth development.

The broad features of tooth genesis in Selachians are similar to those of the placoid scales, with, however, one fairly important exception. That is, that in the skin covering the jaw there develops a "replacement groove" (Kerr, 1919) which was probably permanently open in Selachian ancestors, as a trough-like downpushing of the epidermis into the underlying corium; this trough, in living forms, has by apposition of its sides become converted into a solid lamina of ectoderm which dips down into the dermis just within the mouth opening.

The structural basis of tooth succession is a curious one. The stretch of skin carrying the teeth, owing to a process of differential growth, gradually moves outwards over the edge of the jaw. Just along the outer margin of the jaw the skin is constantly undergoing a slow process of absorption. This absorption is compensated for by the development of new skin (with tooth germs) from the bottom of the replacement groove already referred to. As the skin, with its teeth, moves forward, the tooth germs complete themselves, each one becoming in turn a functional tooth which by the time it has reached the absorption zone is worn out and ready to be shed.

This idea of tooth succession in elasmobranchs has been strenuously opposed by Cawston (1938), who states quite definitely (loc. cit.) that such succession does not take place. He claims that the dentition of sharks is "a complete entity", that shedding of teeth under natural conditions does not occur, and that there is no replacement of lost teeth from the posterior rows.

The mature jaw, according to Cawston, "contains a relatively constant number of teeth throughout life, and those found in any specimen are those with which it was born". The latter "remain in the jaw throughout its (the shark's) life, gradually increasing in size, even though remaining recumbent and out of use".

I do not think that Cawston's theory is weakened by its implication that the posterior rows of teeth in a shark's jaw are without function, in spite of being very well developed. Somewhat similar examples are to be found in other members of the fish group. Whitley (1940) points out that in the large Devil Ray the dentition is useless, being covered with skin. In certain toadfishes, tooth germs are present but lie beneath the actual working surface of the jaw, which consists of dense, hard bone.

At the same time I do not think that Cawston has presented completely convincing arguments in support of his theory. He bases his argument mainly on the examination of adult dentitions. The issue could quite well be decided by experiment. A suitable small species of shark, kept in an aquarium, could have some of its front teeth removed, those teeth lying immediately behind these being suitably marked so that any forward migration would be detectable. It might also be instructive to cut thin sections of the "gum" directly behind the last tooth of an antero-posterior series to see whether this "gum" contained any early stages of tooth germs. That would show whether or not Cawston is right in saying that the dentition is "a complete entity".

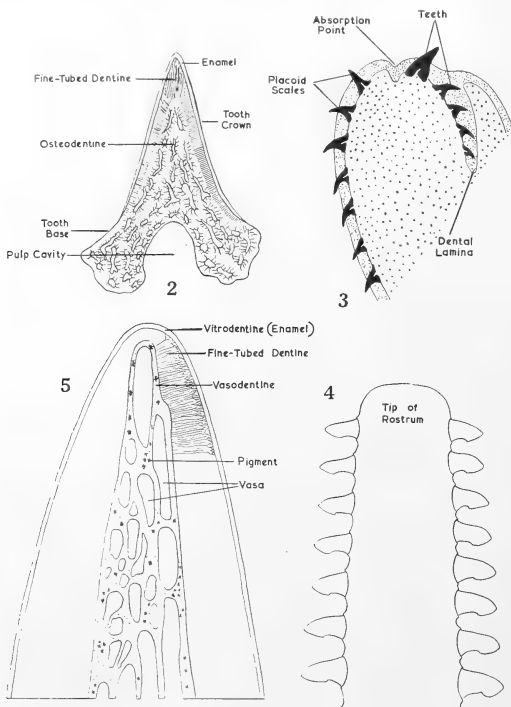


Fig. 2.—Longitudinal section through an elasmobranch tooth. (After Ridewood.)

Fig. 3.—Longitudinal section through the developing lower jaw of a shark, showing tooth succession, and the close resemblance between teeth and placoid scales. (After Graham Kerr.)

Fig. 4.—Anterior end of the rostrum of a sawfish (*Pristis*), with rostral teeth. (After Engel.)

Fig. 5.—Horizontal section through the tip of an unworn rostral tooth of *Pristis*, showing vasodentine with its canals (vasa), and the fine branched dentine tubules which arise from these. (After Engel.)

Rostral Teeth.

In two Selachian families the snout is drawn out into a long flattened cartilaginous rostrum bearing teeth along each margin (Fig. 4). The first family, the Pristiophoridae, contains the saw sharks. The second, the Pristidae, contains the sawfishes, which are more closely related to rays than to sharks. Both types are represented in the Australian fauna. The local species of saw fish, *Pristis zijsron* Bleeker (Whitley, 1940), is a truly

formidable creature which reaches a length of twenty-four feet. Of this, the toothed rostrum would occupy about seven feet.

The common species of saw shark, *Pristiophorus cirratus* (Latham) seldom exceeds four feet, and of this a little over one foot would be occupied by the toothed rostrum.

The structure and development of these rostral teeth have been most fully investigated by Engel (1910), in whose paper reference to the work of earlier investigators will be found. The following account is based on his researches. He worked on various species of the Pristidae.

Engel discovered that adult teeth are comparatively useless for the complete elucidation of structure. This fact, which seems to have escaped the realization of earlier workers, explains a good deal of the confusion which exists in early literature on the subject. The unsuitability of adult teeth for structural study is due to the quite extraordinary amount of wear that takes place as a result of the animal's feeding habits.

Apart from an undoubted defensive function, the rostrum is also used to stir up the bottom in the search for food, and the abrasive action of the sand is enough to wear away a considerable proportion of the tooth. This gives an entirely false conception of its complete structure, for not only is the original enamel or vitrodentine cap missing in such a tooth, but some of the outer dentine layers are lost as well, and the dentine canals open directly on the surface, giving the latter the appearance of a fine sieve.

The largest tooth examined by Engel (loc. cit.) came from the rostrum of *Pristis antiqorum* and was no less than 10.4 cm. in length. Of this, 4.5 cm., or nearly half, was embedded in a deep alveolus in the side of the rostrum.

Each tooth has the form of an elongated cone, tapering rather suddenly towards the end into a fairly sharp point. For a complete understanding of the tooth structure it is necessary to examine the teeth of very young individuals, and also of unborn embryos, because not only do the teeth begin to wear as soon as the animal commences an active life, but also, with increasing age, the central pulp cavity is almost completely obliterated by a mass of vascular dentine (vasodentine).

The wide tubes of the vasodentine (Fig. 5) traverse the tooth substance and penetrate right to the point, branching and anastomosing so as to form a complicated network of tubes or "vasa", the larger of which are occupied by blood capillaries. Towards the tip of the tooth the number of these canals decreases, so that in this region there is far more ground substance than canal space. Still finer tubules (Fig. 5) are given off from these apical vasa and are difficult to trace because of their small size, but they lie within a layer of more typical compact dentine and are complexly branched at their ends. The tooth is capped with enamel or vitrodentine, which is only seen in the teeth of very young individuals. As mentioned above, it is soon worn away.

In its broad outlines the development of the rostral tooth is similar to that of the placoid scale, with the exception that as in the case of jaw teeth the enamel organ, instead of being the simple up-pushing of Malpighian cells enclosing the dermal papilla shown in Figure 1, sinks deeply inwards towards the corium, being joined to the rest of the epidermis by a solid "neck" of ectodermal tissue (Fig. 6).

The investigations of Engel (loc. cit.) indicated that the corium papilla was already well formed by the time the enamel organ became evident. He almost implies (loc. cit., p. 84) that enamel organ formation is evoked by the papilla, although he does not express it precisely in those terms.

Fin Spines.

Certain sharks, such as *Acanthias* and *Heterodontus* and *Spinax*, have a powerful spine in front of each dorsal fin. The structure and development of these spines is described in a very lengthy paper by Markert (1896), from whose account most of the following has been extracted.

Each spine (Fig. 7) is in the form of a very high, rather curved, three-sided pyramid. It is roughly triangular in cross section and the apex of the triangle is directed forward, while the base faces posteriorly. We can therefore distinguish one

posterior surface and two others which are directed anteriorly and laterally. These two "anterior surfaces" are pigmented.

The spine is embedded in the fish's body for about half its length and is held in position not only by skin and fibrous tissue but by one of the cartilaginous elements of the fin skeleton which is inserted like a conical peg into the extensive lumen (pulp cavity) of the spine. The cartilage does not extend quite as far as the apex of the pulp cavity.

The projecting part of the spine (the crown) is pointed and has its two anterior surfaces covered by a hard shiny coat of enamel, which, however, is missing from the posterior surface. This curious distribution of enamel is a direct result of the unusual

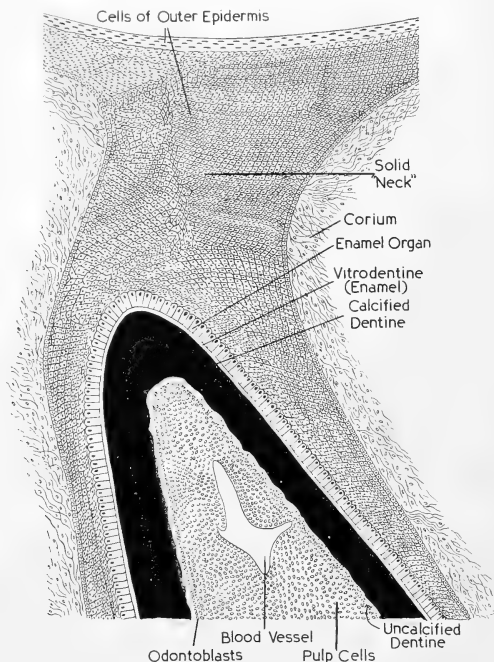


Fig. 6.—Horizontal section through a developing rostral tooth of *Pristis*. (After Engel.)

relationship between enamel organ and spine papilla during development, and will be referred to below when dealing with the early stages of spine genesis.

The posterior surface of the spine fits hard up against the basal cartilage of the fin and has a groove (Fig. 8) which, in Markert's words, is "filled with a soft skin". The latter is most likely a poison gland (see Evans, below), although Markert did not describe it as such.

The main mass ("Stamm") of the spine consists of typical dentine traversed by numerous branching canals. Some of these dentinal tubules arise from the main pulp cavity (Fig. 9) and run centrifugally. Others arise from the outer limit of the dentine and run inwards, i.e., centripetally.

Towards the base of the spine the dentine is relatively thin, but it increases in thickness towards the apex. In the latter region the pulp cavity is reduced to a relatively narrow canal which in a badly worn spine may actually open to the outside.

The two anterior surfaces of the crown of the spine are covered by an additional layer which Markert terms the "Mantel". As seen in the sectional view (Fig. 8), this fails to extend over the posterior surfaces and consists of three layers. From without inwards, these are respectively the enamel or vitrodentine, a heavily pigmented layer, and a layer of dentine containing a network of pulp canals. Branched dentine tubules run from these and penetrate into the dentine of the "Stamm".

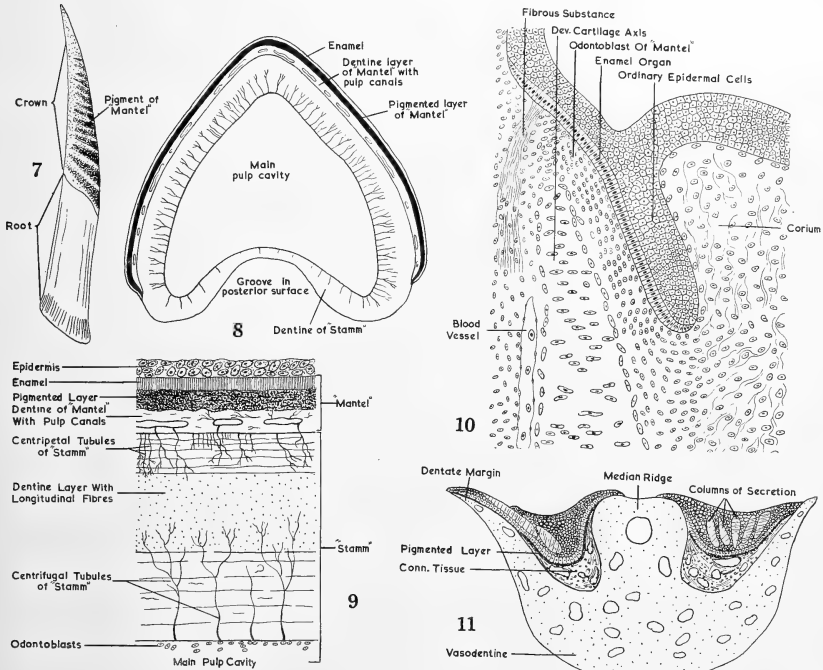


Fig. 7.—A dorsal fin spine of *Acanthias*. Actual length, 2.56". (After Markert.)

Fig. 8.—Transverse section through the fin spine of *Acanthias* about half-way down from the tip. Cartilage axis not shown. (After Markert.)

Fig. 9.—Enlarged view of portion of anterior wall of fin spine of *Acanthias* showing details of composition of "Stamm" (main part), and of "Mantel" (anterior covering of exposed part of spine). The level of this section is just below where the spine emerges from the epidermis. (After Markert.)

Fig. 10.—An early stage in the development of the fin spine of *Acanthias*. (After Markert.)

Fig. 11.—A transverse section through the poison spine from the tail of a ray, *Trygon (Dasyatis?) pastinaca*. (After Evans.)

In that part of the "Mantel" which lies beneath the skin, the pulp canals open into the surrounding corium.

The pigmented layer of the "Mantel" consists mainly of longitudinally-running fibres in a homogeneous ground substance which is heavily charged with dark pigment granules. It is this layer, showing through the glassy enamel, which gives the anterior surfaces of the spine their dark appearance.

The spine has its own peculiar features of development. The enamel organ develops as a solid tongue of epidermis (Fig. 10) which pushes down into the underlying corium.

A short distance posterior to this (to the left in the figure) there is a mesenchymatous condensation which is the beginning of the cartilaginous supporting axis of the spine. Only the Malpighian cells facing this condensation become an enamel organ. The cells on the other face of the epidermal downpushing are not concerned here. Between enamel organ and the rudiment of the cartilage axis the dermal cells become odontoblasts and will eventually begin to lay down dentine.

Owing to the unusual relationship between the enamel organ and these odontoblasts (i.e., at no time is the enamel organ in the form of a cap over the latter), enamel, when it does form, will be deposited only on the front and sides, and none on the back, of the developing spine. This, as we have seen, is the actual enamel distribution in the completed structure.

Actually, the very first hard substance to appear does so in an entirely distinct region—distinct, that is, from the position of the enamel organ and the odontoblasts already mentioned. The substance concerned is actually dentine, and the site of its formation is posterior to the cartilage axis of the spine. The first hint of its presence is a bundle of fibrous substance (langsfasrige Substanz), which is subsequently converted into dentine. This begins to extend ventrally, in the form of a curved plate which has its concavity directed towards the cartilage axis. It eventually extends down to the base of the latter, and in this region wraps itself right round the cartilage.

That sounds rather complicated, and you can best picture the shape of the dentine plate if you think of it as a curved, pointed trowel, directed upwards and having the lower end wrapped around to form the tube in which the handle (in this case the cartilage axis) fits.

At the same time the odontoblasts in the vicinity of the enamel organ have begun to form dentine. This likewise develops as a curved plate, the concavity of which, directed towards the cartilage axis, opposes the posterior curved plate.

Roughly speaking, the basal part of the posterior curved plate, which encircles the cartilage axis in the manner already described, forms the root of the spine where it is attached to the body. The rest of the posterior plate will form most of the crown of the spine, and the anterior plate becomes applied to this as the "Mantel" which is subsequently invested by the enamel. The concluding details of development are very complicated and need not concern us here.

Markert (loc. cit.) comments on the very large size of the enamel organ compared with the small amount of enamel that is actually laid down. He is unable to say whether the enamel is a product of the enamel organ or of the odontoblasts.

I feel that it will not be out of place here to discuss these fin spines, and also the caudal spines of certain rays, as carriers of definite poison glands. In this regard I would like to bring before your notice an important but apparently not well known paper on the subject by Evans (1923). This author investigated the fin spines of a dogfish (*Acanthias vulgaris*), the Port Jackson Shark (*Heterodontus philippi*), a ghost shark (*Chimaera monstrosa*) and a ray (*Trygon pastinaca*—*Dasyatis pastinaca*?) and the spines of a number of fossil forms. In the latter case he was interested in the possible presence of a "poison groove" on the posterior surface.

The structure of the poison gland in the living types examined shows differences in detail, but there is a strong overall resemblance. In *Heterodontus*, the poison apparatus consists of a number of glandular follicles supported by fibrous partitions and lying in the groove on the posterior surface of the fin spine. The follicles probably discharge their secretion towards the margins of the spine, since their orifices are laterally directed. The poison spine from the tail of a ray *Trygon* shows similar conditions (Fig. 11).

To the best of my knowledge no further research on this interesting problem has been stimulated by Evans's work. At least we now know that the poison gland lies on the spine itself and not in the tissues at the base, as was formerly thought. Failure to find such a gland in the tissues at the base has led to the belief that the poisoning which people suffer when wounded by one of these spines is due to the presence of decaying mucus. It should be particularly interesting to investigate the poison spine of our common stingray, *Urolophus testaceus*.

So far then, in reviewing skeletal structures in Selachians, we have seen that there is an astonishing overall resemblance, both in make-up and in development, between placoid scales, jaw teeth, rostral teeth and fin spines. There may be differences in detail, but these are minor compared with the similarities. It is now our task to consider scale structure in the great group Osteichthyes, the bony fishes.

Scale Structure in the Osteichthyes.

Compared with their modern relatives, archaic bony fishes (see classification table, p. xxxiv), had an extremely heavy armour. It consisted typically of thick bony overlapping scales covered with a shiny enamel-like material. Scale structure in the two major groups—the Actinopterygii and the Choanichthyes—differed widely. In the early Choanichthyes the scales were of the “cosmoid” type, so called because of the presence of a dentine-like tissue, cosmine (see below), covered by a thin layer of enamel. While the Actinopterygian scale might in some cases possess a cosmine-like layer, this was overlaid by a thick, shiny, laminated coating of calcified tissue called ganoin. Such scales belong to the “ganoid” type.

The scales of modern Choanichthyes (with the exception of *Latimeria*, whose scales are described below) have degenerated into thin leathery plates, the structure of which is very similar to that of the scales of modern teleosts. Ganoid scales are retained in a modified form by some living Actinopterygians (e.g., *Polypterus* and *Lepidosteus*), but in teleosts, which constitute by far the major proportion of surviving bony fishes, the dermal armour typically consists of a series of thin overlapping bony plates which have lost all trace of ganoin. In a few teleosts the scales are missing altogether (e.g., some catfishes), while in others, e.g., some Siluroids and Plectognaths, they develop into bony plates which in complexity rival almost anything possessed by their extinct ancestors.

The study of ganoid scales has been very much simplified by Goodrich (1907, 1909), who points out that in spite of a wide range of variation these scales can be divided into two main types, the “palaeoniscid” and the “lepidosteid”. We will take the palaeoniscid type first.

Palaeoniscid Scales.

Our example is the scale of *Eurynotus*, a palaeoniscid genus from the Lower Carboniferous. Each scale (Fig. 12) is a roughly rhomboidal plate, produced into a bony articulating peg at one side. The scales overlap one another partially, and in each one there is an anterior region, of bone only, which is concealed from view through being overlapped by the scale in front. The posterior exposed part of the scale, which is of more complex structure, has a toothed edge and is covered by a layer of hard shiny ganoin with a pitted surface.

The basal part of the scale is seen in section (Fig. 13) to be made up of a number of bony layers provided with numerous bone cells. This type of bone is called “isopedine”. The isopedine layers turn up at their edges—i.e., at the margin of the scale—and are continuous with a corresponding number of ganoin layers which constitute the uppermost part of the scale.

The isopedine laminae are pierced by a number of vertical vascular channels which communicate with a network of horizontally-disposed vascular canals, between ganoin and isopedine. Numbers of finely branched tubules arise vertically from the horizontal network, the layer which they penetrate bearing a superficial resemblance to true cosmine (see below). Certain of the vertical vascular channels continue upwards beyond the horizontal network piercing all the ganoin layers, and open on to the upper surface of the scale. This produces the pitted appearance already referred to.

Although, naturally, embryological material is lacking, the structure of this type of scale gives some clues as to the nature of its growth.

The oldest part of the scale is in the centre, and the scale grows by simultaneous additions to the three layers—the isopedine, the cosmine-like one, and the ganoin. With the addition of successive “skins” of these, the scale would grow thicker with age.

Lepidosteid Scales.

Examples of these are found in the living genus *Lepidosteus* (the gar pike) from fresh-water streams of North and Central America.

Although simpler in structure than the "palaeoniscid" kind just described, this scale (Fig. 14) is undoubtedly referable to the ganoid type. The greater part of the bulk consists of laminae of isopidine which has few vascular channels. The isopidine laminae are penetrated at right angles by numbers of fine tubes which in the first part of their course are unbranched. They tend to converge towards the centre of the scale, and at their terminations they break up into a series of delicate tubules which

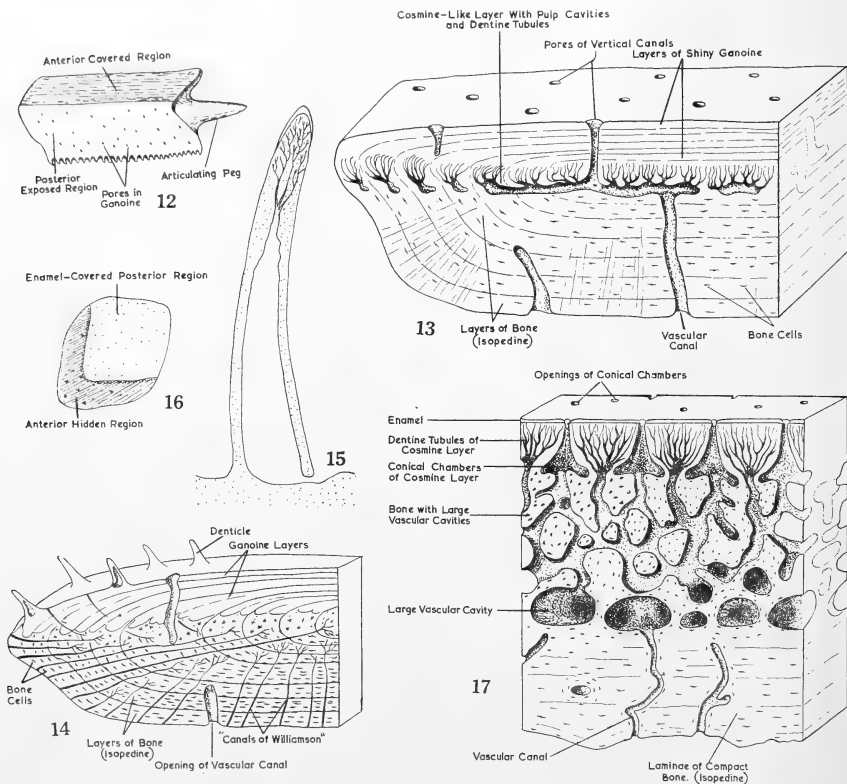


Fig. 12.—A bony scale from the Carboniferous Palaeoniscid genus *Eurymotus*. (After Goodrich.)

Fig. 13.—A section through portion of the posterior region of the "palaeoniscid" type of ganoid scale, belonging to *Eurymotus*. (After Goodrich.)

Fig. 14.—A section through the posterior region of the "lepidosteid" type of ganoid scale, belonging to the modern genus *Lepidosteus* (the gar pike). (After Goodrich.)

Fig. 15.—A vertical section through one of the denticles of the *Lepidosteus* scale, showing aperture at base, pulp cavity, dentine tubules and enamel cap. (After Nickerson.)

Fig. 16.—A bony "cosmoid" scale from the Devonian Crossopterygian *Megalichthys*. (After Goodrich.)

Fig. 17.—A sectional view of portion of the posterior region of the "cosmoid" scale of *Megalichthys*. (After Goodrich.)

are arranged beneath the ganoine layers in such a regular manner that Williamson (1849) was persuaded to regard this portion of the scale as a slightly modified cosmine layer.

Goodrich (1907) disagrees with this view, pointing out that the lepidosteid scale has no vascular network giving rise to canaliculi, nor does it have pulp cavities. In other words, there is no question of a true cosmine layer (see below) here.

Each of the tubes penetrating the isopedine layers at right angles from below, according to Goodrich (1913), belongs to one cell which lies external to the scale (on the scale surface) and which sends a long cytoplasmic process down the tube. According to Goodrich (loc. cit.), "probably these remarkable cells are merely modified bone cells, which instead of being buried in the ostein matrix remain outside it while retaining their connection by means of the long processes with the place they originally held".

Goodrich goes further to show that this remarkable structure is found in the cranial plates and other dermal bones of lepidosteids and amiids, both living and extinct, and even extends to the endoskeleton. The skull bones, the ribs and even the centra of the vertebrae showed the same tubes, branching at their inner ends.* One possible use to which this discovery could be put would be the identification of even minute skeletal fragments, especially with regard to fossil material. A suitable examination would immediately show whether such a fragment belonged to the lepidosteids or amiids, or to some other group.

The *Lepidosteus* scale has its ganoine component very well developed (Fig. 14) and the latter is produced superficially in very young fish into a number of denticles. One curious point in the history of these denticles is that in *Lepidosteus* their number decreases as the fish grow older. This may be due merely to ordinary wear and tear, but the fact remains that eventually they have completely disappeared from the central part of the scale, and only a few remain near the posterior edge. Nickerson (1893) believes they are lost by resorption.

Each of these denticles (Fig. 15) has a structure recalling that of a placoid scale. There is a small enamel cap and a main mass of dentine-like substance, with fine branching tubes and a pulp cavity. At the base of the denticle there is a laterally-directed aperture which in life is concealed by the skin.

The Cosmoid Scale.

As an example of this type we will select the scale of *Megalichthys*, a Devonian Crossopterygian. This scale has been described in great detail by Williamson (1849); a shorter but entirely adequate account will be found in Goodrich (1907) or Goodrich (1909).

In surface view (Fig. 16) it is a rhomboidal plate with the anterior covered part consisting of bone alone, while the posterior exposed portion, which also has a rhomboidal outline, is more complex. Actually this region of the scale is in three layers (Fig. 17). At the base there is laminated bony isopedine, perforated by vascular canals, and containing numerous bone cells. Overlying the isopedine there is a layer of spongy bone with large vascular spaces which, further towards the surface, are organized into a series of horizontally-running vascular channels. From this region are given off dorsally two types of chamber. One type expands out into a conical space opening at its apex on to the surface of the scale by means of a small pore which perforates the thin superficial coat of enamel. Numbers of these pores give the scale surface a pitted appearance.

The second type, which appears to be of the nature of a pulp cavity, gives off bunches of fine branching tubes.

The conical chambers, alternating with the pulp cavities in a beautifully regular manner, together with the intervening tissue, constitute the so-called "cosmine" layer.

* A full discussion on the nature of these tubes will be found in Ørvig (1951), pp. 362-366. Ørvig calls them "canals of Williamson" and describes them as "vascular canals undergoing degeneration".

of the scale. *Megalichthys* scales have this cosmine layer developed to a very high degree and it occurs, variously modified, in many other fossil Crossopterygians. The cosmine layer is not present on the anterior covered part of the scale.

The structure of the scale is such as to permit some speculation as to its method of growth. This takes place in two ways. New layers of isopedine can be added below, thus increasing the scale thickness, while additional vascular cavities, cosmine, and the thin glassy surface layer of enamel are added at the edge.

"Cosmine", as originally defined by Williamson (1849) did not have the restricted significance subsequently proposed for it by Goodrich. Williamson applied the term to a dentine-like substance that he found in ganoid scales, and also to a very different kind of bony material in the Triassic form, *Lepidotus*. Goodrich (1907) prefers to restrict the significance of "cosmine" to the layer just described in *Megalichthys*, with its regularly alternating series of pulp cavities and conical chambers.

True cosmine scales are characteristic of fossil Crossopterygians, but in living representatives of the Choanichthyes the scales, by comparison, are much simpler.

Prior to 1938 it would have been correct to say that the only surviving representatives of what had formerly been a very large group of fishes (the Choanichthyes) are the three freshwater lungfish genera *Epiceratodus* from Queensland, Australia, *Protopterus* from South Africa, and *Lepidosiren* from South America. In the first two the scales are relatively thin overlapping bony plates rather like those of teleosts (see below), while in the eel-like *Lepidosiren* the skin is soft and has a few scales of even more reduced character. We are thus deprived of the opportunity of studying the embryological development of the highly interesting cosmoid scale just described.

This opportunity is lost to us forever, but there has been one compensation in the form of the capture in December, 1938, of a living coelacanth fish, *Latimeria*, off the coast of South Africa. The coelacanths were stout-bodied fishes, representing a specialized side-branch of the Crossopterygians which lived in Mesozoic seas, and the last fossil remains of which have been found in Cretaceous sediments.

As this group had long been considered extinct, the initial sensation created by the discovery in 1938 of a living representative of the group (*Latimeria*) was naturally very great (see Whitley, 1940). This sensation was, however, almost equalled by the dismay of the scientific world at learning that through an unfortunate series of events the fish—surely the most valuable zoological specimen in the world—had not been properly preserved; indeed, little remained of it but the skeleton (damaged) and the stuffed skin. Practically all of the viscera were lost or were in such a bad state of preservation that nothing could be done with them.

An heroic effort was made by Smith (1941) to describe the remains, and it is a tribute to his patience and industry that he wrung practically the last shred of information from the parts of the animal that had been made available to him.

A special and highly interesting paper on the structure of the scales was prepared by Roux (1942). I wish to devote some time to this, because the paper is not readily available.

The Scales of Latimeria.

The scales of *Latimeria* are superficially similar to the ctenoid scales of teleosts (see below), because the posterior exposed region is ornamented with a series of backwardly-directed denticles. The scales are of large size (1.1" × 1.32") and overlap one another in typical fashion. The posterior exposed part of the scale only amounts to one-seventh to one-quarter of the total area and bears, as already noticed, a number of elongated denticles oriented in the direction of the long axis. The denticles are blunt and rounded, but posteriorly each one bears a short, backwardly-directed spine. Spines are not present in every case. The denticles vary in size, and in some scales show traces of a radial arrangement with respect to the centre of the scale (Fig. 18).

The exposed part of the scale is typically heavily pigmented, this being due to the presence on its surface of a layer of stellate pigment cells lying between the projecting denticles. The latter also have pigment cells in their pulp cavities which show through the transparent dentine.

The anterior region of the scale is normally hidden from view through being overlapped by the scale in front, and presents the appearance of a more or less typical teleost scale, with its concentric circuli or striations, representing lines of growth. The whole of this hidden part of the scale is finely corrugated. The corrugations are quite distinct from the growth annuli; they radiate out from the apex of the scale

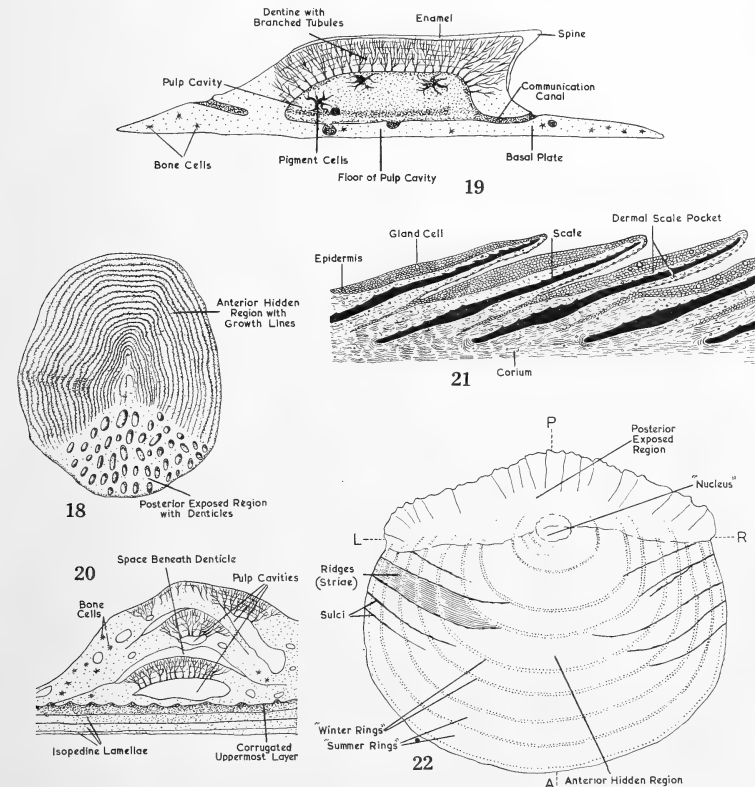


Fig. 18.—Surface view of scale of *Latimeria*, a living coelacanth fish from South Africa. (After Roux.)

Fig. 19.—Longitudinal section through one of the denticles of the *Latimeria* scale. (After Roux.)

Fig. 20.—A section through three superposed denticles of the *Latimeria* scale. (After Roux.)

Fig. 21.—Diagrammatic representation of the relationship between the scales, the scale pockets, the epidermis, and the dermis in a teleost fish.

Fig. 22.—Diagram of a herring scale to show main features (based on photograph by Lea). A-P, main axis of scale; L-R, transverse axis of scale.

at right angles to the latter. They occur in the thin homogeneous osseous layer which lies on top of the laminated isopodine of the scale base, and even beneath the denticles on the posterior surface (Fig. 20).

The basal part of the scale consists of more or less typical isopodine, arranged as a series of laminae which are fibrillar. The fibres of any given lamina run parallel to one another, but the fibres of adjacent laminae cross at an angle of approximately 72 degrees. The fibres of every fifth lamina run in the same direction.

The isopedine layers are traversed by a number of large (vascular?) canals, some of which penetrate into the pulp cavities of the denticles, while others run right through to the dorsal surface of the scale, their openings being visible as tiny pits.

Within the laminae there are numerous lacunae containing bone cells. Lacunae also occur in the corrugated homogeneous osseous layer on the surface of the isopedine.

The structure of the denticles (Fig. 19) presents features of considerable interest. Roux (1942) identifies them as typical placoid teeth, each one consisting of a projecting dentine cone with a tiny cap of enamel, and continuous below with a flattened basal plate.

The whole structure, cone and basal plate, can, after partial decalcification, be detached from the rest of the scale without much difficulty. The dentine of the cone is laminated, has a central pulp cavity, and is traversed by a series of fine branching canals, which may even penetrate into the enamel layer. Roux, apart from mentioning the pigment cells in the pulp cavities, does not describe any other cell types in this part of the scale. This may be due to the fact that the scales, after being fixed in formalin some time after death, reached him in the dry state.

Although completely continuous with the dentine cone, the basal plate is not of uniform structure throughout. The region immediately adjacent to the cone, apart from being fibrillar, appears to be quite homogeneous, with neither dentine canals nor lacunae with bone cells. But in the peripheral part of the basal plate there are lacunae with radiating canaliculi—i.e., bone cells are present. The basal plate shuts off the pulp cavity completely from the rest of the scale, but the cavity sends out horizontal canals which open on the dorsal surface of the basal plate.

Vertical sections made through the posterior part of the scale show several denticles superimposed on one another within the thickness of the scale (Fig. 20). As many as four denticles may be superimposed in this way, and under such circumstances all dentine cones except the most superficial (i.e., the youngest) show signs of degeneration; the basal plates, however, tend to retain their original form and their canals of communication.

Thus arises, in the words of Roux (1942, p. 11), "a layer of sparsely-lacunated osseous tissue with many canals branching and anastomosing through it!" And further ". . . in certain regions no traces of denticles or individual basal plates could be distinguished any longer, but only an osseous layer of considerable thickness containing numerous large canals which may occasionally send short branches to the surface of the scale".

This superposition of denticles—i.e., the enclosure of an originally superficial structure in the substance of the scale—is related to the somewhat similar process of ganoine enclosure observed in the case of *Polypterus* (p. xl), and possibly is some indication of the method of growth.

The structure of the *Latimeria* scale can be summarized as follows:

The anterior, hidden region is much larger in area than the posterior exposed part and consists of two layers, an upper corrugated osseous one with concentric ridges and of homogeneous composition and a lower laminated isopedine layer. These two components also occur in the posterior region, but are overlain by a series of dentinal tubercles with basal plates, pulp cavities and small enamel caps.

The *Latimeria* scale, then, obviously does not correspond very closely with the typical cosmoid form already described and which is characteristic of the Crossopterygians as a group. It lacks the regular series of conical chambers and pulp cavities which are the hallmark of the cosmoid scale. Quoting Smith (1940): "The scales probably represent an advanced stage of modification of the primitive cosmoid type, in which the cancellate bone layer has disappeared, with consequent reduction of thickness of the scale. That the ancestral form bore true cosmoid scales is very probable."

The Scales of Teleosts.

The teleosts, from the evolutionary viewpoint, have been easily the most successful group of the bony fishes, and, represented by thousands of species, are the predominant fish types today, both in the ocean and in fresh water.

Mention has already been made that their scales, in the main, are of great structural uniformity; some aberrant groups, such as certain Siluroids and Plectognaths, have once more developed a heavier type of dermal armour that approaches in complexity the structures I have been describing in fossil groups. I do not propose to deal with these aberrant forms in this Address. Appropriate references will be found in Ørving (1951) and Goetsch (1921).

In a typical teleost the scales are thin, flexible, bony plates which are arranged in rows that run diagonally with respect to the long axis of the fish. The number of these scale rows may in some species correspond closely with the general metamerism of the body (i.e., with the myotomes and vertebrae), but the amount of disagreement in other species is very high. Any cases of close correspondence between scale rows and metamerism must be regarded as being of doubtful significance.

The adult teleost scale is completely enclosed in dermal cells constituting the so-called scale pocket (Fig. 21). The scales are disposed obliquely in the skin with the anterior ends held firmly in the deeper, fibrous layer of the dermis. Typically, the epidermis dips down as a solid strand between adjacent scale pockets, and the free posterior margin of the scale forms a slight projection on the surface.

Neighbouring pockets are bound together by strands of connective tissue which, with the already-mentioned fibrous connection at the front end of the scale, helps to anchor the latter in the skin.

Each scale is partly overlapped by three others, so that only a small portion of its total surface is actually exposed.

In spite of variations in detail, it is possible to give a general representation of gross scale anatomy (Fig. 22). Two axes are usually distinguishable, an antero-posterior one (the "main axis") drawn through the mid-points of anterior and posterior edges, and also a transverse axis (the "base line"—Lea, 1919) crossing the first one at right angles and coinciding in its course with the boundary between exposed and unexposed portions. This description applies perfectly to the herring scale, where the boundary is quite distinct. In other scales, where this boundary is not quite so clear, the base line would be described as a line drawn at right angles to the main axis and passing through the middle of the youngest part of the scale (the "centrum" or "nucleus"). The latter is usually easy to see because it is the point where the surface pattern of the scale (the striae) has obviously commenced to form. It does not necessarily correspond with the geometrical centre of the scale.

The exposed posterior part of the scale is frequently different in appearance from the anterior hidden part. The latter is typically ornamented with a series of ridges and grooves (sulci) which are developed in the upper of the two layers of which the scale is composed. The pattern formed by the ridges varies as between different species and may differ in different parts of the body in the same individual. The posterior, exposed part of the scale in many fish (e.g., clupeoids) lacks the ridges, or striae as they are sometimes termed, but in other species (e.g., the tiger flathead, *Neoplattycephalus macrodon*—see Dakin, 1931, Pl. 2, fig. 1) ridges occur in both regions equally.

Two main types of "normal" teleost scales occur, the classification being based on the ornamentation of the posterior region. If the latter has spines over its surface or along the posterior edge only, the scale is of the "ctenoid" type. This name is derived from the comb-like appearance produced by the row of spines along the posterior edge. The "cycloid" type of scale, on the other hand, lacks any ornamentation of spines on the posterior part and its hinder border is usually smoothly rounded.

Further information on the ridges (striae) and the grooves (sulci) will be given below. First it will be necessary to consider the histological structure of the scale.

The Histological Structure of the Scale.

The teleost scale is nearly always two-layered, although according to Williamson (1851) there may occasionally be a third layer in between. He describes this third layer in a large teleost scale that came into his possession unaccompanied by any information as to its source. In some clupeids there may also be traces of this third layer, but the two-layered condition is more typical.

The basal layer of the scale is fibrous, usually uncalcified, and usually devoid of cells. It is composed of a number of lamellae which contain collagen and another substance, ichthyolepidin. Pevsner (1926) maintains that there is very little collagen present because the basal plate is very little affected by treatment with alkalis. She thinks that instead of collagen the plate contains elastin.

In many scales the fibres of each lamella are parallel to one another but lie at an angle to the fibres of the adjacent lamellae. In some clupeid scales (e.g., the herring) this parallel arrangement is not present. Instead, the fibres of adjacent lamellae run in complicated whorls, as well as respectively radially and tangentially (the "en tourbillon" formation—Lea, 1919) (see Fig. 23).

Whatever the details of the arrangement, the resulting structure must be very strong. This system of fibres crossing one another at an angle recalls the principle behind the manufacture of laminated plywood—fibres of successive layers crossing at an angle to endow the wood with the greatest possible amount of strength for a given cross section.

The entire basal plate, then, consists of a series of superposed lamellae. The very first one to be laid down would be very small; the next one, formed beneath this, a little larger and so on, and the completed structure could be looked upon as a very much flattened cone, made up of a number of layers, one on top of the other (Fig. 24). The apex of the cone would be formed by the youngest and smallest layer. The one immediately beneath would be a little larger in extent and slightly older, and so on. The figure also gives some indication of the difference in direction of the fibres in adjacent lamellae. The thickness of each layer is insignificant compared with its superficial extent, and viewed from above the edge of each successive plate would be visible as an "outcrop". The most basal layer of all would be the largest and would also be the latest one to have formed.

Thus we see that the basal plate can grow in two ways. It can get thicker by the addition of new lamellae below and can also grow centrifugally, each new layer being greater in area than the preceding one. This type of growth is more complex than that of the upper layer, which grows by lateral extension.

This upper part, known either as the "hyalodontine" or "osseous" layer, is of homogeneous structure, fairly uniform thickness and is calcified. It contains both calcium carbonate and tricalcium phosphate. It rests directly on the basal plate and is usually devoid of cells. The complex sculptured pattern (ridges and grooves) of the teleost scale resides in this layer, and a section through the scale shows a characteristic "sawtooth" appearance due to the presence of these ridges (Fig. 24).

The surface pattern varies, and the matter is of sufficient importance to warrant closer attention, because it finds important application in fisheries biology in the matter of age estimation in fishes. Six different modifications of the surface pattern will be described.

The Clupeoid Type (Fig. 23).

In this scale (Lea, 1919; Lee, 1920) the posterior part of the scale (the posterior field) is relatively plain with an irregular edge, while the anterior field is traversed by a number of curved ridges (striae), the general direction of which is transverse to the main axis. A number of furrows or sulci run in from the edge roughly parallel with the striae. These are areas of non-calcification and will be referred to in greater detail later (p. xxxi). The centrum or nucleus of the scale (the oldest part) lies at the intersection of the two axes and embraces part of both anterior and posterior fields.

Developed concentrically with respect to the nucleus is a series of narrow almost transparent zones or rings. These have been shown to correspond with periods of winter growth and owe their transparency to the fact that here the striae of the osseous layer are, through some peculiar optical quality, almost invisible. It will be noticed that the striae which are visible elsewhere in the scale are not concentric with these "winter rings" but cross them at varying angles. It is possible to demonstrate another quite distinct set of "winter rings" in the basal plate below by examining the scale

in polarized light. These rings correspond fairly well in their course with those of the osseous layer. For an explanation of their origin see Lea (1919) and Paget (1920).

The Salmonid Type (see Lee, 1920, Fig. 2).

This scale too has clearly marked striae on the anterior field only. There are successive bands in which the striae are respectively closely crowded and widely spaced. The zone of closely packed striae represents winter growth, while a summer growth zone is indicated by the wider spacing of the striae.

The Smelt Scale (see Lee, 1920, Fig. 3).

Both fields have striae with a generally concentric disposition, but the anterior field (much the smaller of the two) has the ridges set very close and is therefore difficult to read. The posterior field at first sight offers little more promise because the striae are few in number, not conspicuously zoned, and are seemingly haphazard in their course. Yet the smelt scale has been successfully interpreted (Masterman, 1913, quoted by Lee, 1920). The basis of this interpretation is that during summer growth the striae run right around the margin of the scale as unbroken lines. With the onset of winter and a slowing down of growth the new striae fail to encircle the scale completely and definite breaks are visible in them posteriorly. In other words, instead of the winter ridges being closed ovals they are crescents, originating posteriorly, the gap between the two limbs of the crescent being in the anterior field. Series of these crescents are laid down during the winter and the intervening breaks come out as transparent zones. With the approach of a new summer, complete striae are laid down once more, and thus we have a winter ring of interrupted striae and a clear area bordered on each side by a zone of complete summer ridges.

The Eel Scale (see Lee, 1920, Fig. 4).

This scale has its entire upper surface ornamented with concentric lines of small round or oval calcareous plates ("Sclerites"). Most of the rows are complete, extending right around the scale, but others are incomplete, recalling the incomplete striae of the smelt scale.

The concentric zones of plates are separated by clear areas in which the fibrous basal plate of the scale is exposed on the upper surface. The clear areas are the winter rings, and the rows of plates are deposited in summer. The plates on the margin of each summer zone are smaller and narrower than the rest, possibly indicating a slower growth rate correlated with changes in temperature or available food, or feeding habits, or all three. An interesting point in connection with eels (fresh water) is that the scales are not acquired until the fish is two years old. Consequently two years have to be added to any estimate of the age based on scale readings.

The Gadoid Scale (see Lee, 1920, Fig. 4).

This scale, exemplified by the haddock or other member of the cod family, is like that of the eel in that it carries concentric rows of sclerites, but these differ both in their form and the closeness with which they are spaced.

Each sclerite is best described as a slightly curved, rectangular envelope with the flap closed, the contour of which corresponds with the general trend of the row to which it belongs. The rows run concentrically, and not only do the sclerites of each row touch one another, but the spacing between the rows is very close. The scale is divided up into a number of zones or bands of winter and summer growth respectively, each zone containing many rows of sclerites. Each individual sclerite of a winter zone is narrow, while the sclerite of a summer zone is wide (Fig. 25).

So, the interpretation of the gadoid scale rests on the fact that narrow sclerites are laid down in the winter and wide ones in the summer.

The Scales of Australian Teleosts.

The scales of most Australian fish so far investigated are not very good for age estimations, in that it is difficult to see anything in the surface sculpture to act as a guide. This, according to some workers, may be due to the smaller differences

between summer and winter temperatures in these seas as compared with European and North American latitudes, where there is a corresponding difference between summer and winter growth. The pioneer in scale interpretation in Australia is faced with the immediate problem of finding some feature in the surface sculpture to work on, and even then he has to prove that this is indeed a true reflection of seasonal growth processes and not of some other physiological event in the life of the fish, e.g., spawning, which may also be recorded on the scale. Extensive and complicated statistical work is involved here. The first successful application to an Australian fish of the scale reading technique was achieved by Kesteven (1942) working on the sea mullet (*Mugil aobula* Gunther). This was followed, seven years later, by an important paper by Blackburn (1949), who successfully interpreted the scale of the Australian pilchard (*Sardinops neopilchardus* Steindach).

Whereas the pilchard scale was of the "clupeoid" type, the mullet scale was rather different from any of the types described above. The whole of the surface is covered with close-set concentric ridges, although the course of these on the posterior field is rather irregular and interrupted by the presence of the cteni or spines that place it in the ctenoid category.

There is no regular alternation of zones of narrow striae and zones of wider ones. Instead, "breaks" occur, showing as interruptions in the regular arrangement of the ridges, and these have been successfully interpreted by Kesteven (loc. cit.) as representing definite events in the life of the fish which can be correlated with its seasonal growth and therefore with age estimation. Kesteven's supporting arguments are too lengthy to be considered here and I refer you to the original paper.

Age Estimation in General.

Awareness that scale structure may be useful in age estimation dates back to the time of Leeuwenhoek in the seventeenth century, but scale reading techniques in their modern form commence with the work of Hoffbauer (1899). Since that time a vast literature on this subject has grown up and full appreciation of it requires a considerable knowledge of mathematics. The literature up till 1928 has been reviewed by Graham (1928); further valuable references will be found in Kesteven (1942) and Blackburn (1949).

The technique of scale interpretation is by no means easy, even in the more clear-cut cases like the salmon or the herring. The actual method employed must depend on the precise way in which winter and summer rings are registered in the osseous layer of the scale. This involves the problem of proving that the pattern shown does, in fact, truly mirror the seasonal phenomena that the investigators claim it does. Optical examination must be combined with elaborate statistical analysis, and even then the method must be tested against other ways of age estimation, such as the length measurement technique of Petersen or the examination of other parts of the skeleton, such as otoliths, which likewise show a periodic structure. It is therefore not surprising that the literature is full of controversy and contradictions.

Even in a fish such as the herring, where the method is now firmly established, scale structure varies in different parts of the body and it is necessary to decide which are the most suitable scales to use. It is also difficult to get a fair sample of all sizes of fish because the different age groups may be widely dispersed and smaller sizes do not frequent the same grounds as the larger fish.

An obvious method for the collection of scale material would be to keep marine fishes in special culture ponds, the living conditions of which are as close as possible to those of the open sea. Scale samples could be collected from these fish at suitable intervals and examined for additional age rings. These could be correlated not only with the age of the fish but also with the amount of growth it had undergone in the intervening period.

This has actually been done on a number of occasions with, however, conflicting results (see Graham, 1928). The main reason for this conflict appears to be that it is almost impossible to duplicate conditions found in the open sea, and the fish behave

atypically. The most consistent results in this direction have been obtained with a freshwater fish, the sturgeon, the actual material being the classical sturgeon culture raised by Professor Ostroumov (Holtzmayer, 1924, quoted by Graham, 1928). Records were kept over a period of ten years (1910-1920). The heavy bony scales of the sturgeon being unsuitable, sections of the first pectoral ray (which, like scales, has a periodic structure) were used. A cross-section of the pectoral ray showed ten clear zones, a wide dark summer zone (by transmitted light), and a narrow light one. The fish was ten years old.

The actual reading of scales is further complicated by the presence of "false rings" (see Blackburn, 1951) which may form in addition to the age rings, probably in response to some marked environmental change such as temperature, feeding habits or breeding. These "false rings" complicate the picture and are an expression of the fact that the scale is a very delicate indicator of the physiological past of the fish. The investigator has to decide which of the rings truly mirror seasonal growth—i.e., age—and which of them reflect other events from the past.

The difficulty in explaining the origin of scale rings on the basis of purely environmental influences alone, such as temperature or food supply, is well exemplified by the work of Mohr (1921), quoted by Graham (1928). Mohr examined scales from three species of the tropical fish *Rasbora*, one of which came from a region where the temperature is the same all the year round. These scales, nevertheless, showed clearly defined rings similar to those of Cyprinids of temperate waters where there is a marked difference between winter and summer temperatures.

From this Mohr suggests that the year zones on the scales must be produced by some *functional rhythm within the fish itself* rather than by environmental factors.

Similar conclusions were reached (for different reasons) by both Dakin (1939) and Fairbridge (1951) in connection with age estimation in the Australian Tiger Flathead *Neoplatycephalus macrodon* (Ogilby) by means of otoliths.

One of the really great pioneers in the field of scale study was Einar Lea who, apart from his excellent work on the structure of the herring scale (Lea, 1919) also extended the work of Walter (quoted by Graham, 1928) on the relationship between the rate of growth of the scale and the growth rate of the fish as a whole. He argued that as the scale added a winter and a summer ring each year, the distance between any two contiguous rings on the scale might be proportional to the amount of growth made by the fish during the same period.

Extensive measurements made on hundreds of scales from the same fish showed that there was a definite connection between the growth of the scale and the growth of the fish as a whole. Expressed as a principle:

$$\frac{\text{Length of scale included in ring of year } \times}{\text{Length of fish at end of year } \times} = \frac{\text{Total length of scale}}{\text{Length of fish at time of capture.}}$$

Subsequent studies showed that this simple mathematical relationship was inaccurate, and that modifications of the original formula were necessary. For further information see Graham (1928).

Having dealt at such length with the technique of scale reading, I would now like to give you an example of its practical application to a fisheries problem.

In the early part of this century it was well known that the important cod and herring fisheries varied considerably from year to year with respect to total yield. Some years were very productive with heavy catches, while other years were very lean. It was thought that these fluctuations were due to mass migrations of the fish, which for unknown reasons might avoid the usual grounds one year yet return to them some other year. An application of age estimation techniques revealed the true reason and showed that the original theory was wide of the mark.

The success of a fishery was found to depend mainly on one particular year group, the individuals of which made up the bulk of the catches. The year 1904 was apparently a very good one for the survival of the herring brood, and these 1904 fish first came under notice four years later, in 1908, when they had reached commercial size and

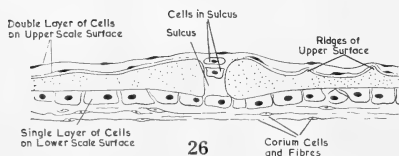
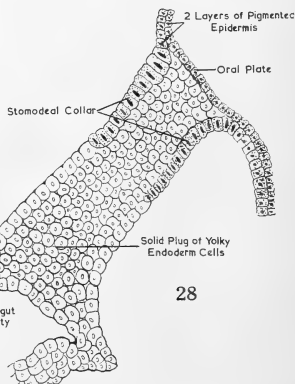
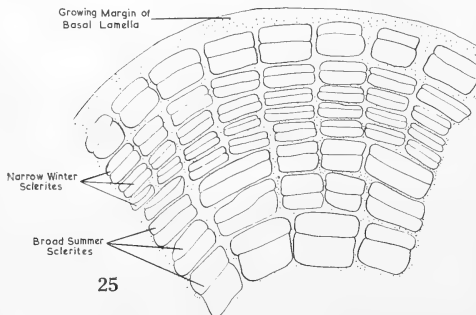
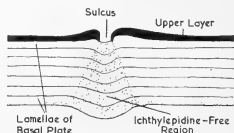
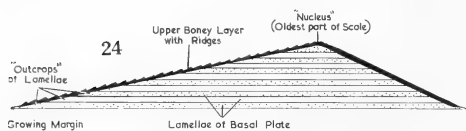
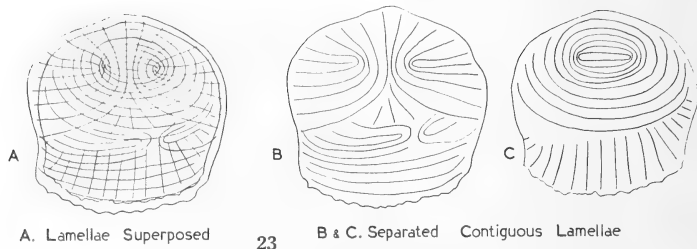


Fig. 23.—Showing how the fibres of adjacent lamellae of the basal plate of the herring scale are arranged to give, when superposed, great strength for a given cross section. (After Lea.)

Fig. 24.—Showing how the basal plate of a teleost scale may be regarded as a flattened cone made up of a number of superposed lamellae of gradually increasing area from above downwards. The fibres in adjacent lamellae run at an angle to one another. Dots are fibres cut in cross-section. (After Lea.)

Fig. 25.—Portion of the upper surface of the gadoid type of scale, showing zones of narrow "Winter sclerites", and of broad "Summer sclerites". (After Graham.)

Fig. 26.—Early stage in the development of the goldfish scale showing the two cell layers of the upper surface of the forming scale, and the single cell layer beneath the latter. (After Neave.)

Fig. 27.—Section across a scale sulcus. (After Neave.)

Fig. 28.—A diagrammatic longitudinal vertical section showing the relationship between the foregut and the epidermis of the embryo of *Amblystoma mexicanum*. (Based on photograph by de Beer.)

were being taken in the fishermen's nets. The greater part of the 1908 catches consisted of these herring, which had been born four years previously.

They also dominated the fishing in 1909, and continued to do so right through the war years. Even in 1918, when they were going on for fifteen years of age, the survivors of this 1904 brood constituted an important part of the fishery.

There was little doubt as to their identification from scales, for apart from the fact that these added a new summer ring and a new winter ring each year, there was a distinctive malformation of the third-year ring which persisted throughout the period mentioned, and which showed that those possessing it belonged to the 1904 brood.

This feature of a fishery being dominated by one, or sometimes two, year classes is something we have come to expect as a normal experience (other examples beside the herring are known), and an important conclusion that may be drawn is that the richness or poverty of a fishing can well depend on some event that has happened years before, such as a good or bad brood year. A heavy mortality in eggs or larvae will not become obvious until some years later, when the fish have reached commercial size and begin to be caught.

On the same basis, age estimations based on scales have enabled predictions to be made as to the possible size of a fishery in future years. Quoting Dakin (1934), "This forecast may eventually include the date a profitable fishery might be expected to commence, the estimated quality of the catches, and the estimated yield. It is the *uncertainty* and *variation* in yield in pelagic fishing which is usually most serious to both fishermen and merchants. Removal of a little of this uncertainty would be of the highest value."

Scale Development.

There are still some matters connected with teleost scales which must claim our attention. An account of the embryonic development must have an important bearing on the interpretation of adult structure, and therefore on the practical application of this to fisheries biology.

The following account is based largely on Neave (1940) and on Paget (1920). The former author worked on the scales of the goldfish (*Carassius auratus*), while Paget studied scale development in the rainbow trout (*Salmo irideus*).

The skin has a typical structure. In the goldfish the epidermis is 6-8 cells deep and provided with scattered gland cells. The underlying dermis is composed of an upper spongy layer with many cells but few fibres, and a lower one in which the fibrous condition predominates. It is laminated, the fibres in any given lamina running parallel to one another, but disposed at an angle to those of adjacent layers.

According to Neave (*loc. cit.*), the osteogenic cells of the actual scale papilla are not derived from the surrounding dermis—that is, not from the dermis in the immediate vicinity of the papilla. The first scales form along the sides of the body and their osteogenic cells come from tissues in the vicinity of the lateral line, migrating to their final position when scale formation is ready to commence.

At each site of scale formation the migrated cells form a sheath which surrounds a fluid or gelatinous intercellular substance. Cells pass into this and form the scale papilla, in the interior of which the laying down of the scale commences. The cells remaining at the periphery, the "follicle cells", continue to contribute osteoblasts to the growing scale margin.

The completed papilla, inside which the scale is developing, comes eventually to consist on the outer side—i.e., the side directed towards the skin—of two cell layers (Fig. 26). There is an outer continuous epithelial layer and an inner coat of cells in intimate contact with the upper surface of the scale and filling the areas between the developing ridges (*striae*). The nuclei are elongated in the direction of the latter, and each cell has in its cytoplasm a clear area surrounded by argyrophil granules. Neave considers that this is a Golgi apparatus. The same structure has been noted by other workers (for references see Neave, 1940), some of whom thought that its presence indicated a definite role on the part of the intimate cell layer in the formation of the bony layer of the scale.

On the undersurface of the scale there is a single layer of cells continuous around the margin with the intimate layer of the upper surface. It persists from the earliest stages of development right up to the time when the fibrous plate of the scale appears. Thereafter, little of it remains, although shrunken nuclei persist for a time as evidence of its former presence.

At the margins of the scale the cells are many-layered and it is only on the upper and lower surfaces that the cell arrangement described above prevails.

The cells of the papilla are largely osteogenic and the first part of the scale to be laid down is the upper hyalodentine or osseous layer. It starts off as a non-calcified mass of collagenous material lying within the papilla, and is subsequently hardened by the secretion of lime salts. Calcification commences in the oldest part of the scale and gradually extends towards the periphery. Neave contends that as long as scale growth continues there is always a recognizable non-calcified (osteoid) margin. A comparatively large osteoid plate is formed before the onset of calcification.

In this regard it is interesting to note that whereas most authors agree that the teleost scale is a purely mesodermal product, Fach (1936), working on minnow scales, asserted that the upper bony layer is formed by the ectoderm. Certain of the epidermal gland cells which come into close relationship with the posterior growing margin of the scale are supposed to secrete a lime-containing fluid ("Kalkmilch") which, conducted by the mesodermal elements, gives rise to the calcareous layer resting on the fibrous plate. Fach (loc. cit.) attempts to demonstrate "lines of communication" between the secretory ectoderm cells and the anterior region of the scale, which is remotely placed with respect to the latter.

Neave (loc. cit.) points out that on general grounds this is unlikely. The distribution of the gland cells (cells of Leydig) in no way encourages a belief that they play a part in scale formation. Even if it could be shown that they secrete calcium salts, they cannot account for the origin of the bony layer, because this, when first laid down, is uncalcified.

The fibrous lower layer of the scale is laid down after the osseous one, according to Neave. It will be recalled that in the beginning there was a definite layer of cells on the undersurface of the scale. As the very first lamella of the fibrous plate begins to form, this cell layer regresses until soon only a few degenerate nuclei remain. Whether these cells take part in the formation of the first lamella is not clear, but in any case subsequent additions of fibrous tissue come directly from the dermis. These additions cause an increase in thickness of the basal plate and also its peripheral extension.

At first the plate is almost entirely collagenous, but later, through the infiltration of the collagen by the second kind of organic substance—ichthyolepidin—present in the basal plate, it loses its characteristic collagen-staining reaction and also becomes less flexible.

The scale papilla, embedded in the skin, at first lies parallel with the body surface, but as development proceeds it tilts obliquely so that the anterior edge becomes buried in the lower layer of the dermis, while the posterior edge pushes outwards against the epidermis causing it to bulge slightly.

This tilting of the scales brings about the imbricated or overlapping arrangement seen in the adult and is due, according to Paget (1920), to the activity of the dermal tissues surrounding the scale papilla and constituting the scale pocket. These latter have in the meantime developed as tracts of dermal tissue between successive scale papillae. Spongy at first, they later become fibrous, completely enclosing the developing scales and helping to hold these firmly in the skin (Fig. 21).

The Formation of Striae.

This is one of the most controversial aspects of scale development. Klaatsch (1890) considered that the striae are produced by the superficial cells of the papilla. Paget (1920) and Pevsner (1926) state that each stria is laid down by a row of superficial cells lying against it and determining its curvature. Neave (1936) ascribes the surface

pattern of ridges to the action of osteoclasts, the ridges being formed not only by a building-up in front but also by a simultaneous hollowing-out behind. Later (1940) he abandons this idea. His earlier view was based upon the finding of wandering cells which might conceivably have osteolytic powers; re-examination of the material convinced him that these cells were far too few in number and also they occurred outside the layer of osteocytes covering the scale surface.

He decides that neither the cells of the outer epithelial layer nor those of the intimate layer can be specific ridge-forming agents, either by deposition or by osteolysis, for these layers are found over wide areas of regenerating scales where no ridges are found. They also occur in other places where the ridges are short and irregular. There may be some correspondence between the orientation of the cells and of the ridges, particularly in the anterior field, but in other parts of the scale there is no such relationship.

He considers that ridge formation is brought about by the presence of scale-forming materials in the intercellular fluid in amounts greater than at the growing edge. These are then deposited at other points nearby, between cells, thus increasing the thickness locally and causing ridge formation. The immediate deposition of osseous substance may be due to the action of the osteoblasts, but these do not determine the course of the striae.

In many regenerate scales the central part is devoid of ridges, the young scale, lying in a large scale pocket, having at first plenty of room for expansion. It can therefore utilize all available material to increase its lateral extent. When the scale approaches the edge of the pocket and marginal growth is slowed down, ridges are formed. He quotes the case of the most anterior of the mid-dorsal scales of the goldfish which abuts against the supratemporal canal. This scale has a very small anterior field, and its main directions for expansion are laterally and posteriorly. The ridges of the anterior field are close-set because of restriction of marginal growth, but in other parts, where there has been more room and greater extension, the ridges are set further apart.

Some reference has already been made to the relationship between the spacing of the ridges (i.e., the growth of the scale) and the growth of the individual (see p. xxvii), but it will be appreciated from the foregoing that the problem is a complex one, involving as it does the fact that the growth of the scale is not uniform in every direction. Neave agrees with Setna (1934) that ridge formation is influenced by "the restrictive action of the scale pocket", but does not believe that this restriction consists in a physical damming-up of material. In the regenerating scale ridges are formed long before the growing scale reaches the edge of the pocket.

The Sulci of the Scale.

Reference has already been made (p. xxiii) to the sulci (furrows or radii) of the scale. In a detached specimen these sulci appear as a series of grooves in the upper surface and from their characteristic arrangement in certain scales (e.g., the mullet) they are occasionally referred to as "radii" or "radial lines". The latter terms have also been applied to those cases where the sulci are not truly radial in their course (e.g., the herring scale), and on the whole the general term "sulcus" is preferable.

Sulci are actual breaks in the continuity of the upper osseous layer of the scale and extend right through to the underlying fibrous plate. They are lines of non-calcification and, however interesting they may be, we still have few clues as to their significance or to their ultimate structure.

Taylor (1916), quoted by Neave (1940), regarded them as lines of flexibility which permit the scales to adapt themselves to the shape and movements of the body. He pointed out that the sulci are always more numerous in scales covering those parts of the body which are subjected to the greatest degree of flexion and extension. In the relatively static regions, e.g., the head, the scales do not show these grooves. Whether Taylor meant these remarks to be confined to the pigfish and the squeteague which formed the subject of his paper, or whether he meant them to be of general application I cannot say, for his paper was unfortunately not available to me.

It is obvious, however, that a wide range of fish should be investigated from the angle of the relationship between the occurrence of scale sulci and body movement. One outstanding feature of scale literature is the amount of contradiction as between different authors working on different species. The scale as a morphological unit is highly variable and what may be true for one species is not necessarily so for another.

Pevsner (1926) considers that the sulci may be channels for the conduction of lymph. In the scales of *Rutilus rutilus* she describes (p. 304) a system of fine canals arising from the sulci and running into the substance of the scale. At the scale margin these canals divide repeatedly to form a network of vessels like blood capillaries. Neave (1940) disagrees with this view. He points out that the sulci are essentially open grooves and are therefore not suited for the conduction of fluid. He admits that they contain cells, but these are merely part of the general cell layer investing the scale (Fig. 26). He dismisses the network of fine vessels at the scale margin as cracks produced by rough handling and claims to have produced similar effects in goldfish scales in this way.

Paget (1920) has no definite suggestions to offer regarding the function of the sulci, but thinks they may be nutrient. He also mentions that in the clupeid scale they are filled with cells, even in the adult. These cells merge into the general tissues of the scale pocket. Fine tubules, simple in the sprat and herring and complexly branched in other clupeids, run down into the layers of the fibrous plate.

Neave (loc. cit.) stresses the great inherent rigidity of the latter due to the presence of ichthyolepidin, and points out that, as the osseous layer is thin anyhow, the sulci, *per se*, would not assist much in increasing flexibility. However, he shows that in goldfish scales the constitution of the fibrous plate immediately beneath each sulcus is different from what it is elsewhere. The conditions are shown in Figure 27. A wedge-shaped area of the plate immediately beneath the sulcus stains well with aniline blue, whereas the rest of the plate takes Orange G. From this he concludes that the wedge-shaped area consists mainly of soft collagen, as evidenced by the staining reaction, the harder ichthyolepidin being absent from here. The flexible condition of the blue-stained area is sometimes shown in section by the bent condition of the lamellae.

It may be concluded from the foregoing that scales with sulci are in fact more flexible than those which lack them, but the fact remains that there are some fish (e.g., the smelt) in which sulci are absent. This point obviously requires further illumination by extended studies on many teleost types. Paget's discoveries (see above) also indicate that the sulci may have a nutritive function, this being the most likely role for the systems of fine canals he describes. Whether these canals occur in all scales with sulci is another matter requiring further research.

The application of scale structure studies to practical problems of age estimation in fish is another field in which many questions remain unanswered. Here we have the curious case of a practical method or application far outstripping real knowledge of the morphological features on which it is based.

Are the osseous and fibrous layers of the scale as physiologically distinct as their respective ontogenies suggest? In herring scales the winter rings do not correspond in their course with the direction of the striae, although where the latter intersect the rings they become modified to give the characteristic clear effect.

Is the development of these rings due to some overriding growth mechanism that has its origin in the fibrous plate? As already mentioned, winter zones can be demonstrated in the latter by means of the polariscope, and these correspond in their course with the clear rings that show on the scale surface under ordinary illumination. The work of Paget (loc. cit., pp. 17-18, and his Fig. xxii) suggests that the primary basis of the winter ring may be the special character of the outcrops of lamellae on the surface of the fibrous plate.

There must be some overall scheme which will describe the growth pattern of scales, but we are not sufficiently *au fait* with details to be able to formulate this. Until such information is forthcoming, the basis of the individual ways in which age rings manifest themselves in scales must remain incompletely solved puzzles.

The Relationship of Scale Types in General.

In accordance with one of the main objects of this address, I have devoted a large amount of time to the teleost scale, and now the relationships between the different scale types in general must be discussed.

In his classical memoirs on fossil fish, Agassiz (quoted by Goodrich, 1907, et al.) used scale structure as a basis for his system of fish classification.

This work was continued and amplified by Williamson, who in two beautifully-produced papers (1849, 1851) described in minute detail the structure of the scales in living and fossil fishes, discussed their mode of growth, and sought to trace evolutionary relationships.

The basis of his theory was the placoid denticle, of the type found in Selachians. He considered that the various types of dermal structure, and more particularly the scales, of other fish groups evolved from the placoid denticle by a series of fusions and, in the bony fishes, by the addition of bony plates from below.

Modified versions of Williamson's theory were proposed by Hertwig, Klaatsch, and a number of other distinguished zoologists, among whom there was not always complete agreement (e.g. see Klaatsch, 1890, for criticisms of Hertwig).

Most were unanimous, however, in their choice of the placoid scale as a starting-point. One of the high points in these attempts to homologize scale structure in terms of placoid scales was reached by Tims (1905), who maintained that each of the calcareous plates (sclerites) on the upper surface of the cod scale, one of the most modified of all scale types, was a minute placoid element that had lost its spine. The concentric lines of striae, he says, are composed of rows of these placoid elements placed edge to edge. In Tims' view, the real morphological unit is the placoid element (sclerite), and the scale as a whole must be regarded as a compound structure consisting of a series of placoid basal plates resting upon the fibrous lower layer.

Even as late as 1915, we find conceptions of scale homology dominated by the placoid interpretation. In a short paper Rosén (1915) seeks to homologize the wide variety of scale types found in fishes. His approach is based on the relationships and relative degree of development of basal plate and spine.

He suggests that the oldest type of scale, phylogenetically, was the "Zahnschuppe", found in fossil Coelolepids, but not possessed by any living elasmobranch. The "Zahnschuppe" was a spine or denticle only, with no basal plate. From it evolved the "Zahnplattenschuppe", a denticle united with the basal plate. The latter consisted of an upper homogeneous layer and a lower fibrous one. In this group he includes the typical placoid scales of selachians as well as the bony scales of *Lepidosteus*, *Polypterus*, some fossil forms belonging to the Heterostraci and Osteostraci, some of the palaeoniscids, and the siluroids among the teleosts.

In his third group ("Plattenschuppen") are those scales which lack denticles, and the individual types are due to various modifications of the basal plate. Thus, in fossil acanthodians, some fossil crossopterygians, some fossil palaeoniscids, the Chondrostei, and certain plectognaths among the teleosts, the plate is very large and frequently ornamented with points or tubercles. In some plectognaths, e.g. *Cyclopterus*, the fibrous part of the basal plate has regressed, and the upper bony layer has become transformed into tubercles and spines.

The final stages of regression are seen in the cycloid scales of teleosts and Dipnoi and in the ctenoid scales of teleosts, where a thin flexible condition has been reached. In Dipnoi, and in ctenoid teleost scales, the upper layer has secondarily developed spiny projections.

Rosén (loc. cit.) claims that his scheme expresses the true genetic relationships of scales and therefore, by implication, the evolutionary process which accounts for their origin. It is difficult to imagine, however, that he intended this scheme to express the phylogenetic relationships of the groups.

I have quoted Rosén at some length as an example of the type of argument that was used in the "placoid controversy". One cannot help feeling that such reasoning is rather

arbitrary and does not necessarily present a true picture of what has happened in scale evolution.

Goodrich (1907) gives a valuable summing-up of the value of scale structure in fish taxonomy, and demonstrates with some success that "the position of a fish in any of the large groups can be determined by an examination of its scale".

He puts this statement to the test by applying it to two groups of fish whose systematic position at the time of writing had been a matter of some dispute—the Polypterini, and the Acanthodians.

Examination of the scale of *Polypterus* (this fish has the "palaeoniscid" type) convinced him that *Polypterus* belongs to the Actinopterygii rather than to the Crossopterygii, the group in which it was placed at that time. Both on the basis of scale structure and of certain other anatomical features, modern zoologists agree that *Polypterus* is an actinopterygian.

Goodrich (loc. cit.) maintained that the structure of the acanthodian scale showed closer affinities with the bony fish than with the elasmobranchs. Modern fish palaeontologists place the acanthodians just below the elasmobranchs in the evolutionary scale. (See Classification Table.)

TABLE OF FISH CLASSIFICATION.

Sub-Phylum CRANIATA.

Section PISCES.

Division and Class: AGNATHA ("jawless fishes").*Sub-Class 1.* Ostracodermi ("ostracoderms").

- Order 1. Cephalaspida = Osteostraci. Late Silurian—end of Devonian.
- Order 2. Anaspida. Late Silurian—Late Devonian.
- Order 3. Heterostraci = Pteraspida. Mid-Ordovician—Upper Devonian.
- Order 4. Coelolepida. Late Silurian—Lower Devonian.

Sub-Class 2. Cyclostomata ("cyclostomes").

- Order 1. Petromyzontes (lampreys). Recent.
- Order 2. Myxinoidei (hagfishes). Recent.

Division: GNATHOSTOMATA ("jawed fishes").*Class 1.* Placodermi ("placoderms").

- Order 1. Acanthodii. Upper Silurian—Lower Permian.
- Order 2. Arthrodira. Lower to Upper Devonian.
- Order 3. Macropetalichthyda. Lower to Upper Devonian.
- Order 4. Antiarchi Pterychiomorphi. Middle to Upper Devonian.
- Order 5. Stegoselachii. Devonian.
- Order 6. Palaeospondyloidea. Middle Devonian.

Class 2. Elasmobranchii = Chondrichthyes ("cartilaginous fishes").

- Order 1. Cladoselachii Pleuropterygii. Devonian—Permian.
- Order 2. Pleuracanthodii. Late Devonian—Triassic.
- Order 3. Selachii (sharks and rays). Devonian—Recent.

The Selachii are divided into four Sub-orders, the Hybodontioidea (Late Devonian—Recent); the Heterodontioidea containing the living genus *Heterodontus* (Port Jackson shark); the Protoselachii containing the three living genera *Hexanchus*, *Heptanchus*, and *Chlamydoselache*; and the Euselachii, containing the remaining dogfishes and sharks which range from Jurassic to Recent, as well as the rays ranging from Jurassic to Recent.

Class 3. Holocephali ("ghost sharks").

- Order 1. Bradyodonti. Devonian—Early Mesozoic.
- Order 2. Chimaerae (living ghost sharks). Triassic or Jurassic—Recent.

Class 4. Teleostomi = Osteichthyes ("bony fishes").*Sub-Class 1.* Actinopterygii.

Super-Order 1. Chondrostei.

Order 1. Palaeoniscoidea. Middle Devonian—Lower Cretaceous.

Order 2. Polypterini. Eocene—Recent. Including the living genera *Polypterus* and *Calamichthys*.Order 3. Acipenseroidi. Living genera *Acipenser* and *Scaphirhynchus* (sturgeons), *Polyodon* and *Psephurus*.

Super-Order 2. *Holostei*.

Order 1. Semionotoidea. Mississippian–Recent. Includes the living genus *Lepidostens* (gar pike).

Order 2. Amioidea. Triassic–Recent. Includes the living genus *Amia* (mudfish or bowfin).

Super-Order 3. *Teleostei* ("teleosts").

Including genera ranging from Lower Jurassic to Recent. Divided into six Orders, which between them contain all the "typical bony fishes" constituting the bulk of the living fish fauna, as well as fossil forms. For further details, see Romer (1950).

Sub-Class 2.

Choanichthyes.

Order 1. Crossopterygii ("crossopterygians").

Divided into two Sub-Orders, the Rhipidista, Lower Devonian to end of Palaeozoic; Coelacanthini, Carboniferous to Recent. The modern genus *Latimeria* is included in this latter Sub-Order.

Order 2. Dipnoi ("lung fishes"). Middle Devonian–Recent.

Includes the modern lungfish genera *Epiceratodus*, *Lepidosiren*, and *Protopterus*, as well as a number of fossil forms.

The full value of Williamson's work (1849, 1851) remained long unrecognized because of the chaotic state of the classification of fossil fish which prevailed in his day and for many years afterwards. Failure of palaeontologists to agree on the correct position of disputed groups prevented a true evaluation of evolutionary relationships.

The past two or three decades of this century have been notable for great research activity in vertebrate palaeontology. Attention has been directed to the study of the minute structure of skeletal tissues, as well as to the general anatomy of fossil types. Our knowledge of the fossil agnathous ostracoderms and of the placoderms has been considerably extended. We now have radically revised ideas as to the antiquity of certain fossil groups, and their sequence in time. Similarly, our attitude towards the evolutionary relationships of the skeletal tissues bone, cartilage, and dentine, has undergone a great change.

These revised ideas more or less undermine the controversy about the placoid origin of scales and other dermal structures, and relegate it to the position of a historical curiosity. This in some ways is a cause for regret, in view of the illustrious names which have been associated with the controversy, and the magnificent researches into scale morphology and scale development which it stimulated.

It is now my task to discuss some of the modern ideas on the subject of early vertebrate evolution in the light of the new knowledge.

Early Vertebrate Evolution.

It was formerly thought that living elasmobranchs are the direct descendants of the most primitive jawed vertebrates, and that elasmobranch ancestors, like their living contemporaries, had internal skeletons of calcified cartilage, and exoskeletons of placoid elements in which there might be some approach to bone structure.

Somewhere along the line of evolution, forms branched off from this primitive stock, and gave rise to the various groups of bony fishes, in which the endoskeleton, although it might pass through a cartilaginous phase during ontogeny, consisted in the adult of a new and distinct kind of tissue-bone.

So, on the older theory, living elasmobranchs are of greater antiquity than living bony fishes, and cartilage is more ancient, phylogenetically, than bone.

Before proceeding to show you how radically our views on this subject have changed, it will be necessary for me to give you a brief summary of the classification of the lower vertebrate groups, because this epitomizes our opinions concerning their evolutionary relationships.

For those requiring fuller information, I would recommend Romer's well-known textbook of palaeontology (Romer, 1950). See also the general scheme of fish classification on page xxxiv.

The most ancient remains of undoubtedly vertebrate origin have been found in Ordovician sediments, but are too fragmentary to permit of any clear idea of the

complete animals. The remains are small fragments which are most likely parts of exoskeletal structures—pieces of armour, which on sectioning prove to consist of bony tissue.

Although these are the oldest vertebrate relics that have come down to us, there is reason to believe that the group was already well established by Ordovician times, and may well date back into the Cambrian, a hundred million years earlier than any of the complete fossils that are known to us.

In late Silurian and early Devonian sediments we encounter the first vertebrate fossils that are complete enough to give an adequate idea of what the original animals were like. These, the ostracoderms, were heavily armoured jawless fishes without paired fins and quite unlike any of the fishes of today, with the possible exception of the Cyclostomes. These, too, are jawless and possibly co-existed with the ostracoderms, but modern representatives have lost all of their dermal armour, and are degenerate, soft-skinned types of semi-parasitic habit.

The ostracoderm head skeleton was well ossified, and consisted of a number of heavy bony plates firmly joined to one another and to the external skeleton of the gill region. The hinder part of the body was encased in stout overlapping scales. They were most likely mud feeders, straining this material through their numerous gill slits.

The Ordovician fragments referred to above (which predate ostracoderms) have been shown to be portions of bony plates with a superficial dentine layer, a middle layer of spongy bone, and a lower one of bone with a laminated structure.

The ostracoderms as known to us had already branched out into distinct groups. Best-known of these are perhaps the cephalaspids, which are abundant in Late Silurian and Lower Devonian rocks. The minute details of skeletal structure in cephalaspids have been worked out in particularly great detail by Stensiö (1927), who finds an enamel-like layer, dentine, and true bone with cells, in the skeletal plates.

Details of the endoskeleton are very obscure (badly preserved), but he considers that it was largely cartilaginous. In *Boreaspis* he describes the presence of perichondral bone, which "is continuous with and passes over into the basal part of the basal layer of the exoskeleton".

The later ostracoderms of the Devonian show a reduction in bony armour as compared with Silurian forms. In these later forms, the bone is regressive, not progressive, in its development. In the little-understood Coelolepids, which are provisionally placed in the ostracoderms, the body was enclosed in minute scales which did not overlap. It was formerly thought that this type of armour represented a further stage in the acquisition of a still heavier bony type of covering, but now the reverse is believed to be true—that it is an example of extreme regression. One further step would take it to the condition of modern sharks with their placoid scales.

Devonian Gnathostomes.

The Devonian period has been called the "age of fishes". This was the time when the more immediate ancestors of modern types flourished, and the variety of forms was far richer than it is today.

Compared with ostracoderms, these new types, which must have originated in late Silurian times, show two very important advances in structure—the acquisition of jaws and of paired fins. Whereas the ostracoderms were most likely bottom feeders, stirring up the mud for the sake of the contained food, these new types of fish, with their jaws, their more streamlined bodies, and their improved locomotion, were able to forsake the bottom and seek their food in mid waters.

The oldest Order of these jawed vertebrates, the Acanthodians or "spiny sharks", flourished along with surviving ostracoderms. Jaws were still in the experimental stage of development, and some types had as many as six or seven sets of paired fins. In the acanthodians, there had been little regression of the external armour, the body being still enclosed in bony plates or scales. The scales were, in fact, very like those of the Actinopterygii (group of higher bony fishes). The endoskeleton, unlike that of modern sharks, contained well-developed bone.

The acanthodians reached their peak in Lower Devonian times, both in numbers and in variety of species. By the Carboniferous, the group had begun to disappear, and the last survivor, which died out in the Lower Permian, was a degenerate type with an elongate body almost devoid of scales, and with no teeth.

The Acanthodii, like the ostracoderms, were apparently fresh-water dwellers, although many of the former seem to have adapted themselves, ultimately, to the salt-water environment.

In the arthrodire, the hinder part of the body was largely naked but the heavy bony armour at the front end was retained. Head and "chest" parts of this were connected by a complicated series of joints and the jaws had a very unusual method of operation. Whereas in a modern vertebrate the mouth is opened by dropping the lower jaw, in the arthrodire the latter was held stationary and the whole head with the upper jaw raised.

We know nothing of any Silurian type that could have been a placoderm ancestor, but from the high degree of development of the skeleton of known forms in this group, it is conceivable that the ancestor, too, included both bone and cartilage in its make-up.

By the end of the Palaeozoic, the majority of sharks had adopted the sea as their place of living. The first representatives of the modern shark Order appeared in the Carboniferous. The elasmobranchs, once well established, were a much larger group than they are today. Of the first two Orders, the Cladoselachii disappeared for ever in Permian times, while the Pleuracanthodii lasted into the Triassic. Of the Order Selachii, the hybodonts became extinct in Cretaceous times, leaving us with three sub-orders of modern sharks and rays. Among these there are three survivors from fossil times—*Heterodontus* (*H. portus-jacksoni* is the Port Jackson shark), fossil remains of which occur in the Jurassic, *Hexanchus* which also dates back to this period, and *Chlamydoselache*, remains of which have been found in Tertiary deposits.

Taken together, these Suborders of the Elasmobranchii, fossil and recent, differed considerably in anatomical characters (such as the skeleton of the paired fins and method of jaw suspension) but for our present purpose, the great feature that unites them is the nature of the skeleton, both internal and external.

The former is reduced to cartilage, calcified to varying degrees, but showing no trace of the bony tissue that was so characteristic of both ostracoderms and placoderms—groups of greater antiquity than the elasmobranchs. The exoskeleton, too, has reduced from a bony armour to a thin covering of placoid scales.

In the aberrant modern ghost sharks (Holocephali) the scales over the skin surface have been lost, but fossil forms possessed a covering of stout denticles.

True bony fishes (Osteichthyes) appeared in fresh waters in the Middle Devonian, but subsequently adopted, in most cases, the marine environment. The early representative of this group lived alongside the more primitive ostracoderms and placoderms, but whereas the latter gradually died out, the former continued to increase in importance, to occupy their predominant place in today's living fish fauna.*

The outstanding feature is the extensive retention of bone in the skeleton. Cartilage may occur along with this, even in some modern teleosts, but bone is the predominant tissue.

With this very brief account we have covered sufficient of the history of the fishes to illuminate what follows.

Right at the bottom of the evolutionary scale, as far as we know it, are the ostracoderms, in which bone, cartilage and dentine were present as characteristic skeletal tissues. The ostracoderms are of greater antiquity than the placoderms, which also had bone, cartilage and dentine. The placoderms in turn predate the elasmobranchs with their skeletons of cartilage only, and the elasmobranchs are of greater antiquity than the Osteichthyes (bony fishes) in which bone is the typical skeletal tissue.

* Certain groups have become extinct. Examples are the Palaeoniscoidei and all Crossopterygii with the exception of the lone genus *Latimeria* (see p. xx).

I have already mentioned the former belief that the ancestors of modern bony fishes were not very different from existing elasmobranchs with their cartilage skeletons. Now our conception of the course of vertebrate evolution has changed drastically, and we see the elasmobranchs in their true perspective. This automatically leads to a revised attitude towards the respective antiquities of dentine, bone and cartilage as skeletal materials. In this regard it is highly interesting to note that the presence of bone in ostracoderm plates has been known for more than ninety years. Huxley (1858), quoted by Goodrich (1909), made this fact known in cephalaspids. Pander (1858), quoted by Goodrich (1909), described bone in fossil remains of placoderms.

At that time though, and indeed for long afterwards, the classification scheme was in a muddle, and the correct evolutionary sequence of the groups was not realized. It will therefore be instructive to re-examine vertebrate evolution from the viewpoint of the phylogeny of the hard tissues.

In the light of the older theory, the placoid element was the basic unit. The dermal bones and bony scales of the Osteichthyes were supposed to have arisen by fusion and progressive development of the basal plates of the placoid scales. This implies that dentine is a tissue of very great antiquity (which is undoubtedly true). Bone in the exoskeleton came about not only as a result of fusion but by an increase in histological complexity. Ossification in the endoskeleton (represented by the "cartilage bones") came later still.

But we have seen that the most primitive vertebrate types (ostracoderms) which survive as fossils show a high degree of bone development in the dermal skeleton, and undoubted bone in the endoskeleton. Bone, dentine,* and cartilage coexist in the one individual, and a study of the evolution of the Agnatha, and of the jawed fishes (gnathostomes) reveals a clear trend towards the regression of bone both internally and externally.

Thus the ancestors of modern bony fishes were not similar to living elasmobranchs. The latter, indeed, present the picture of a group that has undergone considerable reduction in both external and internal skeletons. The latter has been reduced to cartilage, and the former to simple placoid scales.

The bony tissues of Osteichthyes have been inherited directly from primitive jawless vertebrates. Those vertebrates with reduced exoskeleton and partial or absent bone formation in the endoskeleton, owe their condition to reduction and specialization.

There is no evidence to show beyond doubt that cartilage, either calcified or non-calcified, was the evolutionary forerunner of bone. Quoting Ørvig (1951), "If the development of the endoskeletal hard tissues in the lower gnathostomes in general is taken into consideration, the calcification of cartilage and the ossification of connective tissue are collateral processes. In its special manner, each of these two processes reflects the certainly very old trend in the vertebrate stock of the precipitation of lime salts in the mesodermal tissues. Consequently, not one of these processes is more primitive than the other."

The Hard Tissues of Teeth and Scales and their Relationship to the Germ Layers.

It has become apparent from what was said in the earlier part of this Address, that there has been disagreement as to the nature and origin of the so-called "enamel" of elasmobranch scales and teeth.

The dispute revolves around three questions: (1) Is this tissue identical with the enamel of higher vertebrates, and therefore an ectodermal product? (2) Is it formed by mesoderm and is it therefore merely a special kind of dentine? (3) Is it a product of the combined action of mesoderm and ectoderm?

Hertwig (1874) considered that enamel was directly produced by the enamel organ, and must therefore be ectodermal in origin. Klaatsch (1890) agreed with this view, and later (1894) went even further, stating that the epidermis (ectoderm) forms most

* No attempt will be made here to discuss the relationships of the many different varieties of dentine with bone and cartilage. For a full treatment of this, see Ørvig, 1951, pp. 381-394.

of the hard substance, i.e. enamel and dentine, in scales and teeth. He claimed that special cells ("scleroblasts") wandered from the epidermis into the mesoderm and proceeded to form the hard substance. In scale formation, for instance, the enamel epithelium continued to make contributions of scleroblasts to the developing structure, thus acting as a sort of germinal layer, and providing new material for scale formation.

Klaatsch naturally met with considerable opposition to this unorthodox view, one opponent even going so far as to say that Klaatsch's results were due to artefacts produced in the preparation of the sections.

Indeed, the whole dispute may well have become a historical curiosity, transgressing as it did, among other things, the precepts of the germ layer theory. Recent work by various authors (see p. xli), while not directly confirming Klaatsch, at least shows that his ideas are not as impossible as they may have sounded at the time.

Weidenreich (1937) regards elasmobranch vitrodentine as enamel, but inclines to the view that both the enamel organ (ectoderm) and the corium (mesoderm) contribute to its formation. In his view the enamel organ forms a secretion which passes through the basal membrane between epidermis and corium, and brings about calcification in the vitrodentine. The fibres of the latter he regards as mesodermal, as is the main mass of dentine. He considers that there is no essential difference between the enamel of elasmobranchs and of mammals, even though the former lacks the prismatic structure of the latter.

Bargmann (1937) disagrees with Weidenreich, and supports his case with a description of the origin of vitrodentine in the teeth of a ray, *Myliobatis*. The basic structure of the developing tooth is typical—an epidermal enamel organ capping a corium papilla, and separated from this by a basement membrane. The formation of hard substance begins with a shrinkage of corium cells away from the basal membrane, and the intervening space becomes filled with a clear fibrous zone which is comparatively free from cells. The fibres are arranged perpendicularly and the zone becomes thicker as the corium retreats further from the basal membrane. This clear area is the site where the vitrodentine will be laid down. Between its perpendicularly-disposed fibres are long cytoplasmic processes, belonging to more deeply-situated mesenchyme cells (odontoblasts). Both fibres and cell processes are embedded in a fine ground substance, presumably calcified. Bargmann (loc. cit.) denies that the enamel organ plays any part in the formation of this vitrodentine, or in its calcification, because it remains quite unchanged in appearance and shows no sign of secretory activity from the time of the first appearance of the vitrodentine until its final and definite differentiation.

Below the vitrodentine, the main mass of dentine (the "Manteldentin") has begun to form from the rest of the tooth papilla, and is at all times in contact with the vitrodentine. The only structural difference between them is that in the early stages the fibres of the "Manteldentin" are coarser and more closely packed.

Both Bargmann (loc. cit.) and Fischer (1937) point out that in the tooth of the cod (a teleost) there is, in addition to the vitrodentine, a cap of true enamel, of ectodermal origin, enveloping the tip of the tooth, thus providing, in their estimation, further evidence for the separate natures of enamel and vitrodentine respectively. Bargmann concludes his paper by saying that his findings in the case of *Myliobatis* do not necessarily indicate that all elasmobranchs lack true enamel.

W. J. Schmidt (quoted by Ørvig, 1951) studied the structure of enamel and dentine under polarized light, and found that the enamel-like tissues of lower vertebrates differ from the enamel of reptiles and mammals in their hydroxy-apatite crystals, and are closer to dentine in this respect. Their birefringence is higher than that of normal dentine, however, because of the almost complete loss of collagen fibres, and because of heavy calcification.

Levi (quoted by Ørvig, 1951) seems to have produced good evidence that the ectoderm participates in, or at least influences, the formation of enamel in the lower vertebrates, which would indicate a closer relationship between true enamel and vitrodentine than was previously believed.

Kvam (quoted by Ørvig, 1951) says that the hard tissue of lower vertebrates is enamel, defining the latter as "the strongly-calcified acid-soluble outer strata in the dental crowns or in parts of these . . . irrespective of . . . genesis, appearance and structure".

He distinguishes between "mesodermal enamels" in the Anamnia, and "ectodermal enamel" in the Amniota. The former arises by a secondary calcification of the dentine's outer stratum. The latter "is deposited outside the dentine".

This summarizing of the position by Kvam indicates that the origin of enamel is a matter of little importance. What really counts is its position and its chemical and physical properties. But if the "enamel" of elasmobranchs is mesodermal, there is still the problem of the significance of the enamel organ. It is difficult to imagine that the latter, which is such a constant and prominent structure in the development of placoid scales and teeth, should play an insignificant role in their development, even though, so far, formal embryological studies have not illuminated the problem very much.

It is also difficult to relegate its significance to the mere role of determining the form of the tooth or scale, as some authors suggest.

Also, what is the causal-analytical relationship between enamel organ and dermal papilla? Is it another case of evocation, and if so, which evokes which? On this latter point there is an indication that the papilla may be the active partner (see later, p. xliii).

There is obviously here a rich field for the experimental embryologist, working preferably on elasmobranch material. The technical difficulties in such a research are likely to be very great.

The next problem that awaits our attention is the relationship between enamel and ganoine. Nickerson (1893) considered that ganoine is formed by the "ganoine membrane", which is of dermal origin and which lies immediately beneath the epidermis. In other words, ganoine is a mesodermal product.

Ørvig (1951) has some interesting comments to make on this point. He is of the opinion that ganoine should be classed as enamel, and indeed that the name "ganoine" should be discarded as superfluous. It cannot be regarded as a type of bone or even as bone-like tissue because of its high birefringence and because in comparatively recent years it has been shown to have a prismatic structure (authors quoted).

The fact that it contains no or very few terminal branches of the dentinal tubes (in *Lepidosteus*) is to be expected because here it lies directly on bone with no dentine (cosmin layer) in between. In the palaeoniscid type of scale, on the other hand, where there is a layer of dentine (cosmin-like substance) the ganoine is penetrated to a small extent by such tubes.

Ørvig points out that the tendency of most authors to regard ganoine as a hard tissue distinct from enamel is based on its embryological history and not on its structure.

Nickerson's observation of the presence of a layer of dermal cells between the epidermis and the first layer of ganoine led him and subsequent authors to believe that ganoine is formed without any contribution from an enamel organ. However, as Ørvig points out, one must also allow for the possibility that the presence of this corium membrane immediately outside the first ganoine layer does not necessarily mean that the membrane gave rise to the latter. It is equally possible that the membrane is formed after the first stratum of ganoine is laid down and that "probably influenced to some extent by the epidermis, it became impregnated with calcium salts and gave rise to a new, more superficial layer of ganoine".

This suggests that the ganoine increases in thickness as a result of a periodic covering of the outer surface of the scale by mesodermal tissue, the latter collaborating with the epidermis to give a new layer of ganoine.

Tretiakoff (1936) had shown that ganoine occurs within the bone tissue of the dorsal fin spines of the chondrosteian genus *Polypterus*, and concluded that this ganoine, isolated from epidermal influence, must be a purely mesodermal product. But Sewertzoff (1932) had shown that such enclosure is a secondary process and that the ganoine layers were originally superficial in position. The ganoine tubercles ornamenting the

dermal bones of *Polypterus* become overgrown by tubercles of a younger generation, with the result that layers of ganoine alternate with layers of dentine. We have already seen that a similar process can occur in the scale denticles of the coelacanth *Latimeria*.

Ørvig's remarks in the concluding part of this section of his paper are worth quoting almost in full. He says: "What we now know concerning the phylogenetic growth and structure of the scales and dermal bones of fishes in general . . . makes it likely that the *Polypterus* scales are grown over periodically by mesodermal tissues, but that this growing over is less pronounced than in the dermal bones and fin spines of the same fish. In my opinion, the growth in thickness of the 'ganoine' of *Polypterus* scales may therefore take place somewhat as follows:

"The first layer of ganoine forms close beneath the epidermis. It is separated from the epidermis by mesodermal tissue which forms over the entire external face of the individual scales. Under the influence of the epidermis, this layer of mesodermal tissue gives rise to a second layer of ganoine superficial to the first one. A third layer of ganoine forms in the same way after the external face of the scale has become grown over by a new layer of mesodermal tissue, etc., until the ganoine consists of several superimposed layers. If it forms in the manner now outlined, in the *Polypterus* scales, the ganoine naturally develops the same way in the *Lepidosteus* scales. As may be gathered from above, there is no conclusive evidence so far that ganoine and enamel in fishes are of different origin. Instead, everything goes to point that ganoine cannot be a substance *sui generis*, but should be regarded as a kind of enamel."

Scales, Teeth, and the Germ Layer Theory.

The respective roles of ectoderm and mesoderm in the development of mammalian teeth appear to be quite clear-cut. The ectoderm forms the enamel organ which lays down enamel, while the remaining tooth elements are of mesodermal origin.

We have just seen that in lower vertebrates the position is not nearly so clear. An enamel organ formed by the epidermis is almost universally present, but the extent of its contribution to the scales and teeth is not properly understood. Opinions as to the role of the enamel organ vary from complete homology with the corresponding organ in the mammals to a denial that it plays any essential part at all. A middle view has it that the enamel layer is formed by the combined action of enamel organ and the underlying dermis. It should, therefore, repay us to look more closely at the problem of scale and tooth genesis from the angle of the germ layer theory.

The foundations of the germ layer theory were laid by Pander in 1817. He was the first to point out that in the normally-developing egg there are three primary germ layers (ectoderm, mesoderm and endoderm), out of which the organ systems develop. Each germ layer, in the early stages of development, is regarded as mutually exclusive. Each one makes its own definite contributions to the embryo.

Von Baer, in 1828, made the additional contention that homologous structures in different animals could be consistently traced back to the corresponding germ layers, an important principle on which the whole of formal comparative embryology is based. This concept was a purely morphological one, designed to systematize the methods of organ formation during development, and in its original form did not envisage that the developmental potencies of the germ layers must be much wider than their "normal" behaviour suggested.

This was eventually shown to be the case as far as the adult organism was concerned. During regenerative processes or asexual reproduction, structures could arise from a tissue derived from a germ layer that would not have formed such a structure in normal development.

An excellent example of this is the formation of new individuals from buds in the reproductive processes of tunicates (Berrill, 1951, p. 467), where in certain cases atrial epithelium, epicardial epithelium and septal mesenchyme (all functionally and histologically unspecialized epithelia), each in its place, will give rise to all tissues except epidermis. In other words, these unspecialized cells can form ectodermal, mesodermal and endodermal structures.

Such a fact does not necessarily weaken the germ layer theory in its original form, which was concerned only with normal development from the egg.

Further difficulties are encountered with muscle development. Muscle is regarded as a typically mesodermal product, but in some Crustaceans (Cyprids) certain of the muscles are formed from ectoderm. The same sort of thing occurs in the annelid genus *Criodrilus*, and one also recalls that most of the musculature of Coelenterates is in the ectoderm.

Returning now to our immediate problem, the genesis of skeletal structures in fishes, I would like to bring before your notice a very important recent paper by de Beer (1947) concerned with the origin of the cranial and visceral skeleton and of the teeth in the Urodele *Amblystoma mexicanum*. This animal is an Amphibian, and therefore very closely related to the fishes.

de Beer shows that in this *Amblystoma* most of the visceral skeleton, a part of the chondrocranium and the odontoblasts come from the ectoderm, while enamel organs may be formed by ectoderm, ectoderm and endoderm, or endoderm alone.

The ectodermal cells in question which give rise to such a variety of skeletal structures are derived from the neural crests. For the benefit of the non-zoological members of my audience, I should like to explain that the neural crests are two longitudinal strips of ectoderm which have proliferated from the upper level of the two sides of the neural tube, one on the right and one on the left. Their main function is to form the cerebral ganglia, and the dorsal ganglia and roots of the spinal nerves.

In the embryo of *Amblystoma mexicanum* the neural crest cells are clearly distinguishable from notochord mesoderm, ordinary mesoderm, and endoderm, both in their yolk and in their pigment content. The neural crest cells have very little yolk, the globules of which average only about 1μ , and whose cell cytoplasm is heavily pigmented. The other cells mentioned are heavily charged with large yolk globules (diam. 10μ) and are completely lacking in pigment.

The neural crest cells soon lose their yolk, but retain their pigment sufficiently far on in development to be quite definite—recognizable, irrespective of whether they remain in their original position at the sides of the nerve tube, or migrate and become associated with mesoderm or endoderm a long way from the site of their origin.

This natural "tagging" of the neural crest cells, therefore, enables them to be traced during their subsequent history.

The visceral arches (the jaw arch, the hyoid and branchial arches), as well as odontoblasts, have hitherto been regarded as typically mesodermal structures, but let us now examine their origin in the light of de Beer's findings.

The visceral arches are conventionally described as arising from condensations of mesenchyme, a loose aggregation of cells, derived from the mesoderm, and filling (for our present purpose) the space between the endoderm of the foregut (where the pharynx will subsequently develop) and the ectoderm.

In his "stage 22 embryo", de Beer (loc. cit., p. 382) describes the "mesenchyme population" of the head, and shows that it has a double origin. The "true" mesenchyme, the cells of which contain large yolk globules and no pigment, does not extend further forward than the eye, nor does it reach further ventrally than the dorsal wall of the gut. All of the rest of the head space is occupied by "ectomesenchyme", of ectodermal origin, and its cells can be readily recognized because of the lack of yolk and because of the pigmentation.

A sheet of ectomesenchyme, continuous with the neural crest of the same side, becomes applied to the side of the pharynx, and by subsequent condensations gives rise to the whole of the cartilaginous visceral skeleton, except, curiously enough, the second basibranchial, which is mesodermal. Here, then, is cartilage which has come from ectoderm. The trabeculae of the skull have a similar origin, but the parachordals are mesodermal products. The whole mixed pattern can be traced back to cell movements which lead to the laying-down of mesodermal mesenchyme and ectodermal mesenchyme in definite areas, and the sharing of these two sorts of mesenchyme in skeleton-formation.

Concerning the origin of odontoblasts and enamel organs, it will first be necessary to explain the nature of the cell layers at the front end of the gut. In the significant stages described, the mouth had not yet broken through. The respective extents of ectoderm and endoderm in the foregut are shown in Fig. 26.

At the front end of the foregut (pharynx) there is a solid plug of endoderm abutting against a single layer of ectoderm cells constituting the oral plate. The solid plug of endoderm is encircled for a certain distance by a collar of ectoderm (the "stomodaeal collar"), continuous with the oral plate.

Subsequently, the first visceral (mandibular) arch will develop at this level. The jaws which ultimately develop in relationship to this arch eventually acquire teeth and, as will be shown in a moment, the ontogenetic history of these teeth with reference to the germ layers is very mixed.

Soon the solid plug of endoderm is resorbed, the oral plate perforated and a mouth is established. The front end of the foregut now consists of the ectodermal collar already noticed, which is continuous behind with the endodermal wall of the pharynx, and which is separated from the latter by a clearly-marked line. The latter is due to the presence of pigment in the ectoderm, and its absence in the endoderm.

This line cuts across the antero-posterior extent of the tooth-forming region of the jaw, a circumstance which will, in turn, have a profound effect on the germinal origin of the enamel organs. Teeth formed anterior to the line of demarcation will have ectodermal enamel organs. In the transition zone the enamel organs will be partly ectodermal and partly endodermal, while any teeth developing still further back, i.e. in the endodermal lining of the pharynx, will have endodermal enamel organs.

This is what de Beer actually found in his preparations, the germinal origin, ectodermal, endodermal, or ectodermal-endodermal, of the organ being determinable in each case from the pigment and/or yolk content of the cells.

The odontoblasts forming the dental papillae arise from neural crest cells that group themselves around the anterior part of the gut in the vicinity of the stomodaeal (ectodermal) collar, and immediately behind this. Like the presumptive visceral arch cells, they are readily identifiable by their pigmented cytoplasm, and comparative lack of yolk.

In tooth formation, the ectodermal odontoblasts become organized into dental papillae which become overlaid by enamel organs. These may be ectodermal, ecto-endodermal, or endodermal according to their location, and tooth development then proceeds. There is no preliminary sinking inwards to form an "enamel band". The teeth develop much in the same way as placoid scales.

However much these events appear to contradict the germ-layer theory, they do throw some light on the problem of the origin of the placoid scales that occur in the pharynx of some selachians, and also of the pharyngeal teeth of some teleosts. These teeth have always been intriguing to zoologists, because their location suggests that the enamel organ can only arise from endoderm. The work of de Beer has shown that this can in fact happen in Urodeles, and it further suggests that there may be a causal relationship between enamel organ and dental papilla. Irrespective of the position of the latter, the overlying tissue, whether ectoderm or endoderm, is induced to form an enamel organ.

It should be mentioned that de Beer was not the first to suggest or to demonstrate the ectodermal origin of cartilage or of tooth elements. In his paper (*loc. cit.*) he gives an admirable review of previous researches, experimental and otherwise, directed to the same end. His own work—the following of the fate of neural crest cells in perfectly normal development, without the aid of experiment—shows once again that the possibilities of straightforward descriptive embryology as a research weapon have been by no means exhausted.

It is now obvious that we must revise our attitude towards the origin of structures found in the scales and teeth of the lower vertebrates.

We have seen that enamel can be of ectodermal, endodermal, or even mesodermal origin, while dentine, derived from odontoblasts, can come from either ectoderm or

mesoderm. What is now needed is a thorough re-examination of the genesis of scales and teeth and related structures in the fishes. It is unfortunate that the selachian embryo should be such a difficult type for experimental research; the free teleost egg and embryo, on the other hand, offer promising material for the causal embryologist.

In endeavouring to express the changed attitude to the germ layer theory as a whole, I can do no better than quote de Beer himself.

He says (*loc. cit.*, p. 393): "rather should the germ layers be considered as a problem of the anatomy of embryos, and less as a problem of the anatomy of the adult. Germ layers exist, and they correspond in widely-different types of organisms, regardless of the exact topographical localization of the materials of which they are composed, and of the fate of these materials . . . there is just sufficient constancy in the origin and fate of the materials of which the germ layers are composed to endow the ghost of the germ layer theory with a provisional descriptive and limited didactic value, in systematizing the description of the results of the chief course of events in the development of many different kinds of animals; provided that it has been remembered that such systematization is without bearing on the question of causal determination of the origin of the structures of the adult organism."

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The Honorary Treasurer, Dr. A. B. Walkom, presented the Balance Sheets for the year ended 29th February, 1952, duly signed by the Auditor, Mr. S. J. Rayment, F.C.A. (Aust.); and his motion that they be received and adopted was carried unanimously.

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

President: S. J. Copland, M.Sc.

Members of Council: D. J. Lee, B.Sc.; F. V. Mercer, B.Sc., Ph.D.; E. Le G. Troughton, C.M.Z.S., F.R.Z.S.; H. S. H. Wardlaw, D.Sc., F.A.C.I.; Professor W. L. Waterhouse, M.C., D.Sc.Agr., D.I.C.; and A. R. Woodhill, D.Sc.Agr.

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

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

GENERAL ACCOUNT. Balance Sheet at 29th February, 1952.

LIABILITIES.		ASSETS.	
£	s. d.	£	s. d.
Capital—		Fixed Assets—	
Amount received from Sir William	14,000 0 0	Commonwealth Loans, at cost ..	15,048 10 0
Macleay during his lifetime	6,000 0 0	Debentures:	
Further sum bequeathed by his Will	20,000 0 0	Metropolitan Water, Sewerage and	
	10,347 1 4	Drainage Board, at cost ..	994 7 6
Contingencies Reserve	30,347 1 4	Science House (one-third share), at	
		cost	14,835 4 4
Accumulated Funds	416 14 10		30,878 1 10
Bookbinding Account	396 5 4	Current Assets—	
Income Account	813 0 2	Cash in hand	10 0 0
Current Liabilities		Commercial Banking Company of	
		Sydney, Ltd.	271 19 8
			281 19 8
			£31,160 1 6

INCOME ACCOUNT. Year Ended 29th February, 1952.

INCOME ACCOUNT.		EXPENDITURE.	
£	s. d.	£	s. d.
To Balance from 1950-51	19 10	By Subscriptions: 1951-52	343 7 0
" Salaries	425 0 0	Arrears	18 18 0
" Printing Proceedings	726 7 6	In advance	22 1 0
" Printing Reprints	287 1 6		
" Blocks	108 17 10	Entrance Fees	384 6 0
" Insurance	1,122 6 10	Interest	11 11 0
" Postage	21 4 11	Science House	520 6 3
" Petty Cash	64 8 0	" Sales	577 0 0
	32 18 7	" N.S.W. Government Grant	172 0 9
		" Fellowships Account (surplus In-	150 0 0
" Audit	97 6 7	come at 29th February, 1952,	
" Printing and Stationery	13 2 6	transferred)	251 3 1
" Expenses	78 19 2	Bank Expenses	2 15 1
" Cleaning	55 12 6	" Grant towards printing	28 16 10
" Bank Expenses	39 15 0	" Sale of reprints	167 11 1
	2 16 8		
" Transfer to Bookbinding Account ..	190 5 10		
" Balance to 1952-53	12 0 9		
	396 5 4		
	£2,265 10 1		£2,265 10 1

AUDITORS REPORT TO MEMBERS.

I have examined the books of account and vouchers of the Linnean Society of New South Wales for the year ended 29th February, 1952, and certify that the above Balance Sheet and accompanying Income Account are correct and in accordance therewith, and in my opinion present the true state of the Society's affairs at 29th February, 1952, as shown by the books. Certificates of the investments have been inspected.

Sydney, 19th March, 1952.

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

A. E. WALKOM,
Hon. Treasurer.
3rd March, 1952.

LINNEAN SOCIETY OF NEW SOUTH WALES
LINNEAN MACLEAY FELLOWSHIPS ACCOUNT.
BALANCE SHEET at 29th February, 1952.

	£	s.	d.		£	s.	d.
LIABILITIES.				ASSETS.			
Accumulated Funds.				Fixed Assets.			
Amount bequeathed by Sir William Macleay	35,000	0	0	Commonwealth Loans, at cost	30,450	0	0
Surplus Income Capitalized	18,582	11	8	Debentures:			
Current Liability.				Metropolitan Water, Sewerage and Drainage Board, at cost	15,006	14	9
Commercial Banking Company of Sydney, Ltd.	287	9	4	Rural Bank of N.S.W., at cost	2,172	15	0
				Inscribed Stock:			
				Metropolitan Water, Sewerage and Drainage Board, at cost	1,005	0	0
				Loans on Mortgage	4,950	0	0
				Current Assets.			
				Commonwealth Savings Bank		285	11 3
	£53,870	1	0				£53,870 1 0

INCOME ACCOUNT. Year Ended 29th February, 1952.

	£	s.	d.		£	s.	d.
To Salaries of Linnean Macleay Fellows	1,391	13	4	By Interest			
" Research and Field Expenses	95	16	0				1,856 18 11
" Payroll Tax	5	15	10				
" Balance, being Surplus Income transferred to General Account	251	3	1				
" Capital Account	112	10	8				
	£1,856	18	11				£1,856 18 11

AUDITOR'S REPORT TO MEMBERS.

I have examined the books of account and vouchers of the Linnean Society of New South Wales for the year ended 29th February, 1952, and certify that the above Balance Sheet and accompanying Income Account are correct and in accordance therewith, and in my opinion present the true state of the Society's affairs at 29th February, 1952, as shown by the books. Certificates of the investments have been inspected.

S. J. RAYMENT, Chartered Accountant (Aust.),
 Auditor.
 3rd March, 1952.
 A. B. WALKOM,
 Hon. Treasurer.

A CHECK LIST OF THE TROMBICULID LARVAE OF ASIA AND AUSTRALASIA.

By CARL E. M. GUNTHER, M.D., B.S., D.T.M. (Syd.), D.T.M. & H. (Eng.),

*Field Medical Officer, Bulolo Gold Dredging Limited, Bulolo,
Territory of Papua-New Guinea.*

[Read 26th March, 1952.]

Synopsis.

This is an analysis of 332 references in the literature to 177 Trombiculid larvae from Asia and Australasia, including the known and suspected vectors of scrub typhus. The mites are arranged systematically in accordance with the latest opinions expressed in the literature consulted, which runs up till the middle of 1951. Under each species is given a full synonymy, and against each name is set a chronological list of references. Common names, distribution, host and location (where known) of type material are listed.

Class ARACHNIDA.

Order ACARINA.

ACARINIDA Wharton, 1945*b*; Wharton & Hardcastle, 1946 (*laps. cal.*).

Superfamily TROMBIDIOIDEA.

Family TROMBICULIDAE Ewing, 1944.

(EWING, H. E., 1944: *Proc. Biol. Soc. Wash.*, lvii, 101.)

PART I.

THE FAMILY TROMBICULIDAE IN ASIA AND AUSTRALASIA.

My justification for so arbitrarily excluding from this check list those members of the Trombiculidae which do not occur in Asia and Australasia is that, having spent most of my spare time for some years studying mite typhus, which occurs only in those regions, I have not had the need, nor indeed the time, to study those genera and species which occur elsewhere.

In the course of my investigations I amassed a large number of references in the literature of the disease and its vectors. At the same time, for my own convenience, I prepared lists and cross-indices of these references, and it occurred to me that these, enlarged and brought up to date, might be of use to other workers in the same field; the result is this check list. The bibliography is not complete—it could not be—but every reference, however slight, that I have been able to find in the literature, is included. Many of these are of only passing interest, and I have indicated, by putting the authors' names in small capitals, those which I consider to be of greater importance.

I can see nothing to be gained by presenting long lists of the full scientific names of the hosts of the various larvae, and I am sure that the amount of information given with each species is enough for all requirements.

To secure exact information as to the location of type material is not always easy, and during the recent war many places lost their specimens. Only where I am quite sure that type material remains have I put in such information. May I invite museums holding type material not mentioned in this list to send me information about it, so that I may include it in the supplement I hope to issue later?

Work on mites is constantly going on, and there must come a time when a writer has to set a deadline, or his work will never reach publication; I have decided that once I have started the final typing of any Part no further additions or alterations can be included. This may entail some overlapping of current work, the more likely because it often takes months for reprints to reach me here. But so long as any part, whether in its latest systematic placing or not, is as complete and as correct as I can make it at the time of its writing, it will achieve its purpose of serving as a basis for future work.

As for the systematics involved, I have followed with only one deviation the trend of recent work. As I see it, the family Trombiculidae consists of:

TROMBICULINAE Ewing, 1929: As modified and keyed by Wharton *et al.* (1951), but with *Guntherana* (Womersley, 1939), removed (see below).

LEEUWENHOEKIINAE Womersley, 1944: As modified and keyed by Wharton *et al.* (1951). I concur with Ewing (1946a) and later writers in not granting this subfamily the rank of a family as suggested by Womersley in 1945.

WALCHINIINAE Ewing, 1946a: As described by Ewing and amplified by Wharton (1947c).

HEMITROMBICULINAE Ewing, 1946a: I cannot see why Wharton (1947c) excluded this subfamily from the Trombiculidae, if indeed his exclusion was valid, since he did not indicate where else he would place it. That it is completely ignored by Wharton *et al.* in 1951 does not alter the situation.

APOLONIINAE Wharton, 1947c: As keyed by Wharton *et al.* (1951).

GUNTHERANINAE, subfam. nov.: As described in Part II of this list. I have long believed that the genus *Guntherana* is morphologically and biologically quite distinct from the other genera of the family, in that the larva has a caudal plate and the adult cements its eggs to the body hairs of the host, and I now propose to place it in its own subfamily.

PART II.

Subfamily GUNTHERANINAE, subfam. nov.

Type genus, *Guntherana* (Womersley, 1939) Womersley & Heaslip, 1943.

Larva bearing two median dorsal plates; the anterior scutum bearing a pair of sensillae and five scutal setae, the caudal plate possibly divided longitudinally, and bearing usually three pairs of setae. All legs with seven segments; empodium claw-like.

Genus GUNTHERANA (Womersley, 1939) Womersley & Heaslip, 1943.

WOMERSLEY, H., 1939: *Trans. Roy. Soc. S. Aust.*, lxiii, ii, 149; WOMERSLEY, H., & HEASLIP, W. G., 1943: *Ibid.*, lxvii, i, 68.

Guntheria Womersley, 1939 (*nec Güntheria* Bleeker, 1862). Gunther, 1940a.

Guntherana Womersley & Heaslip, 1943. Ewing, 1946a; Lawrence, 1949; Wharton *et al.*, 1951.

Genotype, *Guntherana kallipygos* (Gunther, 1939), Womersley & Heaslip, 1943.

GUNTHERANA KALLIPYGOS (Gunther, 1939) Wharton, 1946.

GUNTER, C. E. M., 1939: *Proc. Linn. Soc. N.S.W.*, lxiv, i-ii, 73; WHARTON, G. W., 1946: *Ecol. Monogr.*, xvi, iii, 151.

Neoschöngastia callipygea Gunther, 1938 (*nom. nud.*).

Neoschöngastia kallipygos Derrick *et al.*, 1939 (*nom. nud.*).

Neoschöngastia kallipygos GUNTHER, 1939a, 1942. Womersley, 1939; Radford, 1942; Wharton *et al.*, 1951.

Neoschöngastia bipygalis GUNTHER, 1939c.

Guntheria kallipygos (Gunther, 1939) Womersley, 1939 (*nom. gen. praeocc.*).

Guntheria bipygalis (Gunther, 1939) Gunther, 1940a, 1940d, 1941a (*nom. gen. praeocc.*). Heaslip, 1941.

Guntherana bipygalis (Gunther, 1939) Womersley & Heaslip, 1943. Blake *et al.*, 1945a; McCulloch, 1946; Radford, 1946b.

Guntherana kallipygos Wharton, 1946b.

Type, *Ovum* (attached to hairs of rat), South Australian Museum.—*Larva*, School of Public Health and Tropical Medicine, University of Sydney.

Paratypes, *Ovum*, S.P.H.T.M., Univ. Syd.—*Larvae*, S. Aust. Mus., Aust. Mus., Brit. Mus., Rocky Mountain Lab., Natal Mus.

New Guinea: Rats (*R. ringens*, *R. browni*, *R. mordax*, *Melomys moncktoni*, *M. stalkeri*, *M. rubex*, *Uromys lamingtonensis*), arboreal "mouse" (*Melomys* sp.), marsupial bandicoots (*Peroryctes raffrayana*, *Echymipera cockerelli*).

Queensland: *R. youngi*, bandicoot (*Isoodon torosus*).

GUNTHERANA PARANA Womersley, 1944.

WOMERSLEY, H., 1944: *Trans. Roy. Soc. S. Aust.*, lxxviii, 1, 82.*Guntherana parana* Womersley, 1944. Blake *et al.*, 1945a; McCulloch, 1946.Type, *Larva*, S. Aust. Mus.New Guinea: Marsupial bandicoot (*Echymipera cockerelli*), free on boots.

PART III.

SUBFAMILY TROMBICULINAE Ewing, 1929.

Ewing, H. E., 1929: *A Manual of External Parasites*, London.Type genus, *Trombicula* Berlese, 1905.TROMBICULINAE EWING, 1929 (*partim*). THOR, 1935, 1936; WOMERSLEY, 1937, 1944;Griffiths, 1945; EWING, 1931, 1938, 1944a, 1944b, 1946a; Michener, 1946b; WHARTON, 1947c; Thor & Willmann, 1947; Fuller, 1948; Lawrence, 1949; WHARTON *et al.*, 1951.TROMBICULININAE Anderson & Wing, 1945 (*laps. cal.*).Following Wharton *et al.*, 1951, this subfamily consists of sixteen genera, only ten of which (marked *) appear in this check list:**Trombicula* Berlese, 1905 (Type, *T. minor* Berlese, 1905).*Dolopsis* Oudemans, 1910 (Type, *D. symoti* Oudemans, 1910).**Schöngastia* Oudemans, 1910 (Type, *Thrombidium vandersandei* Oudemans, 1905).*Reidlinea* Oudemans, 1914 (Type, *R. coeca* Oudemans, 1914).**Neoschöngastia* Ewing, 1929 (Type, *Schöngastia americana* Hirst, 1921).*Endotrombicula* Ewing, 1931 (Type, *E. penetrans* Ewing, 1931).*Euschöngastia* Ewing, 1938 (Type, *Schöngastia sciuricola* Ewing, 1925 = *E. americana* Ewing, 1938).**Myotrombicula* Womersley & Heaslip, 1943 (Type, *M. vespertilionis* Womersley & Heaslip, 1943).**Heastipia* Ewing, 1944 (Type, *Trombiculoides gateri* Womersley & Heaslip, 1943).**Ascoschöngastia* Ewing, 1946 (Type, *Neoschöngastia malayensis* Gater, 1932).**Oenoschöngastia* Womersley & Kohls, 1947 (Type, *O. cana* Womersley & Kohls, 1947).**Novotrombicula* Womersley & Kohls, 1947 (Type, *N. owiensis* Womersley & Kohls, 1947).*Tecomatlana* Hoffmann, 1947 (Type, *T. sandovali* Hoffmann, 1947).*Sauriscus* Lawrence, 1949 (Type, *S. ewingi* Lawrence, 1949).**Mackienia* Traub & Evans, 1950 (Type, *M. empodiformia* Traub & Evans, 1950).**Trisetica* Traub & Evans, 1950 (Type, *T. melvini* Traub & Evans, 1950).Of these, both *Trombicula* and *Endotrombicula* have acquired subgenera.

PART IV.

GENUS TROMBICULA Berlese, 1905 (*sensu lato*).BERLESE, A., 1905: *Redia*, ii, ii, 155.Genotype, *Trombicula minor* Berlese, 1905 (*loc. cit. supra*).

There are five major difficulties facing the student of this genus:

(i) The genotypic material no longer exists.

(ii) Recent work by Brennan & Wharton (1950) and Wharton *et al.* (1951) has necessitated the introduction of subgenera, and it looks as if it will take some years to review the Asian and Australasian species and assign them to their places among the subgenera.(iii) The great confusion which has existed in the synonymies of *T. minor*, *T. hirsti*, and *T. mediocris* has only just been cleared up (Gunther, 1951)—and now, on top of that, certain authorities have stated that *T. hirsti* is synonymous with *T. wichmanni*.

(iv) The work of Philip (1947b) has shown that very many of our conceptions regarding the Japanese species have been entirely wrong.

(v) Philip & Kohls (1948) flatly reduced *T. deliensis* to the status of a variety of *T. akamushi*.

Most of these points are dealt with in Parts V to VIII, but the new subgenera must be dealt with here, as well as in their various Parts. In 1950 Brennan & Wharton

erected the subgenus *Neotrombicula* and resurrected *Trägårdhula* Berlese, 1912, while Kuwata *et al.* described *Trombicula* (*Leptotrombidium*) *fuji*; in 1951 Wharton *et al.* give a key to six subgenera of *Trombicula*:

Blankaartia Oudemans, 1911 (Type, *Trombidium nitoticum* Trägårdh, 1905).

Leptotrombidium Nagayo *et al.*, 1916a (Type, *Trombidium akamushi* Brumpt, 1910).

Neotrombicula Hirst, 1925 (Type, *Acarus autumnalis* Shaw, 1790).

Eutrombicula Ewing, 1938 (Type, *Microtrombidium alfreddugési* Oudemans, 1910).

Fonsecia Radford, 1946 (Type, *Trombicula ewingi* Fonseca, 1932).

Trombiculindus Radford, 1948 (Type, *T. squamosus* Radford, 1948).

Trägårdhula, along with *Pentagonella* Thor and *Megatrombicula* Michener, they regard as included in *Blankaartia*. Moreover, they leave two lines in their key for "*Trombicula sensu lato* (Species for which no subgenera have been proposed)". Since, except for *T. akamushi*, *T. fuji*, *Trombiculindus squamosus*, and *Fonsecia coluberina*, none of the species with which this list is concerned can be allotted to subgenera, I propose to treat *Trombicula* here only *sensu lato*, listing the subgenera in their former places as synonyms, including with them their subgeneric references.

In subsequent Parts, I have grouped the various species, ignoring chronological order, in a way that will enable the difficulties listed above to be more easily grappled with. An index of synonyms will form a later Part, so that any name can easily be found when needed.

Genus TROMBICULA (*s.l.*).

Microtrombidium Haller, 1882 (*partim*). Oudemans, 1909, 1910b, 1912b; Hirst, 1915a, 1915b, 1925a; von Goosmann, 1917; Miyajima & Okumura, 1917a, 1917b; Ewing, 1920; Warburton, 1928; Vitzthum, 1929; Brumpt, 1949.

Trombidium BERLESE, 1888 (*nec* *Trombidium Fabricius*, 1775). Oudemans, 1905, 1906; Nagayo *et al.*, 1915e, 1915f, 1916, 1917a, 1917b; Banks, 1915; Miyajima & Okumura, 1917a, 1917b; Kitashima & Miyajima, 1918b; Kawamura, 1926; Walch, 1927; Warburton, 1928; Vitzthum, 1929; Blake *et al.*, 1945c; Thor & Willmann, 1947; FULLER, 1949.

Thrombidium Brumpt, 1910, 1949. Oudemans, 1912a, 1912b; Kishida, 1917.

Trombicula Berlese, 1905, 1912. Oudemans, 1910c, 1928; Banks, 1915; Miyajima, 1917; Nagayo *et al.*, 1918, 1919, 1920a, 1920b, 1920c, 1921; Tanaka, Hatori, 1919; EWING, 1920, 1925, 1926, 1928, 1929, 1938, 1942, 1946a; Hirst, 1925b, 1926; Walch, Sambon, 1927; Warburton, 1928; Vitzthum, Patton & Evans, 1929; Gater, 1932; Thor, 1935, 1936; Fonseca, 1936; Womersley, 1937, 1939; Gunther, 1941c; Griffiths, 1945; Wharton, 1946a, 1947b; MICHENER, 1946b, 1946c, 1946d; Thor & Willmann, 1947; PHILIP, 1947b; Lawrence, Jenkins, 1949; Richards, PHILIP & FULLER, BRENNAN & WHARTON, 1950; WHARTON *et al.*, 1951.

Thrombicula André, 1928, 1932. Brumpt, 1949.

Blankaartia Oudemans, 1911. WOMERSLEY, 1937; WHARTON *et al.*, 1951.

Subgenus *Blankaartia* (Oudemans, 1911) Wharton *et al.*, 1951 (= *Trägårdhula* Berlese, 1912 = *Pentagonella* Thor., 1936 = *Megatrombicula* Michener, 1946).

Subgenus *Trägårdhula* Berlese, 1912. BRENNAN & WHARTON, 1950; WHARTON *et al.*, 1951.

Kedania Kishida, 1909 (?), 1917. KAWAMURA, 1926; Kaiwa *et al.*, 1929; Tanaka *et al.*, 1930; Gater, 1932; PHILIP, 1947a, 1947b; PHILIP & KOHLS, 1948; PHILIP & FULLER, 1950.

Leptotrombidium NAGAYO *et al.*, 1917a, 1918. KAWAMURA, 1926; Ewing, 1942; PHILIP, 1947b; KUWATA *et al.*, 1950; WHARTON *et al.*, 1951.

Subgenus *Leptotrombidium* KUWATA *et al.*, 1950.

Subgenus *Leptotrombidium* (Nagayo *et al.*, 1916) WHARTON *et al.*, 1951.

Neotrombicula Hirst, 1925b, 1926. EWING, 1929, 1946a; Womersley, 1937; Lawrence, 1949; Philip & Fuller, BRENNAN & WHARTON, 1950; WHARTON *et al.*, 1951.

Subgenus *Neotrombicula* BRENNAN & WHARTON, 1950 (= *Eutrombicula* Ewing, 1938).

Subgenus *Neotrombicula* WHARTON *et al.*, 1951.

- Pentagonella* Thor, 1936. Womersley & Heaslip, 1943; EWING, 1946a; Thor & Willmann, 1947; Lawrence, 1949; BRENNAN & WHARTON, 1950; WHARTON *et al.*, 1951.
- Eutrombicula* EWING, 1938, 1942, 1943, 1944a, 1946a. Radford, 1942; Womersley & Heaslip, 1943; MICHENER, 1946a, 1946c; Philip & Woodward, 1946b; Thor & Willmann, 1947; Fuller, 1947b; WHARTON, 1947b; Womersley & Kohls, 1947; Lawrence, Jenkins, 1949; BRENNAN & WHARTON, 1950; WHARTON *et al.*, 1951.
- Subgenus *Eutrombicula* Thor & Willmann, 1947. Fuller, 1948; Jenkins, 1949; WHARTON *et al.*, 1951.
- Fonsecia* Radford, 1942, 1946c. Womersley & Heaslip, 1943; Ewing, 1944a, 1944b; Sayers *et al.*, 1947; Lawrence, 1949.
- Fonsecia* Radford, 1946. WHARTON *et al.*, 1951.
- Subgenus *Fonsecia* WHARTON *et al.*, 1951.
- Acariscus* EWING, 1943, 1944a. WOMERSLEY, 1944; WHARTON, 1945b, 1947b; MICHENER, 1946a, 1946c; Philip & Woodward, 1946b; Lawrence, 1949.
- Crotiscus* Ewing, 1944a. Lawrence, 1949; WHARTON *et al.*, 1951.
- Megatrombicula* MICHENER, 1946b, 1946d. Lawrence, 1949; BRENNAN & WHARTON, 1950; WHARTON *et al.*, 1951.
- Trombiculindus* Radford, 1948. WHARTON *et al.*, 1951.
- Subgenus *Trombiculindus* WHARTON *et al.*, 1951.
- Leptotrombicula* Manson-Bahr, 1948.
- (*non*) *Leptus* Latreille, 1804. Miyajima & Okumura, 1917b; Nagayo *et al.*, 1917b; Miyajima, 1917; Okumura, 1918; Kitashima & Miyajima, 1918b; Tanaka, 1918, 1919; Kawamura, 1926; Warburton, 1928; Kaiwa *et al.*, 1929; Gater, 1932; Blake *et al.*, 1945a; PHILIP, 1947b.
- (*non*) *Trombicula* Berlese, 1905. André, 1929.

PART V.

TROMBICULA MINOR, T. MEDIOCRIS, & T. HIRSTI.

The type and paratype of *T. minor* Berlese, 1905, have been destroyed, and the procuring of a neotype is likely to be difficult. The site where a topotype must be searched for is not only very limited in extent but is also difficult of access (certain caves at Tjompea in Java); moreover, the available data on which to base a neotype are not very comprehensive or detailed. All this is dealt with in my paper: "On *Trombicula minor* Berlese, 1905" (1951).

In 1939 I bred the nymph of *T. hirsti* var. *buloloensis* (*mihi*), and Womersley identified it with *T. minor* and with *T. hirsti* Sambon, 1927. I concurred in this, and in 1940 worked out the logical synonymy of *T. minor* based on these premises. Then in the Pacific War years, when the vectors of mite typhus were subjected to widespread intensive research, there arose two schools of thought, one accepting that *T. minor* and *T. hirsti* were synonymous, the other remaining unconvinced. In 1950 I consulted Herr Carl Willmann (the only living man who has seen and studied the genotype), and he confirmed that *T. hirsti* was not *T. minor*. But meanwhile both views had been widely adopted in the literature, and it is safe to assume that since 1942 any mention of "*T. minor*", unless specifically designated as referring to the genotype, should be read as "*T. hirsti*".

But that is not all—from 1946 on, there has been an increasing number of opinions that *T. hirsti* is synonymous with *T. wichmanni* (Oudemans, 1905). I cannot concede their complete identity, and am convinced that they are divisible at least into distinct subgenera. This will be discussed in Part VI; meanwhile I am listing them as distinct species.

TROMBICULA MINOR Berlese, 1905.

BERLESE, A., 1905. *Redia*, ii, ii, 155.

Trombicula minor Berlese, 1905, 1912. EWING, 1920, 1938, 1942, 1944; WILLMANN, 1941; Womersley, 1944; Thor & Willmann, 1947; PHILIP, 1947b; Jenkins, 1949; GUNTHER, WHARTON *et al.*, 1951.

Trombicula minor Brumpt, 1949.

Trombicula minor Berlese, 1904. Gunther, 1939b, 1940c; Womersley, 1939.

(non) *Trombicula minor* Berlese, 1904 (= *T. hirsti* Sambon, 1927). Heaslip, 1941; Womersley & Heaslip, 1943; Finnegan, 1945.

(non) *Trombicula minor* Berlese, 1905 (= *T. hirsti* Sambon, 1927). Gunther, 1939b, 1940a, 1940c, 1940d, 1941c, 1942; Womersley, 1939, 1944; Manson-Bahr, 1940; Ewing, 1942, 1944b; Ahlm & Lipshutz, Williams, Cook, 1944; McCulloch, 1944, 1946, 1947; Blake *et al.*, 1945a; Fischbach & Howell, 1945; Dumbleton, Fenner, H.M. Stat. Off., 1946; Philip & Woodward, 1946b; Fuller, 1947b; Philip & Kohls, Kohls, 1948; Philip & Traub, 1950.

(non) *Trombicula wichmanni* (Oudemans, 1905). McCulloch, 1946; Fuller, 1947b; Philip & Kohls, Kohls, 1948; Audy & Harrison, 1950.

(non) *Trombicula mediocris* Berlese, 1912. GUNTER, 1940c, 1941c; Womersley & Heaslip, 1943.

(non) *Trombicula pseudoakamushi* Hatori, 1919 (= *T. hirsti* Sambon, 1927, *nec T. pseudoakamushi* Kaiwa *et al.*, 1929, *non* Tanaka *et al.*, 1930, *non* 1916). Gunther, 1940c, 1941c; Fuller, 1947b.

(non) *Trombicula pseudoakamushi* (variatio *deliensis*) Walch, 1924a. Gunther, 1940c, 1941c; Womersley & Heaslip, 1943; Womersley, 1944.

(non) *Trombicula pseudoakamushi* (variatio *deliensis* ?) Walch, 1925. Gunther, 1940c.

(non) *Trombicula hirsti* Sambon, 1927. Womersley, 1939; Gunther, 1940c; Heaslip, 1941; Ewing, 1942, 1944c; Womersley & Heaslip, 1943; Womersley, 1944; Dumbleton, 1946.

(non) *Trombicula hirsti* var. *morobensis* Gunther, 1938. Gunther, 1939b, 1940c; Womersley & Heaslip, 1943; Womersley, 1944.

(non) *Trombicula hirsti* var. *buloloensis* Gunther, 1939a, 1939b, 1940a, 1940c, 1940d, 1942. Womersley, 1939, 1944; Ewing, Radford, 1942; Womersley & Heaslip, 1943; Blake *et al.*, 1945a.

(non) *Trombicula buloloensis* (Gunther, 1939) Blake *et al.*, 1945a. Philip & Woodward, 1946b; Fuller, 1947b; Kohls, Philip & Kohls, 1948.

(non) *Trombicula minor* var. *deliensis* (Walch, 1923) Womersley & Heaslip, 1943. Womersley, 1944; Dumbleton, 1946.

(non) *Trombicula hatorii* Womersley & Heaslip, 1943.

(non) *Schongastia minor* (? = *T. hirsti* Sambon, 1927) U.S. War Dept., 1944.

(non) *Neoschongastia minor* (? = *T. hirsti* Sambon, 1927) Bull. U.S. Army Med. Dept., 1944.

(non) *Trombicula minor* (Willmann, 1941) (? = *T. hirsti* Sambon, 1927), No. 2 E.F.U. 1945.

Type and Paratype, *Adults*: Formerly at Hamburg Museum, but destroyed, 1943 (Gunther, 1951).

Java: ? bats (original specimens sifted from guano in cave at Tjompea).

TROMBICULA MEDIOCRIS Berlese, 1912.

BERLESE, A., 1912. *Redia*, viii, i, 1.

Trombicula mediocris BERLESE, 1912. Miyajima, 1917; Hatori, 1920; Kawamura *et al.*, 1921; Walch, 1923; Gater, 1932; GUNTER, 1940c, 1941c, 1951; Womersley & Heaslip, 1943; Thor & Willmann, 1947.

Trombicula mediocris (J. de Vidas, 1945) Brumpt, 1949.

(non) *Trombicula minor* Berlese, 1905 (= *T. hirsti* Sambon, 1927). Gunther, 1940c, 1941c; Womersley & Heaslip, 1943.

(non) *Trombicula pseudoakamushi* Hatori, 1919. Miyajima, 1917.

Type: Adult.

Java: Taken free at Buitenzorg.

TROMBICULA HIRSTI Sambon, 1927.

SAMBON, L. W., 1927: *Ann. Mag. Nat. Hist.*, ix, xx, 157.

Trombicula hirsti SAMBON, 1927 (*nec* *T. hirsti* Hirst, 1929). Ewing, 1928, 1942; Patton & Evans, 1929; Gater, Matheson, 1932; WOMERSLEY, 1939, 1944; GUNTHER, 1939a, 1940a, 1940c, 1940d, 1942, 1951; Heaslip, 1941; Radford, 1942; Womersley & Heaslip, 1943; Farner & Katsampes, Williams, Cilento, 1944; Hayakawa Tanaka *et al.*, Hayakawa & Muro, Finnegan, No. 2 E.F.U., 1945; Dumbleton, Roy, 1946; PHILIP & WOODWARD, 1946b; Thor & Willmann, Hayakawa & Hokari, 1947; Chandler, 1949.

Trombicula hirsti Brumpt, 1949.

Trombicula hirsti (Gater, 1932) Blake *et al.*, 1945a.

Eutrombicula hirsti Philip & Woodward, 1946b.

Trombicula minor Berlese, 1904. Gunther, 1939b, 1940c; Womersley, 1939; Heaslip, 1941; Womersley & Heaslip, 1943; Finnegan, 1945.

Trombicula minor Berlese, 1905. Gunther, 1940a, 1940d, 1941c, 1942; Manson-Bahr, 1940; Ewing, 1942, 1944b; Ahlm & Lipshutz, Womersley, Williams, Cook, 1944; McCulloch, 1944, 1946, 1947; Blake *et al.*, 1945a; Fischbach & Howell, 1945; Dumbleton, Fenner, H.M. Stat. Off., 1946; Philip & Woodward, 1946b; Fuller, 1947b; PHILIP & KOHLS, Kohls, 1948; Philip & Traub, 1950.

Trombicula minor (Willmann, 1941) No. 2 E.F.U., 1945.

(?) *Schongastia minor* U.S. War Dept., 1944.

(?) *Neoschongastia minor* Bull. U.S. Army Med. Dept., 1944.

Trombicula hirsti var. *morobensis* Gunther, 1938, 1939a, 1939b, 1940c, 1951 (*nom. nud.*). Womersley & Heaslip, 1943; Womersley, Farner & Katsampes, 1944.

Trombicula hirsti var. *bulotoensis* GUNTHER, 1939a, 1939b, 1940c, 1940d, 1942, 1951. Womersley, 1939, 1944; EWING, 1942, 1944c; Womersley & Heaslip, 1943; Radford, 1946b.

Trombicula hirsti var. *boloensis* Farner & Katsampes, 1944 (*laps. cal.*).

Trombicula bulotoensis (Gunther, 1939) Blake *et al.*, 1945a. Kohls *et al.*, 1945; McCulloch, 1946; Bushland, 1946a, 1946b; Philip & Woodward, 1946b; Griffiths, 1947; Fuller, 1947b; Kohls, Philip & Kohls, 1948.

Trombidium bulotoensis Blake *et al.*, 1945c.

Eutrombicula bulotoensis (Gunther, 1939) Wharton, 1946a.

(*non*) *Trombicula hirsti* Sambon, 1927 (= *T. hirsti* Hirst, 1929 = *T. samboni* Womersley, 1939). Hirst, 1929a, 1929c, 1929d; Womersley, 1934, 1936, 1937.

(*non*) *Trombicula minor* Berlese, 1905. Gunther, 1940c.

(*non*) *Trombicula wichmanni* (Oudemans, 1905). McCulloch, 1946; Fuller, 1947b; Philip & Kohls, Kohls, 1948; Audy & Harrison, 1950 (= *T. minor* Berlese, 1905 [= *T. hirsti* Sambon, 1927]); McCulloch, 1946; Griffiths, 1947 (= *T. bulotoensis* Gunther, 1939); McCulloch, 1946 (= *T. minor* var. *deliensis* Walch, 1923).

Scrub-itch mite (Australia: Jackson, 1908); *tungau* (Malaya: Patton & Evans, 1929); *bush-mokka*, *pipi*, *gugung* (New Guinea: Gunther, 1939a); *sanana*, *tigali*, *dedigalogala* (Papua: Gunther, 1939a).

Types, Larva: British Museum. Nymph: S. Aust. Museum.

Paratype, Nymph: School Pub. Health Trop. Med., Univ. Sydney.

Hypotypes, Larvae: Brit. Mus.; S.P.H.T.M., Univ. Sydney; Aust. Mus.; S. Aust. Mus.; Natal Mus.; Rocky Mountain Lab.; Univ. Calif.; Liverpool School Trop. Med.; Tulane Univ.; P.H.D., Brisbane; Hosp. Generale, Mexico City; coll. van Eyndhoven; coll. Rosas Costa.

Queensland, Malaya, New Guinea: Man.

Queensland: Possum (*Trichosurus johnstoni*), bandicoots (*Perameles nasuta*, *Isoodon obesulus*, *I. torosus*), free on boots.

Malaya: Rats (*R. jalorensis*, *R. diardi*), shrew (*Tupaia ferruginea*), *Gallus gallus*.

New Guinea: Pig (*Sus papuensis*), wallaby, rat (*R. gestri*), bandicoot (*Echymipera cockerelli*), ground birds (*Megapodius reinwardt*, *Talegalla jobiensis*, *Gallicolumba jobiensis*, *Casuarus casuarinus*), swamp birds (*Amaurornis nigrifrons*, *Porphyrio melanotus*), catbird (*Ailuroedus melanocephalus*), pitta (*P. mackloti*), free on boots.

Celebes: Rat.

PART VI.

TROMBICULA WICHMANNI & T. HAKEI.

The following authorities have given, in effect, their opinion that *T. hirsti* Sambon, 1927, is synonymous with *T. wichmanni* (Oudemans, 1905), in that they have affirmed the identity of *T. wichmanni* with various synonyms of *T. hirsti*:

FULLER, 1947*b*; KOHLS, 1948; PHILIP & KOHLS, 1948; Audy & Harrison, 1950: *T. wichmanni* = *T. minor* (= *T. hirsti*).

McCulloch, 1946: *T. wichmanni* = *T. minor* var. *deliensis* (= *T. hirsti*).

McCulloch, 1946; Griffiths, 1947: *T. wichmanni* = *T. buloloensis* (= *T. hirsti*).

It must be pointed out, however, that all of these opinions were given before the practical possibilities of developing suitable subgenera of the Trombiculæ had been fully examined. I am reasonably familiar with both *T. wichmanni* and *T. hirsti*, and I am not convinced that there is no definable demarcation, at least at subgeneric level, between them; at any rate, I am listing them here as distinct species.

T. hakei is included in this Part because it has been suggested that it is synonymous with *T. wichmanni*.

TROMBICULA WICHMANNI (Oudemans, 1905) Hirst, 1917.

OUDEMANS, A. C., 1905: *Ent. Ber. Ned. Ent. Ver.*, i, xxii, 216; HIRST, S., 1917: *Brit. Mus. (Nat. Hist.) Econ. Ser.*, vi.

Trombidium wichmanni Oudemans, 1905, 1906, 1909 (*nom. gen. praeocc.*). Fantham *et al.*, 1916; Matheson, 1932; Gunther, 1941*c*.

Allotrombidium wichmanni Oudemans, 1906. Womersley & Heaslip, 1943.

Trombidium (Heterotrombidium) wichmanni Verdun, 1909. Womersley & Heaslip, 1943.

Microtrombidium wichmanni Oudemans, 1912*a*. Ewing & Hartzell, 1918; Warburton, 1928; Manson-Bahr, 1929; Gunther, 1941*c*; Womersley & Heaslip, 1943; Brumpt, 1949.

Trombicula wichmanni HIRST, 1917. Oudemans, 1912*b*, 1913, 1916; Walch, 1923, 1924*a*; Sambon, 1927; Patton & Evans, 1929; Gater, 1930; Gunther, 1939*a*, 1940*a*, 1940*b*, 1940*d*, 1941*c*, 1942, 1951; Womersley, 1939, 1944; Radford, 1942; Womersley & Heaslip, 1943; Finnegan, 1945; Philip *et al.*, McCulloch, 1946; Philip & Woodward, 1946*b*; Ewing, 1946*a*; Thor & Willmann, Griffiths, 1947; Philip & Kohls, Kohls, 1948; Chandler, 1949; Audy & Harrison, 1950; Wharton *et al.*, 1951.

Eutrombicula wichmanni Ewing, 1938. Sayers *et al.*, 1945; Philip & Woodward, 1946*b*; Fuller, 1947*b*; Philip, 1947*b*; Philip & Fuller, 1950.

(*non*) *Trombicula minor* (= *T. hirsti* Sambon, 1927). Fuller, 1947*b*; Philip & Kohls, Kohls, 1948; Audy & Harrison, 1950.

(*non*) *Trombicula buloloensis* (Gunther, 1939): McCulloch, 1946; Griffiths, 1947.

(*non*) *Trombicula hatorii* Womersley & Heaslip, 1943; Philip, 1947*b*; Philip & Fuller, 1950.

(*non*) *Trombicula minor* var. *deliensis*: McCulloch, 1946.

Gonone (Celebes: Oudemans, 1906).

Type, Larva.

Hypotypes, Larvae: School Pub. Health Trop. Med., Univ. Sydney; British Museum; Aust. Mus.; S. Aust. Mus.

Celebes, Philippine Is.: Man.

British North Borneo: Mouse deer (*Tragulus borneanus*).

Philippine Is.: Rats (*R. mindanensis*, *R. calcis*).

Dutch New Guinea: Goura pigeon (*Goura scheepmakeri*).

Brunei, Balikpapan, Morotai, New Guinea: Free.

TROMBICULA HAKEI Radford, 1946.

RADFORD, C. D., 1946: *Proc. Zool. Soc. Lond.*, cxvii, ii, 247.

Trombicula hakei Radford, 1946*c*.

(*non*) *Trombicula wichmanni* (Oudemans, 1905). Fuller, *vide* Sayers *et al.*, 1947.

Type, Larva: British Museum.

Imphal (India): Snake (*Coluber radiatus*), cobra (*Naia fasciatus*).

PART VII.

THE JAPANESE & FORMOSAN TROMBICULAE, & T. OBSCURA.

That nearly all of the very important work by the Japanese is in their own language, and is therefore quite inaccessible to occidental workers, has led to many misconceptions. When Dr. C. B. Philip of the Rocky Mountain Laboratory had the various Japanese papers translated, he made many surprising discoveries (Philip, 1947b). I am deeply indebted to him for giving me access to these translations.

In the first place, it is obvious that papers on mite systematics did not reach Japan until 1915, and did not reach the majority of workers until 1917. Previous to then, the Japanese called the vector of mite typhus (and sometimes some of its allies) "the akamushi" (= red mite); various other species came to be called "the pseudoakamushi"—the Tanaka school applied this name to those species more closely allied to akamushi, whereas Hatori applied it to the Japanese harvest mite.

Nagayo and his varying associates were the leaders in adopting conventional nomenclature (Nagayo *et al.*, 1915c: "*Trombidium* and the Akamushi"). Then, in 1917, they devised *Leptotrombidium* because *Trombidium* Berlese, 1888, used by Brumpt for *T. akamushi*, was preoccupied by *Trombidium* Fabricius, 1775—hence also *Microtrombidium akamushi* Hirst, 1915a and *Leptus akamushi* Miyajima & Okumura, 1917b; but as soon as they had the opportunity of comparing their nymphs and adults with Berlese's *Trombicula minor*, it became obvious that *Trombicula* had priority, and so in Nagayo *et al.*, 1918, we find *Trombicula akamushi*, and in 1919, *T. akamushi akamushi*, *T. akamushi* nov. var. *pallida*, and *T. palpalis* nov. sp.; in 1920 they added *T. intermedia* (1920b) and *T. scutellaris* (1920c).

Meanwhile, in 1917, Miyajima identified the pseudoakamushi (= harvest mite) first as *Leptus autumnalis* and later as *Trombicula mediocris* (both refuted by Hatori in 1920); Kishida stated that in 1909 he had used "Kedania tanakai" for *Thrombidium akamushi* Brumpt, 1910; Nagayo *et al.* introduced "the tsutsugamushi" as a substitute for the akamushi, which had acquired a more special application; and Miyajima & Okumura classified the akamushi into "thin-haired" and "coarse-haired" types (to which Kawamura *et al.* later added an "intermediate" type).

Kawamura *et al.* in 1920 made another classification of the akamushi and its allies, into Types A, B, C, and D (and later, Type E, in Kawamura, 1926). Meanwhile, in 1918, Tanaka gave a definite description of the pseudoakamushi (= one of the allies of the akamushi, not the harvest mite).

It is an important point that no mention of *Trombicula pseudoakamushi* as such is to be found until Hatori, 1919, or of *Trombicula autumnalis japonica* until Kaiwa *et al.*, 1929; until these dates, the names used by all writers (including Tanaka) were "the pseudoakamushi" and "the Japanese *Trombicula autumnalis*".

In 1921 Nagayo *et al.* correlated the 1917-1920 work, and gave their list of "the kinds of the tsutsugamushi":

Trombicula akamushi: Type A, thin-haired.

T. pallida: Type D, coarse-haired, equivalent to Tanaka's pseudoakamushi.

T. palpalis: Type C.

T. intermedia.

T. scutellaris: Type B.

In 1929 Kaiwa *et al.* described "*T. pseudoakamushi* A and B" (not the harvest mite), and stated that "A" was equivalent to *T. pallida* and "B" to *T. palparis* (*sic*); they also stated that *T. akamushi* was equivalent to "*Kedania tanakai* Kishida, 1909", and that *T. autumnalis japonica* was *Leptus autumnalis japonica*. Tanaka *et al.*, 1930, use these same names, but claim that Tanaka used *T. pseudoakamushi* in 1916.

As for the pseudoakamushi (= harvest mite), Hatori described it under the name *Trombicula pseudoakamushi* in 1919, but claimed (1920) that he had used that name in 1917.

From all of this there emerge three problematical names: *Kedania tanakai* Kishida, 1909; *T. pseudoakamushi* Tanaka, 1916; and *T. pseudoakamushi* Hatori, 1917. Nobody has so far been able to locate the publications in which these names, actually so written,

at the dates claimed for them, are alleged to have appeared. As far as actual records go, the name *Kedania tanakai* appears to have been first used by Kishida in 1917, and so it must at the present time be regarded as a synonym of *T. akamushi* (Brumpt, 1910). Similarly, there exists no evidence that *Trombicula pseudoakamushi* was used before Hatori in 1919 (for the Japanese harvest mite); certainly in none of Tanaka's available papers does he use the name until 1930, while it was previously used by Kaiwa *et al.* in 1929—they stated that it was equal to *T. pallida* (Nagayo *et al.*, 1919). Consequently we can no longer accept *T. pseudoakamushi* Tanaka, 1916, as the prior name, with *T. pallida* as a synonym—*T. pallida* has precedence, and *T. pseudoakamushi* of Tanaka and of Kaiwa *et al.* becomes a synonym of *T. pallida*.

This leaves *T. pseudoakamushi* Hatori, 1919, with precedence—it had drifted uncertainly about in limbo for years until Womersley & Heaslip rescued it in 1943 and labelled it *T. hatorii*. There is no record to be found of Hatori's having used this actual name in 1917, and we must accept its date as 1919. Still, there is another difficulty about this species: there is a lot of indirect evidence that *T. hirsti* Sambon, 1927, and *T. pseudoakamushi* are identical. Theoretically this is almost certainly so—but I am not aware that anybody has as yet compared actual specimens. If it were so, then *T. pseudoakamushi* would take precedence; but I am listing them separately here until further studies have been made.

Another point about the Japanese mites is that Ewing (1925) stated that probably *T. pallida*, *T. palpalis*, *T. intermedia*, and *T. scutellaris* were only seasonal variations of *T. akamushi*. In 1940 my teacher and very good friend, the late Frank H. Taylor, to whom I was indebted for much valuable help and advice, collected all the authenticated specimens in Australia and sent them to me for examination; in my opinion these are all valid and distinct species.

I have grouped the Japanese and Formosan Trombiculae together in this Part for convenience, and have added *T. obscura* Womersley, 1944, since it seems almost certainly doomed to become a synonym of *T. akamushi*.

TROMBICULA AKAMUSHI (Brumpt, 1910) Hirst, 1917.

BRUMPT, E., 1910: Précis de Parasitologie, 2 Ed., Paris, 506; HIRST, S., 1917: Brit. Mus. (Nat. Hist.) Econ. Ser., vi.

Trombidium akamushi Brumpt, 1910, 1949 (*nom. gen. praeocc.*). Fantham *et al.*, 1916; Kishida, 1917.

Trombidium akamushi Brumpt, 1910: Nagayo *et al.*, 1915e, 1915f, 1916b, 1917a; Miyajima & Okumura, 1917a, 1917b.

Microtrombidium akamushi Hirst, 1915a, 1915b. Miyajima & Okumura, 1917b; Warburton, 1928; Gater, 1932; Gunther, 1939b; Manson-Bahr, 1948.

Kedania tanakai Kishida, 1909 (?), 1917. Kawamura, 1926; Kaiwa *et al.*, 1929; Tanaka *et al.*, 1930; PHILIP, 1947b; PHILIP & KOHLS, 1948.

Microtrombidium brumpti Hirst, 1915a (*laps. mem.*). Ewing, 1920; Gater, 1932.

Leptotrombidium akamushi Nagayo *et al.*, 1917a. Kawamura, 1926; Gater, 1932; Ewing, 1942; PHILIP, 1947b.

Leptotrombicula akamushi Manson-Bahr, 1948.

Leptus akamushi Miyajima & Okumura, 1917b (*nom. gen. praeocc.*).

Trombicula akamushi Hirst, 1917, 1929a. Nagayo *et al.*, 1918, 1919, 1920a, 1920b, 1920c, 1921; Hayashi *et al.*, 1918; Hatori, 1919; Kawamura *et al.*, 1920a, 1920b, 1921; Kawamura & Yamaguchi, 1921; Walch, 1922a, 1923, 1924a; Walch & Keukenschrijver, 1924; Ewing, 1925, 1928, 1929, 1937, 1942, 1944a, 1944b, 1944c; KAWAMURA, 1926; Sambon, 1927; Fletcher *et al.*, Warburton, 1928; Fletcher & Field, Stitt, Patton & Evans, Kaiwa *et al.*, 1929; Manson-Bahr, 1929, 1940, 1948; Tanaka *et al.*, 1930; Lewthwaite, 1930, 1945a, 1945b; GATER, 1930, 1932; Patton, 1931; Matheson, Fonseca, 1932; Lewthwaite & Savoore, 1936a, 1936b, 1936c, 1936d, 1940; Chandler, 1936, 1949; Kawamura & Ikeda, 1936; Mühlens *et al.*, Sugimoto, Riley & Johansen, 1938; Gunther, 1939a, 1940a, 1940d, 1942; Kawamura & Yamamiya, Herms, 1939; Heaslip, Poynton, 1941; Morishta, Culbertson, 1942; Radford, 1942, 1946a; Womersley &

Heaslip, 1943; Banerjea & Bhattacharya, 1943, 1945; Ahlm & Lipshutz, Farnier & Katsampes, Williams, Nauss, Strong, Cook, Bercovitz, Logue, Bull. U.S. Army Med. Dept., Womersley, Cilento, Kouwenaar & Wolff, 1944; U.S. War Dept., 1944, 1948; Rogers & Megaw, 1944, 1946; Fischbach & Howell, Craig & Faust, Tidy, Finnegan, No. 2 E.F.U., Megaw, Anderson & Wing, 1945; Mackie *et al.*, 1945, 1946; BLAKE *et al.*, 1945a, 1945c; Philip & Kohls, 1945, 1948; Philip & Tamiya, Farnier, Wharton & Carver, Johnson & Wharton, H.M. Stat. Off., McCulloch, Roy, 1946; Philip *et al.*, 1946, 1949; Wharton, 1946a, 1946b, 1947b; Philip & Woodward, 1946b; Thor & Willmann, Sayers *et al.*, Griffiths, Audy, Mohr, Hayakawa & Hokari, Sadusk, 1947; PHILIP, 1947a, 1947b, 1948, 1949; Dubois & van den Bergh, Cockings, Smart, Kohls, 1948; Audy & Harrison, Traub & Frick, Jones, Traub *et al.*, Philip & Fuller, Pullen, 1950; WHARTON *et al.*, 1951.

Trombicula akamushi akamushi Nagayo *et al.*, 1919.

Trombicula fletcheri Womersley & Heaslip, 1943. Womersley, Cook, Ahlm & Lipshutz, 1944; McCulloch, 1944, 1946; Kohls *et al.*, Finnegan, Fischbach & Howell, 1945; PHILIP & KOHLS, 1945, 1948; Blake *et al.*, 1945a, 1945b, 1945c; PHILIP *et al.*, 1946; WHARTON, 1946a; PHILIP & WOODWARD, 1946b; Bushland, 1946a; Southcott, Sadusk, Irons *et al.*, GRIFFITHS, Sayers *et al.*, 1947; PHILIP, 1947b, 1948; KOHLS, 1948; Chandler, 1949; Audy & Harrison, Pullen, 1950.

Trombicula fletcheri Womersley & Heaslip, 1945. Brumpt, 1949.

(?) *Trombicula obscura* Womersley, 1944. Sayers *et al.*, 1947; (?) Philip & Kohls, 1948.

(non) *Trombidium coarctatum* Berlese, 1888 (= *Trombicula coarctata* Berlese, 1912).

Kitashima & Miyajima, 1918b; Manson-Bahr, 1929; Gater, 1932; Heaslip, 1941.

(non) *Trombicula pallida* (Nagayo *et al.*, 1919). Ewing, 1925.

(non) *Trombicula palpatis* Nagayo *et al.*, 1919. Ewing, 1925.

(non) *Trombicula intermedia* Nagayo *et al.*, 1920b. Ewing, 1925.

(non) *Trombicula scutellaris* Nagayo *et al.*, 1920c. Ewing, 1925.

(non) *Trombicula pseudoakamushi* Kaiwa *et al.*, 1929 non Tanaka, 1916. Gater, 1932.

(non) *Trombicula deliensis* Walch, 1922a. Gater, 1930, 1932; Heaslip, 1941; Philip & Woodward, 1946b; PHILIP & KOHLS, PHILIP, 1948.

Akamushi Baelz & Kawakani, 1879; *kedani* Tanaka, 1899; pseudoakamushi, *shimamushi*, *yochu* Tanaka, 1916; *tsutsugamushi* Nagayo *et al.*, 1917a; "thin-haired type" Miyajima & Okumura, 1917a; type A Kawamura *et al.*, 1920a.

Types: *Adult*, *nymph*, & *larva*: Kitasato Research Institute.

Paratypes & Hypotypes, *Adult*: Brit. Mus., S.P.H.T.M., Univ. Syd.—*Nymph*: U.S. Nat. Mus.—*Larva*: Brit. Mus., S.P.H.T.M., Univ. Syd., U.S. Nat. Mus., Molteno Inst., Rocky Mountain Lab.

Japan, Malaya: Man.

Japan, Formosa: Dog, buffalo, mouse (*Mus musculus*), field mouse (*Apodemus agrarius*), rats (*R. rattus*, *R. norvegicus*, *R. rufescens*), pheasant (*Phasianus formosanus*), *Gallus gallus*, quail (*Turnix taigoo*).

Japan: Rats (*R. alexandrinus*, *R. manipulus*, *Arvicola hatanadzumi*), mice (*Mus speciosus*, *M. jerdoni*), vole (*Microtus montebelloi*), cat, horse, warbler (*Acrocephalus orientalis*).

Formosa: Ox, *Rattus losea*, mice (*Mus formosanus*, *Apodemus ningpoensis*), shrews (*Crociodura murina*, *Suncus swinhoei*), pheasant (*Centrococtyx javanicus*).

Malaya: Rats (*R. diardi*, *R. jalorensis*, *R. argentifer*, *R. whiteheadi*, *R. browni*, *Trichys fasciculata*).

Burma: Rats (*R. rattus*, *R. slandensis*, *R. yunnanensis*).

Maldivé Is.: *R. alexandrinus*.

Ceylon: *R. kandianus*.

Nepal: *R. fulvescens*.

China: *R. bowersi*.

Philippine Is.: Rats (*R. umbriventer*, *R. mindanensis*).

Pescadores Is.: *R. norvegicus*, *R. rufescens*, birds.

New Guinea: Rats (*R. browni*, *R. mordax*, *R. praetor*, *R. gestri*), bandicoot (*Echymipera cockerelli*).

TROMBICULA PSEUDOAKAMUSHI Hatori, 1919.

- HATORI, J., 1919: *Ann. Trop. Med. Parasit.*, xiii, 233.
- Trombicula pseudoakamushi* Hatori, 1917 (?) *ſide* Hatori, 1919.
- Trombicula pseudoakamushi* Hatori, 1919 (*non* *T. pseudoakamushi* Tanaka, 1916 (?) *nec* Kaiwa *et al.*, 1929 *nec* Tanaka *et al.*, 1930). Hatori, 1920; Kawamura *et al.*, 1921; Walch, 1923, 1924a, 1925, 1927; Walch & Keukenschrijver, 1924; KAWAMURA, 1926; Fletcher *et al.*, 1928; Hirst, 1929a; Patton & Evans, 1929; Gater, 1932; GUNTHER, 1939a, 1940a, 1940c, 1941c, 1951; Radford, 1942, 1946b; Womersley & Heaslip, 1943; Blake *et al.*, 1945a; Hayakawa & Muro, Hayakawa, Tanaka *et al.*, 1945; Fuller, 1947b; PHILIP, 1947b; Hayakawa & Hokari, 1947.
- Trombicula pseudoakamushi* Hatori, 1918. GUNTER, 1940a.
- Trombicula pseudoakamushi* (*variatio deliensis*) Walch, 1924a. GUNTER, 1940c, 1941c, 1951; Blake *et al.*, 1945a.
- Trombicula pseudoakamushi* (*variatio deliensis* ?) Walch, 1925. GUNTER, 1940c, 1951; Finnegan, 1945.
- Trombicula pseudoakamushi* var. *deliensis* Walch, 1923. Womersley & Heaslip, 1943; Womersley, 1944; Dumbleton, McCulloch, 1946.
- Trombicula hatorii* Womersley & Heaslip, 1943. Womersley, 1944; Finnegan, 1945; McCULLOCH, 1946; PHILIP & WOODWARD, 1946b; PHILIP, 1947b.
- (*non*) *Trombidium holosericeum* Linné. Nagayo *et al.*, 1917b.
- (*non*) *Trombicula mediocris* Berlese, 1912. Miyajima, 1917 (?), *ſide* Hatori, 1920; Kawamura & Yamaguchi, 1921.
- (*non*) *Leptus autumnalis* (Shaw, 1790). Miyajima, 1917; Tanaka, 1918; Hatori, 1920.
- (*non*) *Trombicula wichmanni* (Oudemans, 1905). PHILIP, 1947b.
- Patau* (Formosa: Patton & Evans, 1929).
- Type, Larva.
- Formosa: Rat (*R. rufescens*), pheasant (*Centrococcyx javanicus*).
- Sumatra: Gibbon (*Hylobates agilis*), pig, cat, goat, quail (*Excalfactoria chinensis*), pheasant (*C. javanicus*), *Gallus gallus*.

TROMBICULA PALLIDA (Nagayo *et al.*, 1919) Nagayo *et al.*, 1920.

- NAGAYO, M., MIYAGAWA, Y., MITAMURA, T., & TAMIYA, T., 1919: *Verhandl. der jap. pathol. Gessellsch. Tokyo*, ix, 107; NAGAYO, M., MITAMURA, T., & TAMIYA, T., 1920: *Jikken Igaku Zasshi*, iii, iv, 265.
- Trombicula akamushi* nov. var. *pallida* NAGAYO *et al.*, 1919.
- Trombicula pallida* Nagayo *et al.*, 1920a, 1920b, 1920c, 1921. Walch, 1922a, 1924a; Ewing, 1925; Kawamura, 1926; Kaiwa *et al.*, 1929; Tanaka *et al.*, 1930; Radford, 1942, 1946a, 1946b; Womersley & Heaslip, 1943; Blake *et al.*, 1945a; Finnegan, No. 2 E.F.U., 1945; Wharton, 1946a; Philip & Tamiya, 1946; PHILIP, 1947a, 1947b; Sayers *et al.*, 1947; Kohls, 1948; Kuwata *et al.*, Philip & Fuller, Traub *et al.*, 1950.
- Trombicula pallida* Nagayo *et al.*, 1927. Sayers *et al.*, 1947.
- Thrombicula pallida* Brumpt, 1949.
- Trombicula pseudoakamushi* Kaiwa *et al.*, 1929 (= Tanaka, 1916 (?) *ſide* Tanaka *et al.*, 1930). Kawamura, 1926; Fletcher & Field, 1929; Gater, 1932; Lewthwaite & Savoer, 1936c; Gunther, 1940a, 1940c; Womersley & Heaslip, 1943; Takekawa, 1948; Philip & Fuller, 1950.
- (*non*) *Trombicula pseudoakamushi* Hatori, 1917 (?), 1919, 1920 (= *T. hatorii* Womersley & Heaslip, 1943 = *T. hirsti* Sambon, 1927).
- (*non*) *Trombicula akamushi* (Brumpt, 1910) Hirst, 1917. Ewing, 1925; Gater, 1932.
- (*non*) *Trombicula palpalis* Nagayo *et al.*, 1919. Ewing, 1925.
- (*non*) *Trombicula intermedia* Nagayo *et al.*, 1920b. Ewing, 1925.
- (*non*) *Trombicula scutellaris* Nagayo *et al.*, 1920c. Ewing, 1925.
- (*non*) *Trombicula palparis* Kaiwa *et al.*, 1929. Gater, 1932.
- Yasodani Tanaka, 1916; nezumidani Tanaka, 1919; "coarse-haired type" Miyajima & Okumura, 1917a; type D Kawamura *et al.*, 1920a; pseudoakamushi of Tanaka (Nagayo *et al.*, 1921); *T. pseudoakamushi* A Kaiwa *et al.*, 1929.

Type, *Nymph* (?) & *Larva*: Kitasato Research Institute.

Paratypes, *Larva*: Brit. Mus., S.P.H.T.M., Univ. Syd.

Japan: Vole (*Microtus montebelloi*), field mouse (*Apodemus speciosus*).

TROMBICULA PALPALIS Nagayo *et al.*, 1919.

NAGAYO, M., MIYAGAWA, Y., MITAMURA, T., & TAMIYA T., 1919: *Verhandl. der jap. pathol. Gessellsch. Tokyo*, ix, 107.

Trombicula palpalis Nagayo *et al.*, 1919, 1920a, 1920b, 1920c, 1921. Walch, 1922a, 1924a; Ewing, 1925; Kawamura, 1926; Patton & Evans, 1929; Radford, 1942, 1946a, 1946b; Womersley & Heaslip, 1943; Blake *et al.*, 1945a; Finnegan, 1945; Wharton, 1946a; Philip & Tamiya, 1946; Sayers *et al.*, Thor & Willmann, 1947; Philip, 1947a, 1947b; Philip & Kohls, 1948; Kuwata *et al.*, Philip & Fuller, 1950.

Trombicula palparis Kaiwa *et al.*, 1929 (*laps. ling.*). Tanaka *et al.*, 1930; Gater, 1932. *Thrombicula palpalis* Brumpt, 1949.

(non) *Trombicula akamushi* (Brumpt, 1910). Ewing, 1925.

(non) *Trombicula pallida* (Nagayo *et al.*, 1919). Ewing, 1925.

(non) *Trombicula intermedia* Nagayo *et al.*, 1920b. Ewing, 1925.

(non) *Trombicula scutellaris* Nagayo *et al.*, 1920c. Ewing, 1925.

Type C Kawamura *et al.*, 1920a; intermediate type Kawamura, 1926; *T. pseudoakamushi* B Kaiwa *et al.*, 1929.

Type, *Nymph* (?) & *larva*: Kitasato Research Institute.

Paratypes, *Larvae*: British Mus., S.P.H.T.M., Univ. Syd.

Japan: *Apodemus speciosus*, rodents and birds.

TROMBICULA INTERMEDIA Nagayo *et al.*, 1920.

NAGAYO, M., MITAMURA, T., & TAMIYA, T., 1920: *Verhandl. der jap. pathol. Gessellsch. Tokyo*, ix, 143.

Trombicula intermedia Nagayo *et al.*, 1920b, 1920c, 1921. Walch, 1922a, 1924a; Ewing, 1925; Kawamura, 1926; Radford, 1942, 1946b; Womersley & Heaslip, 1943; Finnegan, 1945; Blake *et al.*, 1945a; Wharton, 1946a; Philip & Tamiya, 1946; Philip, 1947a, 1947b; Sayers *et al.*, 1947; Kohls, 1948; Kuwata *et al.*, Philip & Fuller, 1950.

Trombicula intermedia Nagayo *et al.*, 1927. Sayers *et al.*, 1947.

Thrombicula intermedia Brumpt, 1949.

(non) *Trombicula akamushi* (Brumpt, 1910). Ewing, 1925.

(non) *Trombicula pallida* (Nagayo *et al.*, 1919). Ewing, 1925.

(non) *Trombicula palpalis* Nagayo *et al.*, 1919. Ewing, 1925.

(non) *Trombicula scutellaris* Nagayo *et al.*, 1920c. Ewing, 1925.

Type, *Larva*: Kitasato Research Institute.

Japan: Vole (*Microtus montebelloi*).

TROMBICULA SCUTELLARIS Nagayo *et al.*, 1920.

NAGAYO, M., MITAMURA, T., & TAMIYA, T., 1920: *Nippon byorigaku Zasshi*, x, 503.

Trombicula scutellaris Nagayo *et al.*, 1920c, 1921. Walch, 1922a, 1924a; Ewing, 1925; Kawamura, 1926; Patton & Evans, 1929; Radford, 1942, 1946a, 1946b; Womersley & Heaslip, 1943; Blake *et al.*, 1945a; Finnegan, 1945; Wharton, 1946a; Sayers *et al.*, 1947; Philip, 1947a, 1947b; Kohls, 1948; Kuwata *et al.*, Traub *et al.*, 1950.

Trombicula scutellaris Nagayo *et al.*, 1919. Wharton, 1946a; Sayers *et al.*, 1947.

(non) *Trombicula akamushi* (Brumpt, 1910). Ewing, 1925.

(non) *Trombicula pallida* (Nagayo *et al.*, 1919). Ewing, 1925.

(non) *Trombicula palpalis* Nagayo *et al.*, 1919. Ewing, 1925.

(non) *Trombicula intermedia* Nagayo *et al.*, 1920b. Ewing, 1925.

Saichukan; type B Kawamura *et al.*, 1920a.

Type, *Larva*: Kitasato Research Institute.

Paratypes, *Larvae*: S.P.H.T.M., Univ. Syd.

Japan: Rodents.

TROMBICULA CORVI (?) Kawamura & Yamaguchi, 1921.

KAWAMURA, R., & YAMAGUCHI, M., 1921: *Kita. Arch. Exper. Med.*, iv, iii, 169.

Trombicula corvi (Hatori, 1919) Kawamura & Yamaguchi, 1921. Walch & Keuken-schrijver, 1924.

Trombicula corvi Kawamura & Yamaguchi, 1921. Kawamura, 1926; Sugimoto, 1938; Womersley & Heaslip, 1943; Finnegan, 1945; Philip & Woodward, 1946b.

I have queried this name merely because it has been stated that Hatori used it in 1919. He certainly mentioned this mite as being found on the house crow, but did not give an adequate description, and if he actually used the name it would have been a *nomen nudum*. but I think that the doubt has arisen only because of the way in which Kawamura and Yamaguchi attributed the species to Hatori; I feel that the mark of interrogation could be omitted with propriety.

Type, *Larva*.

Formosa: Crow (*Corvus splendens*).

TROMBICULA ISSHIKII Sugimoto, 1938.

SUGIMOTO, M., 1938: *J. Jap. Soc. Vet. Sci.*, xvii, i, 58.

Trombicula isschikii Sugimoto, 1938. Radford, 1942.

Trombicula issikii Womersley & Heaslip, 1943 (*laps. cal.*). Finnegan, 1945; Philip & Woodward, 1946b.

Type, *Larva*.

Formosa: Snipe (*Capella hardwickii*).

TROMBICULA JAPONICA (Kaiwa et al., 1929).

KAIWA, J., TERAMURA, S., & KAGAYA, J., 1929: *Zentralbl. f. Bakt., Parasit., u. Insekt.*, cxvi, vi/viii, 23.

Trombicula autumnalis japonica Kaiwa et al., 1929.

Leptus autumnalis japonica Kaiwa et al., 1929.

Trombicula autumnalis japonica Tanaka et al., 1916 (?) *vide* Tanaka et al., 1930. Gater, 1932; Gunther, 1940c; Womersley & Heaslip, 1943; PHILIP, 1947b.

Trombicula japonica (Tanaka, 1916) Womersley & Heaslip, 1943. Finnegan, 1945; Blake et al., 1945a; Wharton, 1946a; Philip & Tamiya, 1946; Philip, 1947a.

Trombicula japonica (Tanaka et al., 1930) PHILIP, 1947b. Philip & Fuller, 1950.

Akidani Okumura, 1918; the Japanese *Leptus autumnalis* Tanaka, 1916.

Type, *Larva*: Kitasato Research Institute.

Japan: Man, field mouse (*Apodemus speciosus*), vole (*Microtus montebelloi*).

TROMBICULA FUJI Kuwata et al., 1950.

KUWATA, T., BERGE, T. O., & PHILIP, C. B., 1950: *J. Parasit.*, xxxvi, i, 1.

Trombicula (Leptotrombidium) fuji Kuwata et al., 1950.

Type, *Larva*: U.S. Nat. Mus.

Paratypes, *Larvae*: Rocky Mountain Lab., Brit. Mus., S. Aust. Mus., coll. Kuwata, coll. Berge, coll. Philip.

Japan: Field mice (*Apodemus speciosus*, *A. geisha*).

TROMBICULA FUJIGMO Philip & Fuller, 1950.

PHILIP, C. B., & FULLER, H. S., 1950: *Parasitology*, xl, i/ii, 50.

Trombicula fujigmo Philip & Fuller, 1950.

Type, *Larva*: U.S. National Museum.

Paratypes, *Larvae*: British Mus., Rocky Mountain Lab., S. Ausf. Mus., coll. Wharton, coll. Tamiya, coll. Fuller, coll. Philip.

Japan: Shrew (*Crocodyura vorax*), *Rattus sladeni*, rat.

TROMBICULA TAMIYAI Philip & Fuller, 1950.

PHILIP, C. B., & FULLER, H. S., 1950: *Parasitology*, xl, i/ii, 50.

Trombicula tamiyai Philip & Fuller, 1950.

Type "E" Kawamura, 1926.

Type, *Larva*: U.S. National Museum.

Paratypes, *Larvae*: British Museum, Rocky Mountain Lab., S. Aust. Mus., coll. Wharton, coll. Tamiya, coll. Fuller, coll. Philip.
Japan: Field vole (*Microtus montebelloi*).

TROMBICULA OBSCURA Womersley, 1944.

WOMERSLEY, H., 1944: *Trans. Roy. Soc. S. Aust.*, lxxviii, i, 82.
Trombicula obscura Womersley, 1944. Wharton, 1946a; Sayers *et al.*, 1947; Kohls, Philip & Kohls, 1948; Traub *et al.*, 1950.
(non?) *Trombicula akamushi* (Brumpt, 1910). Sayers *et al.*, 1947; (?) Philip & Kohls, 1948.
(non?) *Trombicula deliensis* Walch, 1922a. (?) Philip & Kohls, 1948.
Type, Larva: South Australian Museum.
New Guinea: Rat.

PART VIII.

TROMBICULA DELIENSIS, T. BURMENSIS, & T. FULLERI.

The following authorities have discussed the probability that *T. deliensis* Walch, 1922 is synonymous with *T. akamushi* (Brumpt, 1910): Gater, 1930, 1932; Heaslip, 1941; Philip & Woodward, 1946b; Philip, 1948. However, Audy & Harrison (1950) are against the idea. Further, Philip & Kohls (1948) stated outright that they reduced *deliensis* to the status of a variety of *akamushi*. Nevertheless, most of these writers at the same time agree to two broad groups, distinguishable as the *deliensis* group and the *akamushi* group. As in the case of *hirsti* and *wichmanni*, I am not yet prepared to concede complete identity, and prefer to list them separately pending further investigation at subgeneric level.

I have included *T. burmensis* and *T. fulleri* in this Part because they are both very close to *T. deliensis* and may even prove to be synonymous when more fully investigated.

TROMBICULA DELIENSIS Walch, 1922.

WALCH, E. W., 1922: *Geneesk. Tijdschr. v. Ned.-Ind.*, lxxii, 5.
Trombicula deliensis WALCH, 1922a, 1923, 1924a, 1925, 1927. Walch & Keukenschrijver, 1923, 1924; Kawamura, 1926; Fletcher *et al.*, Warburton, 1928; Ewing, 1928, 1944a, 1944b, 1944c, 1945; Hirst, 1929a; Patton & Evans, Fletcher and Field, 1929; Manson-Bahr, 1929, 1940; Lewthwaite, 1930, 1945a, 1945b; Gater, 1930, 1932; Matheson, 1932; Dinger, 1933; Lewthwaite & Savoor, 1936a, 1936b, 1936c, 1936d, 1940; Chandler, 1936, 1949; Mehta, 1937; Herms, 1939; Gunther, 1939a, 1940a, 1940d, 1941c, 1942; Poynton, Heaslip, 1941; Radford, 1942, 1946a, 1946b, 1946c; Kouwenaar & Wolff, Burnet, 1942; Womersley & Heaslip, 1943; Banerjee & Bhattacharya, 1943, 1945; Takekawa *et al.*, Ahm & Lipshutz, Womersley, Farnar & Katsampes, Cilento, Williams, Takekawa, Cook, Bercovitz, 1944; Rogers & Megaw, 1944, 1946; U.S. War Dept., 1944, 1948; Blake *et al.*, 1945a, 1945c; Finnegan, No. 2 E.F.U., Gurbuksh Singh, Craig & Faust, Browning, Fischbach & Howell, Hayakawa Ichikawa *et al.*, Kohls *et al.*, Megaw, 1945; Mackie *et al.*, 1945, 1946; PHILIP & KOHLS, 1945, 1948; Wharton, 1946a, 1947b; Errington *et al.*, Philip & Sullivan, Roy, Michener & Fuller, H.M. Stat. Off., 1946; McCulloch, 1946, 1947; Philip & Woodward, 1946a, 1946b; Sayers *et al.*, Southcott, Millspaugh & Fuller, Hayakawa & Hokari, Griffiths, Mohr, Sadusk, Thor & Willmann, 1947; Audy, 1947, 1950; Fuller, 1947a, 1947b; PHILIP, 1947a, 1947b, 1948, 1949; Cockings, Dubois & van den Berghe, KOHLS, Smart, 1948; Gispens *et al.*, Traub, PHILIP *et al.*, 1949; Audy & Harrison, Krishnan, Pullen, Traub & Frick, Traub *et al.*, 1950; Traub & Evans, 1950b.
Trombicula delhiensis Stitt, 1929. Strong, 1944.
Thrombicula delhiensis Brumpt, 1949.
Trombicula diliensis Hayakawa Tanaka *et al.*, 1945. (This species is named from Deli, Sumatra, not from Delhi, India, or Dili, Timor.)
Trombicula vanderghinstei Gunther, 1940a, 1940d. Heaslip, 1941; Womersley & Heaslip, 1943; Womersley, 1944; Blake *et al.*, 1945a; Audy & Harrison, 1950.

Trombicula waltchi Womersley & Heaslip, 1943. Cook, U.S. War Dept., Womersley, 1944; McCulloch, 1944, 1946, 1947; Kohls *et al.*, Browning, Finnegan, Ewing, 1945; Blake *et al.*, 1945a, 1945c; Philip & Kohls, 1945, 1948; Philip *et al.*, 1946, 1949; Wharton, 1946a; Bushland, 1946a; Dumbleton, Mackie *et al.*, 1946; Philip & Woodward, 1946b; Sayers *et al.*, Griffiths, Sadusk, 1947; Kohls, 1948; Audy & Harrison, 1950.

(non) *Trombicula akamushi* (Brumpt, 1910). Gater, 1930, 1932; Heaslip, 1941; Philip & Woodward, 1946b; PHILIP & KOHLS, PHILIP, 1948.

Types, *Adult*: British Museum.—*Nymph*: British Museum.—*Larva*.

Hypotypes, *Larvae*: Brit. Mus., U.S. Nat. Mus., Molteno Inst., Kitasato Res. Inst., S. Aust. Mus., S.P.H.T.M., Univ. Syd., Aust. Mus., Rocky Mountain Lab.—*Adult*: Coll. Radford.

Sumatra, Malaya: Man.

Sumatra: Rats (*R. diardi*, *R. concolor*), pheasant (*Centrococcyx javanicus*), *Rhinorthra chlorophaea*.

Malaya: Rats (*R. diardi*, *R. jalorensis*, *R. concolor*, *R. mülleri*, *R. ciliatus*, *R. vociferans*, *Trichys fasciculata*), squirrels (*Sciurus humei*, *S. miniatus*, *S. nigrovittatus*, *Rhinosciurus tupaoides*), shrew (*Tupaia ferruginea*). *Paradoxurus hermaphroditus*, barking deer (*Tragulus fulviventor*).

India: Rodents.

Java, Indochina, South-west China: Not specified.

Ceylon: Bandicoot (*Bandicota malabarica*), rat (*R. kandiensis*), shrew (*Suncus giganteus*), gerbille (*Tatera ceylonica*), squirrel (*Funambulus favonicus*), crow (*Corvus splendens*), pheasant (*Centropus parroti*), *Endynamis scolopaceus*.

Maldive Is.: *R. norvegicus*, *R. alexandrinus*, shrew (*Suncus giganteus*).

Burma: Rats (*R. concolor*, *R. norvegicus*, *R. rattus*, *R. yunnanensis*, *R. sladenis*, *R. brunnesculus*, *R. tistae*, *R. manipulus*, *R. fulvescens*, *R. nitidus*), mice (*Mus bactrianus*, *Diomys crumpi*, *Hadromys humei*, *Dremomys lokriæ*), shrews (*Tupaia belangeri*, *Suncus fulvocinereus*, *S. griffithi*, *S. murinus*, *Crocidura vorax*, *Anourosorex assamensis*), civets (*Viverra picta*, *Paradoxurus hermaphroditus*), barking deer (*Muntiacus muntjak*), monkey (*Macacus assamensis*), squirrels (*Callosciurus pygerrhus*, *C. lockroides*), bandicoots (*Bandicota bengalensis*, *B. nemorivaga*), *Gallus gallus*, *Felis domestica*, quail (*Turnix plumbipes*), hoopoe (*Upapa longirostris*), mongoose (*Herpestes* sp.), pheasant (*Centropus intermedius*).

Nepal: *R. fulvescens*.

Kanpat: *R. manipulus*.

Yunnan: *R. bowersi*.

Philippine Is.: *R. mindanensis*, *R. umbriventer*.

Formosa: *R. losca*.

New Guinea: Rats (*R. browni*, *R. mordax*, *R. praetor*, *R. gestri*, *Melomys* sp.), wallaby, bandicoot (*Echymipera cockerelli*), rail (*Rallus philippensis*), free.

Queensland: Rats and bandicoots.

TROMBICULA BURMENSIS Ewing, 1945.

EWING, H. E., 1945: *Proc. Ent. Soc. Wash.*, xlvii, iii, 63.

Trombicula burmensis Ewing, 1945. Wharton, 1946a.

Type, *Larva*: U.S. National Museum.

Burma: Rats.

TROMBICULA FULLERI Ewing, 1945.

EWING, H. E., 1945: *Proc. Ent. Soc. Wash.*, xlvii, iii, 63.

Trombicula fulleri Ewing, 1945. Wharton, 1946a; Sayers *et al.*, 1947; Kohls, 1948; Traub *et al.*, 1950.

Type, *Larva*: U.S. National Museum.

Burma: Shrews

PART IX.

THE TROMBICULAE OF MALAYA & THE EAST INDIES.

Certain of these species have already been dealt with in previous Parts:

T. minor Berlese, 1905 (Java), Part V; *T. mediocris* Berlese, 1912 (Java), Part V; *T. wichmanni* (Oudemans, 1905) (Celebes & B.N. Borneo), Part VI; *T. akamushi* (Brumpt, 1910) (Malaya), Part VII; *T. deliensis* Walch, 1922 (Sumatra, Java, & Malaya), Part VIII; *T. hirsti* Sambon, 1927 (Malaya, Sumatra, & Celebes), Part V.

TROMBICULA ACUSCUTELLARIS Walch, 1923.

WALCH, E. W., 1923: *Kita. Arch. Exper. Med.*, v, iii, 63.

Trombicula acuscutellaris Walch, 1923, 1925. Patton & Evans, 1929; Gater, 1932; Lewthwaite & Savoer, 1936c; Thor, 1936; Mehta, 1937; Gunther, 1941c; Radford, 1942, 1946b; Williams, 1944; Blake *et al.*, 1945a; Finnegan, 1945; Mackie *et al.*, Roy, Philip *et al.*, 1946; Ewing, 1946a; Wharton, 1946b; Philip & Woodward, 1946b; Thor & Willmann, 1947; Fuller, 1947b; Philip, 1947b; Sayers *et al.*, 1947.

Thrombicula acuscutellaris Walch, 1922. Brumpt, 1949.

Trombidium acuscutellare Walch, 1927.

Pentagonella acuscutellaris Thor, 1936.

Trombicula (Pentagonella) acuscutellaris (Walch, 1923) Womersley & Heaslip, 1943.

Type, *Nymph*: British Museum.—*Larva*.

Hypotypes, *Larva*: British Museum.—*Nymph*: Coll. Radford.

Malaya: Man.

Malaya & Sumatra: *R. diardi*.

Ceylon & Maldive Is.: *R. norvegicus*.

TROMBICULA DENSIPILIATA Walch, 1923.

WALCH, E. W., 1923: *Kita. Arch. Exper. Med.*, v, iii, 63.

Trombicula densipiliata Walch, 1923, 1925. Patton & Evans, 1929; Gunther, 1941c; Radford, 1942, 1946b; Womersley & Heaslip, 1943; Finnegan, 1945; Blake *et al.*, 1945a; Dumbleton, 1946.

Type, *Larva*.

Sumatra: Rat.

Nissan Is., New Guinea: Rat.

TROMBICULA (?) KEUKENSCHRIJVERI Walch, 1924.

WALCH, E. W., 1924: *Trans. 5th Bienn. Cong. Far East. Ass. Trop. Med.*, 583.

Trombicula keukenschrijveri Walch, 1924a, 1924b, 1925. Walch & Keukenschrijver, 1924; Gater, 1932; Gunther, 1941c; Blake *et al.*, 1945a; Wharton, 1946a; Philip & Woodward, 1946b.

Trombicula keukenschrijveri Walch, 1923: Womersley & Heaslip, 1943; Finnegan, 1945.

Apparently Walch did not acknowledge any other genus but *Trombicula* (cf. *Trombicula vandersandei* Walch, 1923, for *Thrombidium van der Sandei* Oudemans, 1905, and *Schöngastia vandersandei* Oudemans, 1912, and various other examples). Therefore we cannot even assume that in the absence of the sensillae Walch placed *keukenschrijveri* in the genus *Trombicula* because of other generic characters, and I retain it here merely because, though it has no ostensible right to this generic placing other than that Walch originally put it there, there is nowhere else to place it, and no sense in pushing it around.

Type, *Larva*.

Paratypes, *Larvae*: British Museum, U.S. National Museum.

Sumatra: Man.

Malaya: *R. ciliatus*.

TROMBICULA RARA Walch, 1924.

WALCH, E. W., 1924: *Trans. 5th Bienn. Cong. Far East. Ass. Trop. Med.*, 583.

Trombicula rara Walch, 1924a, 1925. Walch & Keukenschrijver, 1924; Gunther, 1941c; Womersley & Heaslip, 1943; Kohls *et al.*, Finnegan, 1945; Blake *et al.*, 1945a; Philip & Woodward, 1946b.

Trombicula (Eutrombicula) rara (Walch, 1924) Philip & Woodward, 1946b.

Type, Larva.

Sumatra: Man.

Dutch New Guinea: Skink (*Lygosoma variegatus*), free.

TROMBICULA (?) HASTATA Gater, 1932.

GATER, B. A. R., 1932: *Parasitology*, xxiv, ii, 143.

Trombicula hastata Gater, 1932. Radford, 1942.

Neoschöngastia hastata Womersley & Heaslip, 1943.

Ascoshöngastia hastata Womersley & Kohls, 1947.

Gater placed *hastata* in the genus *Trombicula* in spite of the absence of sensillae. Its anteromedian and posterolateral scutal setae are leaf-shaped. Now, in 1940, I described *N. foliata* from New Guinea—*foliata* has its posterolateral scutal setae (but not its anteromedian) broad and leaf-shaped, and because of this partial resemblance Womersley & Heaslip (1943) transferred *hastata* to *Neoschöngastia*, and in 1947 Womersley & Kohls went further and made it *Ascoshöngastia*. These workers are probably quite right, but until the type of the sensillae of *hastata* is established I can see no justification in transferring it about on purely hypothetical grounds.

Type, Larva: British Museum.

Malaya: *R. surifer*.

TROMBICULA MUNDA Gater, 1932.

GATER, B. A. R., 1932: *Parasitology*, xxiv, ii, 143.

Trombicula munda Gater, 1932. Radford, 1942; Womersley & Heaslip, 1943; Finnegan, 1945; Audy, 1947; Philip & Fuller, 1950.

Type, Larva: British Museum.

Paratypes, Larvae: U.S. National Museum, Molteno Institute.

Malaya: Rats (*R. diardi*, *R. mülleri*, *R. malaisia*).

TROMBICULA SPICEA Gater, 1932.

GATER, B. A. R., 1932: *Parasitology*, xxiv, ii, 143.

Trombicula spicea Gater, 1932. Radford, 1942; Womersley & Heaslip, 1943; Finnegan, 1945; Philip & Fuller, 1950.

Type, Larva: British Museum.

Paratypes, Larvae: U.S. National Museum, Molteno Institute.

Malaya: Rats (*R. malaisia*, *R. mülleri*).

TROMBICULA BODENSIS Gunther, 1940.

GUNTHER, C. E. M., 1940: PROC. LINN. SOC. N.S.W., lxxv, iii/iv, 479.

Trombicula bodensis Gunther, 1940b. Womersley & Heaslip, 1943; Finnegan, 1945; Philip *et al.*, McCulloch, 1946; Philip & Woodward, 1946b.

Type, Larva: School Public Health Tropical Medicine, Univ. Sydney.

Paratypes, Larvae: British Museum, Australian Museum, South Australian Museum.

B.N. Borneo: Mouse deer (*Tragulus borneanus*).

Philippine Is.: Rat.

TROMBICULA BATUI Philip & Traub, 1950.

PHILIP, C. B., & TRAUB, R., 1950: *J. Parasit.*, xxxvi, i, 29.

Trombicula batui Philip & Traub, 1950.

Holotype, Larva: U.S. National Museum (Type No. 1865).

Paratypes, Larvae: British Museum, Rocky Mountain Laboratory (No. AP 25759), Chicago Natural History Museum.

Batu caves, Selangor: Bat (*Eonycteris spelaea*).

TROMBICULA INSOLLI Philip & Traub, 1950.

PHILIP, C. B., & TRAUB, R., 1950: *J. Parasit.*, xxxvi, i, 29.

Trombicula insolli Philip & Traub, 1950.

Holotype, Larva: U.S. National Museum (No. 1866).

Paratypes, Larvae: British Museum, Rocky Mountain Laboratory.

Batu caves, Selangor: Bat (*Eonycteris spelaea*).

PART X.

THE TROMBICULAE OF INDIA & BURMA.

The following species have already been dealt with in previous Parts:

T. akamushi (Brumpt, 1910) (Burma, Ceylon, Maldive Is., Nepal), Part VII; *T. deliensis* Walch, 1922 (India, Ceylon, Maldive Is., Kanpat, Nepal, Burma), Part VIII; *T. burmensis* Ewing, 1945 (Burma), Part VIII; *T. fulleri* Ewing, 1945 (Burma), Part VIII; *T. hakei* Radford, 1946 (Imphal), Part VI.

TROMBICULA GLIRICOLENS (Hirst, 1915) Radford, 1942.

HIRST, S., 1915: *Bull. Ent. Res.*, vi, iii, 183; RADFORD, C. D., 1942: *Parasitology*, xxxiv, 55.

Microtrombidium gliricolens Hirst, 1915b.

Trombicula gliricolens Radford, 1942. Womersley & Heaslip, 1943; Finnegan, 1945; Dumbleton, 1946.

Type, *Larva*: British Museum.

Bengal: *Mus rattus*.

TROMBICULA CERVULICOLA Ewing, 1931.

EWING, H. E., 1931: *Proc. U.S. Nat. Mus.*, lxxx, No. 2908, 1.

Trombicula cervulicola Ewing, 1931. Radford, 1942; Womersley & Heaslip, 1943.

Type, *Larva*: U.S. National Museum.

India: Barking deer (*Muntiacus aureus*).

TROMBICULA COLUBERINA (Radford, 1946).

RADFORD, C. D., 1946: *Proc. Zool. Soc.*, cxvi, ii, 247.

Fonsecia coluberina Radford, 1946c. Sayers *et al.*, 1947.

Strictly speaking, following the new subgenera of Wharton *et al.*, 1951, this species should be listed as *Trombicula (Fonsecia) coluberina* (Radford, 1946), but, as already explained, it is not feasible to introduce subgenera in this list.

Type, *Larva*: British Museum.

Paratypes: Coll. Radford, coll. André, U.S. Nat. Mus.

India: Snake (*Coluber radiatus*).

TROMBICULA SQUAMOSUS (Radford, 1948).

RADFORD, C. D., 1948: *Proc. Zool. Soc.*, cxviii, i, 126.

Trombiculindus squamosus Radford, 1948.

This species has been made the type of the new subgenus *Trombiculindus* Wharton *et al.*, 1951, and should therefore be listed as *Trombicula (Trombiculindus) squamosus* (Radford, 1948), but I am not using subgenera in this list.

Lectotype, *Larva*: British Museum.

Paratypes, *Larvae*: U.S. Nat. Mus., S. Aust. Mus., coll. Willmann, Musée d'Hist. Natur., Paris, coll. Kalra, coll. du Toit, coll. Radford, coll. André, coll. Brennan.

India: Rat.

PART XI.

THE TROMBICULAE OF THE SOUTH-WEST PACIFIC.

The following species have already been dealt with in previous Parts:

T. wichmanni (Oudemans, 1905) (Philippine Is., New Guinea), Part VI; *T. akamushi* (Brumpt, 1910) (Philippine Is., New Guinea), Part VII; *T. deliensis* Walch, 1922 (Philippine Is., New Guinea), Part VIII; *T. densipiliata* Walch, 1923 (Nissan Is., N.G.), Part IX; *T. rara* Walch, 1924 (Dutch New Guinea), Part IX; *T. hirsti* Sambon, 1927 (New Guinea), Part V; *T. obscura* Womersley, 1944 (New Guinea), Part VII.

T. quadriense Womersley & Heaslip, 1943 (British Solomon Islands) will be dealt with in Part XII.

TROMBICULA PIERCEI Ewing, 1933.

EWING, H. E., 1933: *Proc. U.S. Nat. Mus.*, lxxxii, xxix, 1.

Trombicula piercei Ewing, 1933. Radford, 1942; Philip & Traub, 1950.

Lectotype & Cotypes, *Larvae*: U.S. National Museum.

Philippine Is.: Bat. (*Hipposideros diademata*).

TROMBICULA RIOI Gunther, 1939.

- GUNTHER, C. E. M., 1939: PROC. LINN. SOC. N.S.W., lxiv, i/ii, 73.
Trombicula edwardsi Gunther, 1938 (*nom. nud.*).
Trombicula rioi Gunther, 1939a, 1940a, 1940d, 1942. Womersley, 1939; Radford, 1942; Womersley & Heaslip, 1943; Blake *et al.*, 1945a; Finnegan, 1945.
 Type, *Larva*: School Public Health Trop. Med., Univ. Sydney.
 Paratypes, *Larvae*: Brit. Mus., Australian Mus., S. Aust. Mus., Rocky Mountain Lab. New Guinea: Bush fowl (*Megapodius reinwardt*).

TROMBICULA ROBUSTA Gunther, 1941.

- GUNTHER, C. E. M., 1941: PROC. LINN. SOC. N.S.W., lxvi, iii/iv, 157.
Trombicula robusta Gunther, 1941b. Womersley & Heaslip, 1943; Finnegan, 1945.
 Type, *Larva*: School Public Health Trop. Med., Univ. Sydney.
 Paratypes, *Larvae*: Australian Museum, British Museum.
 New Guinea: Catbird (*Ailuroedus melanocephalus*), pitta (*P. mackloti*).

TROMBICULA KOHLSI Womersley, 1944.

- WOMERSLEY, H., 1944: *Trans. Roy. Soc. S. Austral.*, lxxviii, i, 82.
Trombicula kohlsi Womersley, 1944. Kohls *et al.*, 1945.
 Type, *Larva*: South Australian Museum.
 New Guinea: Skink (*Lygosoma variegatus*), free.

TROMBICULA SCINCOIDES Womersley, 1944.

- WOMERSLEY, H., 1944: *Trans. Roy. Soc. S. Austral.*, lxxviii, i, 82.
Trombicula scincoides Womersley, 1944. Blake *et al.*, 1945a; Kohls *et al.*, 1945; Philip & Woodward, 1946b; Bushland, 1946b; Philip *et al.*, 1946.
 Type, *Larva*: South Australian Museum.
 New Guinea: Skink (*Lygosoma bicarinatus*), lizards (*Leiolepisma fuscum*, *L. albertisii*), free.
 Philippine Is.: Skinks, lizards.

TROMBICULA FRITTSI Wharton, 1945.

- WHARTON, G. W., 1945: *J. Parasit.*, xxxi, iv, 282.
Trombicula frittsi Wharton, 1945a. Philip & Fuller, 1950.
 Type, *Larva*: U.S. National Museum. Paratype, *Larva*: Coll. Radford.
 Bougainville Is.: *Rattus praetor*, *Gehyra oceanica*, *Varanus indica*.

TROMBICULA ANOUS (Wharton, 1945).

- WHARTON, G. W., 1945: *J. Parasit.*, xxxi, vi, 401.
Acariscus anous Wharton, 1945b, 1946b, 1947b.
 Type, *Larva*: U.S. National Museum.
 Paratypes, *Larvae*: U.S. National Museum, S. Australian Museum, coll. Radford.
 Guam: Noddy (*Anous stolidus*), tattler (*Heteroscelus incanus*).

TROMBICULA PLUVIUS (Wharton, 1945).

- WHARTON, G. W., 1945: *J. Parasit.*, xxxi, vi, 401.
Acariscus pluvius Wharton, 1945b, 1946b, 1947b.
 Type, *Larva*: U.S. National Museum.
 Paratypes, *Larvae*: U.S. National Museum, S. Australian Museum, coll. Radford.
 Guam, Bougainville Is.: Plover (*Pluvialis dominica*), noddies (*Anous tenuirostris*, *A. stolidus*), tattler (*Heteroscelus incanus*).

TROMBICULA NISSANI Dumbleton, 1946.

- DUMBLETON, L. J., 1946: *Trans. Roy. Soc. N.Z.*, lxxvi, iii, 409.
Trombicula nissani Dumbleton, 1946.
 Type & Paratypes, *Larvae*: South Australian Museum.
 Nissan Is., N.G.: Tree kangaroo.

TROMBICULA GYMNODACTYLA (Womersley & Kohls, 1947).

WOMERSLEY, H., & KOHLS, G. M., 1947: *Trans. Roy. Soc. S. Aust.*, lxxi, i, 3.

Trombicula gymnodactyla McCulloch, 1946 (*nom. nud.*).

Eutrombicula gymnodactyla Womersley & Kohls, 1947.

Eutrombicula (*Acariscus*) *gymnodactyla* Womersley & Kohls, 1947.

McCulloch (1946) published a paper in which he mentioned "*Trombicula gymnodactyla* (Womersley MS.)". Womersley & Kohls (1947) published the full description of their species as *Eutrombicula gymnodactyla* and *Eutrombicula* (*Acariscus*) *gymnodactyla* in the same paper, explaining that they regarded *Acariscus* as a synonym of *Eutrombicula*.

Type, Larva: South Australian Museum.

Paratypes, Larvae: South Australian Museum, U.S. National Mus.

Dutch New Guinea: *Gymnodactyla louisiadensis*.

PART XII.

THE TROMBICULAE OF AUSTRALIA & NEW ZEALAND.

The following species have already been dealt with in previous Parts:

T. deliensis Walch, 1922 (Australia), Part VIII; *T. hirsti* Sambon, 1927 (Australia), Part V.

Although this check list purports to deal only with larvae, I have already included two species known only from the adults (*T. minor* and *T. deliensis*), and I am including here three more (*T. signata*, *T. tindalei*, and *T. translucens*).

TROMBICULA NOVAE-HOLLANDIAE Hirst, 1929.

HIRST, S., 1929: *Proc. Zool. Soc. Lond.*, ii, 165.

Trombicula novae-hollandiae Hirst, 1929b, 1929c, 1929d. Womersley, 1934, 1936, 1937, 1939; Gunther, 1939a; Radford, 1942; Womersley & Heaslip, 1943; Finnegan, 1945.

Type, Larva: British Museum.

Paratype, Larva: South Australian Museum.

Australia: *Rattus greyii*, rat-kangaroo (*Potorous tridactylus*).

TROMBICULA SAMBONI (Hirst, 1929) Womersley, 1939.

HIRST, S., 1929: *Ann. Mag. Nat. Hist.*, x, iii, 564; WOMERSLEY, H., 1939: *Trans. Roy. Soc. S. Aust.*, lxiii, ii, 149.

Trombicula hirsti Sambon, 1927. Hirst, 1929a, 1929c, 1929d. Womersley, 1934, 1936, 1937.

Trombicula samboni Womersley, 1939. Womersley & Heaslip, 1943; Gill *et al.*, 1945; McCulloch, 1946, 1947; Fuller, 1947b.

Trombicula samboni Womersley, 1936. Finnegan, 1945.

Trombicula sanboni McCulloch, 1944 (*laps. cal.*).

(*non*) *Trombicula hirsti* Sambon, 1927.

T. hirsti occurs in the northern part of Australia. Both Hirst and Womersley, working with similar specimens from South Australia, believed that they were working with *hirsti*, but in 1939 Womersley obtained some of Sambon's paratypes and discovered that the southern specimens were different; these he named *T. samboni*.

Type, Larva: South Australian Museum.

South Australia: Man.

TROMBICULA SIGNATA Womersley, 1934.

WOMERSLEY, H., 1934: *Rec. S. Aust. Mus.*, v, ii, 179.

Trombicula signata Womersley, 1934, 1937.

Type, Adult: South Australian Museum.

Western Australia: Free.

TROMBICULA TINDALEI Womersley, 1936.

WOMERSLEY, H., 1936: *Linn. Soc. J.: Zool.*, xl, clxix, 107.

Trombicula tindalei Womersley, 1936, 1937.

Type, *Adult*: S. Australian Museum.

Kangaroo Is., S. Australia: Free.

TROMBICULA MACROPUS Womersley, 1936.

WOMERSLEY, H., 1936: *Linn. Soc. J.: Zool.*, xl, clxix, 107.

Trombicula macropus Womersley, 1936, 1939. Gunther, 1939a; Womersley & Heaslip, 1943; Finnegan, 1945.

Trombicula macropus Womersley, 1934. Womersley, 1937.

Type, *Larva*: South Australian Museum.

Northern Territory, Australia: Wallaby (*Macropus* sp.).

TROMBICULA CHIROPTERA Womersley & Heaslip, 1943.

WOMERSLEY, H., & HEASLIP, W. G., 1943: *Trans. Roy. Soc. S. Aust.*, lxxvii, i, 68.

Trombicula chiroptera Womersley & Heaslip, 1943. Finnegan, 1945.

Type, *Larva*: South Australian Museum.

South Australia (?): Rats (?), *Chalinolabus gouldi*.

TROMBICULA QUADRIENSE Womersley & Heaslip, 1943.

WOMERSLEY, H., & HEASLIP, W. G., 1943: *Trans. Roy. Soc. S. Aust.*, lxxvii, i, 68.

Trombicula quadriense Womersley & Heaslip, 1943. Finnegan, 1945; Dumbleton, 1946.

Type, *Larva*: South Australian Museum.

Queensland: *Rattus assimilis*, *Hydromys chrysogaster*, rat.

TROMBICULA SARCINA Womersley, 1944.

WOMERSLEY, H., 1944: *Trans. Roy. Soc. S. Aust.*, lxxviii, i, 82.

Trombicula sarcina Womersley, 1944. Legg, 1944; Gill *et al.*, 1945; McCulloch, 1947; Chandler, 1949.

Type, *Larva*: South Australian Museum.

Queensland: Man, sheep, dog, kangaroo (*Macropus major*), wallaroos, wallabies, apostle bird (*Struthidia cinerea*), free.

TROMBICULA TRANSLUCENS Womersley, 1944.

WOMERSLEY, H., 1944: *Trans. Roy. Soc. S. Aust.*, lxxviii, i, 82.

Trombicula translucens Womersley, 1944.

Type, *Adult*: South Australian Museum.

Queensland: Free.

TROMBICULA NAULTINI Dumbleton, 1946.

DUMBLETON, L. J., 1946: *Trans. Roy. Soc. N.Z.*, lxxvi, iii, 409.

Trombicula naultini Dumbleton, 1946.

Type, *Larva*: Entomol. Division, Nelson, N.Z.

New Zealand: *Naultinus elegans*.

PART XIII.

GENUS SCHÖNGASTIA Oudemans, 1910.

OUDEMANS, A. C., 1910: *Ent. Ber. Ned. Ent. Ver.*, iii, liv, 86.

Schöngastia Oudemans, 1910a, 1912b. Walch, 1927; Sambon, 1928; Hirst, 1929a; Vitzthum, 1929; Ewing, 1929, 1938, 1944a, 1944b; Gater, 1932; Thor, 1935, 1936; Womersley, 1937, 1939; Gunther, 1939a, 1941c; Womersley & Heaslip, 1943; Thor & Willmann, 1947; Lawrence, 1949; Wharton *et al.*, 1951.

Schöngastia Warburton, 1928 (*laps. cal.*).

(*non*) *Trombicula* Berlese, 1905: Walch, 1923, 1924a, 1925, 1927; Walch & Keuken-schrijver, 1923, 1924; Fletcher *et al.*, 1928; Patton & Evans, Manson-Bahr, 1929.

(*non*) *Leptus* Latreille, 1804; Warburton, 1928.

(*non*) *Schöngastia* Oudemans, 1910: Hirst, 1929*a*, 1929*b*, 1929*c*, 1929*d*; Womersley, 1934, 1937; Radford, 1942; U.S. War Dept., 1944.

(*non*) *Neoschöngastia* Ewing, 1929. Radford, 1942; Womersley & Heaslip, 1943.

Genotype, *Schöngastia vandersandei* (Oudemans, 1905) Oudemans, 1912.

A peculiar thing has happened with regard to a member of this genus: Wharton *et al.*, in 1951, made their first division of the larval Trombiculidae on the basis of the numbers of leg segments (which does not appeal to me, from the practical aspect, as a good starting-point). Now, *S. oudemansi* (Walch, 1923) has seven leg-segments in legs I, but six in legs II and III—a similar condition to that existing in *Neoschöngastia impar* Gunther, 1939. Apart from this variation in leg segments, *S. oudemansi* has all the characteristics of the genus *Schöngastia*—yet we are threatened with its being taken out of its seat in the Trombiculinae and placed, as the type of a new genus, into the Walchiinae alongside totally different genera such as *Walchia* and *Gahrlipeia*. This seems artificial to me, and I am leaving *S. oudemansi* for the present in the genus *Schöngastia*.

Apart from this one point, my arrangement of this Part is quite orthodox. I have not accepted as fully proven the identification of *S. blestowei* with *S. vandersandei*, and of *S. pusilla* with *S. schüffneri*, but have retained them as distinct.

SCHÖNGASTIA VANDERSANDEI (Oudemans, 1905) Oudemans, 1912.

OUDEMANS, A. C., 1905: *Ent. Ber. Ned. Ent. Ver.*, i, xxii, 216; Idem, 1912: *Zool. Jahrb.*, xiv, i, 1.

Thrombidium van der Sandei Oudemans, 1905, 1906, 1910*c*. Fantham *et al.*, 1916.

Schöngastia vandersandei Oudemans, 1912*b*, 1913, 1916. Hirst, 1917; Ewing & Hartzell, 1918; Sambon, 1927; Gunther, 1939*a*, 1940*d*, 1941*c*. 1942; Womersley, 1939; Radford, 1942; Womersley & Heaslip, 1943; Ewing, 1944*a*, 1944*b*; Finnegan, 1945; Dumbleton, 1946; Thor & Willmann, 1947; Philip & Kohls, 1948; Traub *et al.*, 1950.

Schöngastia van der sandei (Oudemans, 1905) Brumpt, 1949.

Trombicula vandersandei Walch, 1923, 1924*a*. Patton & Evans, 1929.

Microtrombidium vandersandei Warburton, 1928.

(*non*) *Schöngastia blestowei* Gunther, 1939*a*. Dumbleton, 1946; Philip & Kohls, 1948; Traub *et al.*, 1950.

Akran (Patton & Evans, 1929), *gonone* (Oudemans, 1906).

Type, Larva.

Dutch New Guinea, British Solomon Is.: Man.

SCHÖNGASTIA OUDEMANSI (Walch, 1923) Gater, 1932.

WALCH, E. W., 1923: *Kita. Arch. Exper. Med.*, v, iii, 63; GATER, B. A. R., 1932: *Parasitology*, xxiv, ii, 143.

Trombicula oudemansi Walch, 1923, 1924*a*, 1925, 1927. Walch & Keukenschrijver, 1924; Fletcher *et al.*, 1928; Patton & Evans, 1929; Hayakawa Tanaka *et al.*, 1945; Hayakawa & Hokari, 1947.

Schöngastia oudemansi Gater, 1932. Gunther, 1939*a*, 1940*b*, 1941*c*; Womersley & Heaslip, 1943; Blake *et al.*, 1945*a*; Radford, 1946*b*; Hayakawa & Hokari, Thor & Willmann, 1947; Audy & Harrison, 1950; WHARTON *et al.*, 1951.

Neoschöngastia oudemansi Walch, 1923. Radford, 1942; Finnegan, 1945.

(*non*) *Microtrombidium oudemansi* von Goosmann, 1917.

Type, Larva.

Paratypes, Larvae: British Museum, U.S. National Mus., Molteno Inst.

Sumatra: Man, rats (*R. jalorensis*, *R. diardi*, *R. concolor*), tiger cat.

Malaya: Rats (*R. diardi*, *R. jalorensis*, *R. mülleri*, *R. ciliatus*), *Trichys fasciculata*, squirrels (*Sciurus miniatus*, *Rhinosciurus laticaudatus*), shrew (*Tupaia ferruginea*), mouse-deer (*Tragulus fulviventer*).

SCHÖNGASTIA SCHÜFFNERI (Walch, 1923) Gunther, 1941.

- WALCH, E. W., 1923: *Kita. Arch. Exper. Med.*, v, iii, 63; GUNTHER, C. E. M., 1941: *Proc. Linn. Soc. N.S.W.*, lxvi, v/vi, 391.
- Trombicula schüffneri* Walch, 1923, 1924a, 1925. Walch & Keukenschrijver, 1923, 1924, 1925; Warburton, Fletcher *et al.*, 1928; Patton & Evans, Manson-Bahr, 1929; Matheson, 1932; Poynton, 1941; Kouwenaar & Wolff, 1942; Farner & Katsampes, Takekawa, 1944; No. 2 E.F.U., Craig & Faust, 1945; Lewthwaite, 1945b; Hayakawa & Hokari, 1947.
- Trombicula schüffneri* Warburton, 1928. Strong, 1944.
- Thrombicula schüffneri* Walch, 1924. Brumpt, 1949.
- Schöngastia schüffneri* Gunther, 1941c. Williams, 1944; Blake *et al.*, 1945a; Wharton, 1946a; Griffiths, Sayers *et al.*, Mohr, Hayakawa & Hokari, 1947; Philip & Kohls, 1948.
- Neoschöngastia schüffneri* Walch, 1923. Radford, 1942; Womersley & Heaslip, 1943; Finnegan, 1945.
- (non) *Schöngastia pusilla* Womersley, 1944. Griffiths, 1947; Philip & Kohls, 1948.
- Type, Larva.
Sumatra: Man, pheasant (*Centrococcyx javanicus*), rodents.

SCHÖNGASTIA PSEUDO-SCHÜFFNERI (Walch, 1927) Gunther, 1941.

- WALCH, E. W., 1927: *Geneesk. Tijdschr. v. Ned.-Ind.*, lxxvii, 922; GUNTHER, C. E. M., 1941: *Proc. Linn. Soc. N.S.W.*, lxxvi, v/vi, 391.
- Trombicula pseudo-schüffneri* Walch, 1927.
- Schöngastia pseudo-schüffneri* Gunther, 1941c.
- Neoschöngastia pseudoschüffneri* Walch, 1927. Womersley & Heaslip, 1943.
- Type, Larva.
Sumatra: Man, *Rattus diardi*.

SCHÖNGASTIA VIETA Gater, 1932.

- GATER, B. A. R., 1932: *Parasitology*, xxiv, ii, 143.
- Schöngastia vieta* Gater, 1932. Radford, 1942; Womersley & Heaslip, 1943.
- Type, Larva: British Museum.
- Paratypes, Larvae: U.S. National Mus., Molteno Inst.
Malaya: Rats (*R. diardi*, *R. jalorensis*, *R. mülleri*).

SCHÖNGASTIA BLESTOWEI Gunther, 1939.

- GUNTHER, C. E. M., 1939: *Proc. Linn. Soc. N.S.W.*, lxxiv, i/ii, 73.
- Schöngastia yeomansi* Gunther, 1938 (*nom. nud.*). Womersley, 1944.
- Schöngastia blestowei* Gunther, 1939a, 1940a, 1940d, 1941c, 1942. Womersley, 1939, 1944; Radford, 1942; Womersley & Heaslip, 1943; McCulloch, 1944, 1946; Finnegan, Kohls *et al.*, Anderson & Wing, Philip & Kohls, 1945; Blake *et al.*, 1945a, 1945c; Wharton, 1946a; Bushland, 1946a, 1946b, 1946c; Dumbleton, 1946; Fuller, 1947b; Griffiths, Southcott, Mohr, 1947; Kohls, Philip & Kohls, 1948; Traub *et al.*, 1950.
- Schöngastia blestowei* (J. de Vidas, 1945) Brumpt, 1949.
- Schöngastia blestowei* v. *megapodius* Womersley & Heaslip, 1943. Finnegan, 1945.
- (?) *Leeuwenhoekia blestowei* Gunther, 1945.
- (non) *Schöngastia vandersandei* (Oudemans, 1905). Dumbleton, 1946; Philip & Kohls, 1948; Traub *et al.*, 1950.
- Bush-mokka, pipi, gugung* (New Guinea: Gunther, 1939a).
- Type, Larva: School Public Health Trop. Med., Univ. Sydney.
- Paratypes, Larvae: British Mus., Australian Mus., S. Australian Mus., Rocky Mountain Lab.
- New Guinea: Man, bush fowl (*Megapodius reinwardt*), lizards, snakes, birds, *Rattus browni*, bandicoot (*Echymipera cockerelli*), wallaby, free.
Philippine Is.: Rats.

SCHÖNGASTIA JAMESI Gunther, 1939.

GUNTER, C. E. M., 1939: PROC. LINN. SOC. N.S.W., lxiv, i/ii, 73.

Schöngastia rotunda Gunther, 1938 (*nom. nud.*).

Schöngastia jamesi Gunther, 1939a, 1940d, 1941c, 1942. Womersley, 1939; Radford, 1942; Womersley & Heaslip, 1943; Finnegan, 1945.

Schöngastia jamesi Blake *et al.*, 1945a (*laps. cal.*).

Type, Larva: School Public Health Trop. Med., Univ. Sydney.

Paratype, Larva: Australian Museum.

New Guinea: Bush fowl (*Megapodius reinwardt*), bandicoot (*Echymipera cockerelli*).

SCHÖNGASTIA TAYLORI Gunther, 1940.

GUNTER, C. E. M., 1940: PROC. LINN. SOC. N.S.W., lxxv, iii/iv, 250.

Schöngastia taylori Gunther, 1940a, 1940d, 1941c. Womersley & Heaslip, 1943; Blake *et al.*, 1945a.

Type, Larva: School Public Health Trop. Med., Univ. Sydney.

Paratypes, Larvae: British Mus., Australian Mus., S. Australian Mus., Rocky Mountain Lab.

New Guinea: Wallaby.

SCHÖNGASTIA KATONIS Womersley & Heaslip, 1943.

WOMERSLEY, H., & HEASLIP, W. G., 1943: *Trans. Roy. Soc. S. Aust.*, lxxvii, i, 68.

Carasou-mite of Kato: Kawamura & Yamaguchi, 1921. Walch, 1923, 1924a.

Schöngastia katonis Womersley & Heaslip, 1943.

Type, Larva.

Parao Is.: Man.

SCHÖNGASTIA PUSILLA Womersley, 1944.

WOMERSLEY, H., 1944: *Trans. Roy. Soc. S. Aust.*, lxxviii, i, 82.

Schöngastia pusilla Womersley, 1944. McCulloch, 1944, 1946; Philip & Kohls, 1945, 1948; Blake *et al.*, 1945a, 1945c; Kohls *et al.*, 1945; Bushland, 1946a, 1946b, 1946c; Fuller, 1947b; Griffiths, Mohr, 1947; Kohls, 1948.

Schöngastia pusilla (J. de Vidas, 1945) Brumpton, 1949.

(non) *Schöngastia schüffneri* (Walch, 1923). Griffiths, 1947; Philip & Kohls, 1948.

Type, Larva: South Australian Museum.

New Guinea: Man, rats, free.

Philippine Is.: Rats.

SCHÖNGASTIA MALDIVENSIS Radford, 1946.

RADFORD, C. D., 1946: *Parasitology*, xxxvii, i/ii, 46.

Schöngastia maldivensis Radford, 1946b.

Types, Nymph & Larva: British Museum.

Paratypes, Nymph: Coll. Radford. Larvae: U.S. Nat. Mus., Coll. Radford, Coll. Brennan, Coll. André.

Maldives Is.: Lizard (*Calotes versicolor*), *R. norvegicus*.

SCHÖNGASTIA PHILIPI Womersley & Kohls, 1947.

WOMERSLEY, H., & KOHLS, G. M., 1947: *Trans. Roy. Soc. S. Aust.*, lxxix, i, 3.

Schöngastia philipi Womersley & Kohls, 1947.

Type, Larva: South Australian Museum.

Paratypes, Larvae: S. Australian Museum, British Museum, U.S. National Museum, Rocky Mountain Laboratory.

Goodenough Is., N.G.: Lizard (*Leiolopisma albertisii*).

NOTE.—For the benefit of anyone seeking names for future species, it should be recorded that a *nomen nudum* (*Schöngastia parva* McCulloch, 1946) and a misidentification (*Schöngastia minor* U.S. War Dept., 1944) have confused these specific names for this genus.

PART XIV.

GENUS NEOSCHÖNGASTIA Ewing, 1929.

- EWING, H. E., 1929: A Manual of External Parasites, London.
- Schöngastia* Oudemans, 1910a (*partim*). Hirst, 1915b, 1929a, 1929b; Ewing, 1925.
- Neoschöngastia* EWING, 1929, 1938, 1942, 1944a, 1944b, 1946b. Gater, 1932; Thor, 1935, 1936; Fonseca, 1936; WOMERSLEY, 1937, 1939; Gunther, 1939a, 1940a, 1942; Womersley & Heaslip, 1943; Radford, 1946c; WOMERSLEY & KOHLS, Thor & Willmann, 1947; Philip & Woodward, 1946b; WHARTON & HARDCASTLE, 1946; Lawrence, 1949; Jones, 1950; WHARTON *et al.*, 1951.
- Paraschöngastia* Womersley, 1939. Gunther, 1940a; EWING, 1942, 1944a, 1944b, 1946b; Wharton & Hardcastle, 1946.
- (*non*) *Trombicula* Berlese, 1905. Walch, 1923, 1924a, 1925, 1927; Fletcher *et al.*, 1928; Patton & Evans, 1929.
- (*non*) *Trombidium* Walch, 1927.
- (*non*) *Schöngastia* Oudemans, 1910a. Hirst, 1929a, 1929b, 1929c, 1929d; Womersley, 1934, 1937.

Genotype, *Neoschöngastia americana* (Hirst, 1921).

In 1939 Womersley investigated several species of *Neoschöngastia* described by me from New Guinea, and erected a new genus, *Paraschöngastia*, to accommodate certain of them. But Ewing (1946b) re-examined the genotype of his genus *Neoschöngastia*, *N. americana* (Hirst, 1921), and found that it had the special scutal characteristics of Womersley's *Paraschöngastia*. Consequently, *Paraschöngastia* reverted as a synonym of *Neoschöngastia*, and Ewing erected *Ascoschöngastia* to accommodate those species of *Neoschöngastia* which lacked the special scutal characteristics. Unfortunately this did not solve things, because Ewing selected *N. malayensis* Gater, 1932, as the genotype of *Ascoschöngastia*, and it has its posterolateral scutal setae placed alongside, not upon, its scutum, and if this is to be regarded as a generic character (and even more trivial characters are being so regarded these days), the remainder of the unspecialized members of *Neoschöngastia* have only *Euschöngastia* Ewing, 1938, to go to, and in Ewing's original definition *Euschöngastia* has 5 to 7 palpal claws in 2 or 3 pairs.

In fact, the whole situation is quite unsatisfactory, as will be evident if we consider, for example, the well-known species originally described by Hirst (1915) as *Schöngastia indica*; this species has been labelled *Neoschöngastia*, *Euschöngastia*, and *Ascoschöngastia* by equally competent authorities within the last few years. The key given by Wharton *et al.* (1951) does not solve the problem either. So I am hereby taking the bull by the horns and regarding *Ascoschöngastia* as containing only *A. malayensis*, and *Euschöngastia* as containing only *E. sciuricola* (Ewing, 1925) Ewing, 1938, and I am listing all other species as *Neoschöngastia* until they are properly sorted out. Indeed, I believe that such a course is inevitable in the present state of our knowledge of the Asian and Australasian species, very few of which could at the present time be allotted with accuracy to those other genera.

NEOSCHÖNGASTIA INDICA (Hirst, 1915) Gater, 1932.

- HIRST, S., 1915: *Bull. Ent. Res.*, vi, iii, 183; GATER, B. A. R., 1932: *Parasitology*, xxiv, ii, 143.
- Schöngastia indica* Hirst, 1915b. Walch, 1927; Finnegan, 1945.
- Trombicula muris* Walch, 1923, 1924a, 1927. Fletcher *et al.*, 1928; Hayakawa & Hokari, 1947.
- Trombicula muris* Walch, 1922. Womersley & Heaslip, 1943.
- Trombicula indica* (*muris*) Patton & Evans, 1929.
- Neoschöngastia indica* Gater, 1932. Gunther, 1941c; Heaslip, 1941; Radford, 1942, 1946b; Womersley & Heaslip, 1943; Blake *et al.*, 1945a; Hayakawa Tanaka *et al.*, Finnegan, 1945; Wharton & Carver, Philip *et al.*, Woodward *et al.*, 1946; Thor & Willmann, Mohr, Hayakawa & Hokari, 1947.

- Neoschöngastia muris* (Walch, 1923). Radford, 1942.
Ascoschöngastia indica Ewing, 1946b. Wharton, 1946b; Philip & Woodward, 1946b; Sayers *et al.*, Griffiths, 1947.
Euschöngastia indica Traub, 1949. Traub *et al.*, Philip & Traub, Audy & Harrison, 1950.
Neoschöngastia cockingsi Radford, 1946c.
Ascoschöngastia cockingsi Ewing, 1946b. Sayers *et al.*, 1947.
 (non) *Microtrombidium muris* Oudemans, 1912b.
 Types, *Adult, Nymph & Larva*: British Museum.
 Paratypes, *Adult*: U.S. National Museum. *Larvae*: Molteno Institute, U.S. National Museum, South Australian Museum, Coll. Radford.
 Sumatra: Rats (*R. diardi*, *R. jalorensis*).
 Celebes: Rats.
 Malaya: Rats (*R. jalorensis*, *R. concolor*, *R. vociferans*, *R. malaisia*).
 Bengal: Mouse (*Nesokia bengalensis*).
 Ceylon: *R. kandinus*.
 Maldive Is.: *R. norvegicus*.
 Burma.
 Philippine Is.: Rats (*R. mindanensis*, *R. calcis*, *R. alexandrinus*, *R. norvegicus*).
 Guam: *Rattus* sp.
 Queensland: Rats and bandicoots.

NEOSCHÖNGASTIA SALMI (Oudemans, 1922) Gunther, 1941.

- OÜDEMANS, A. C., 1922: *Ent. Ber. Ned. Ent. Ver.*, vi, cxxvi, 81; GUNTHER, C. E. M., 1941: *PROC. LINN. SOC. N.S.W.*, lxvi, v/vi, 391.
Schöngastia salmi Oudemans, 1922. Salm, 1923.
Schöngastia (Trombicula) salmi Walch, 1927.
Neoschöngastia salmi Gunther, 1941c.
Schöngastia salmi (incertae sedis) Womersley, 1944.
 Type, *Larva*.
 Java: (Host not specified.)

NEOSCHÖNGASTIA GALLINARUM (?) (Hatori, 1920) Sugimoto, 1936.

- HATORI, J., 1920: *Taiwan Igaku Zasshi*, No. 209, 317; SUGIMOTO, M., 1936: *J. Jap. Soc. Vet. Sci.*, xv, i, 201.
Trombicula (?) gallinarum Hatori, 1920 (? *nom. nud.*).
Trombicula gallinarum Hatori, 1919 (?). KAWAMURA & YAMAGUCHI, 1921; Walch, 1923, 1924a, 1925; Kawamura, 1926; Fletcher *et al.*, 1928; Patton & Evans, 1929.
Trombicula gallinarum Kawamura & Yamaguchi. Womersley & Heaslip, 1943.
Neoschöngastia gallinarum (Hatori, 1920). Sugimoto, 1936a, 1936b, 1938; Radford, 1942, 1946b.
Neoschöngastia gallinarum (Kawamura & Yamaguchi, 1921). Ewing, 1946a; Philip & Woodward, 1946b; Wharton & Hardcastle, 1946.
Paraschöngastia gallinarum (Kawamura & Yamaguchi, 1921). Womersley & Heaslip, 1943.
 Types, *Nymph & larva*: Taihoku University Museum.
 Formosa: Crow (*Corvus colonorum*), pheasant (*Centropus lignator*), *Alcedo japonica*, *Gallus gallus*, sparrow (*Passer tivanensis*), *Caprimulgus monticola*.
 Malaya: *G. gallus*.

NEOSCHÖNGASTIA GLOBULARE (Walch, 1927) Gunther, 1941.

- WALCH, E. W., 1927: *Geneesk. Tijdschr. v. Ned.-Ind.*, lxxvii, 922; GUNTHER, C. E. M., 1941; *PROC. LINN. SOC. N.S.W.*, lxvi, v/vi, 391.
Trombidium (Trombicula ?) globulare Walch, 1927.
 "Trombidium globulare" Gater, 1932.
Neoschöngastia globulare Gunther, 1941c. Womersley & Heaslip, 1943.
 Type, *Larva*.
 Celebes: Rat.

NEOSCHÖNGASTIA ANTIPODIANUM (Hirst, 1929) Gunther, 1939.

HIRST, S., 1929: *Proc. Zool. Soc. Lond.*, ii, 165; GUNTHER, C. E. M., 1939: *Proc. Linn. Soc. N.S.W.*, lxiv, i/ii, 73.

Schöngastia antipodianum Hirst, 1929b. Womersley, 1934, 1937; Radford, 1942.

Neoschöngastia antipodianum Gunther, 1939a. Womersley, 1939; Womersley & Heaslip, 1943.

Type, *Larva*: British Museum.

Kangaroo I., S. Australia: *R. greyii*.

NEOSCHÖNGASTIA COORONGENSE (Hirst, 1929) Gunther, 1939.

HIRST, S., 1929: *Ann. Mag. Nat. Hist.*, x, iii, 564; GUNTHER, C. E. M., 1939: *Proc. Linn. Soc. N.S.W.*, lxiv, i/ii, 73.

Schöngastia coorongense Hirst, 1929a, 1929c, 1929d. Womersley, 1934; Radford, 1942.

Schöngastia coorongensis Womersley, 1937 (*laps. cal.*).

Neoschöngastia coorongense Gunther, 1939a. Womersley, 1939; Heaslip, 1941; Womersley & Heaslip, 1943.

Ascoshöngastia coorongense Philip, 1947c. Womersley & Kohls, 1947.

Type, *Larva*: British Museum.

Paratype, *Larva*: South Australian Museum.

Australia: Rats and bandicoots.

NEOSCHÖNGASTIA DASYCERCI (Hirst, 1929) Gunther, 1939.

HIRST, S., 1929: *Proc. Zool. Soc. Lond.*, ii, 165; GUNTHER, C. E. M., 1939; *Proc. Linn. Soc. N.S.W.*, lxiv, i/ii, 73.

Schöngastia dasycerci Hirst, 1929b. Womersley, 1934, 1937; Radford, 1942.

Neoschöngastia dasycerci Gunther, 1939a. Womersley, 1939; Womersley & Heaslip, 1943.

Type, *Larva*: British Museum.

Paratype, *Larva*: South Australian Museum.

S. Australia: Marsupial mouse (*Dasyercus cristicauda*).

NEOSCHÖNGASTIA (?) DEBILIS Gater, 1932.

GATER, B. A. R., 1932: *Parasitology*, xxiv, ii, 143.

Neoschöngastia debilis Gater, 1932. Radford, 1942; Womersley & Heaslip, 1943.

In the absence of sensillae, the placing of this species is provisional.

Type, *Larva*: British Museum.

Malaya: *R. cremoriventer*.

NEOSCHÖNGASTIA LACUNOSA Gater, 1932.

GATER, B. A. R., 1932: *Parasitology*, xxiv, ii, 143.

Neoschöngastia lacunosa Gater, 1932. Radford, 1942; Womersley & Heaslip, 1943.

Euschöngastia lacunosa Audy & Harrison, 1950.

Type, *Larva*: British Museum.

Paratypes, *Larvae*: U.S. National Museum, Molteno Institute.

Malaya: *R. vociferans*.

NEOSCHÖNGASTIA MUTABILIS Gater, 1932.

GATER, B. A. R., 1932: *Parasitology*, xxiv, ii, 143.

Neoschöngastia mutabilis Gater, 1932. Gunther, 1939a; Radford, 1942; Womersley & Heaslip, 1943.

Ascoshöngastia mutabilis Ewing, 1946b. Audy, Sayers *et al.*, 1947.

Type, *Larva*: British Museum.

Paratypes, *Larvae*: U.S. National Museum, Molteno Institute.

Malaya: *R. vociferans*.

Burma: *R. brunnesculus*, shrew (*Tupaia belangeri*).

NEOSCHÖNGASTIA PETROGALE (Womersley, 1934) Gunther, 1939.

WOMERSLEY, H., 1934: *Rec. S. Aust. Mus.*, v, ii, 179; GUNTHER, C. E. M., 1939: *PROC. LINN. SOC. N.S.W.*, lxiv, i/ii, 73.

Schöngastia petrogale Womersley, 1934, 1937. Radford, 1942.

Neoschöngastia petrogale Gunther, 1939a. Womersley, 1939; Heaslip, 1941; Womersley & Heaslip, 1943.

Type, *Larva*: South Australian Museum.

S. Australia: Wallaby (*Macropus* sp.).

NEOSCHÖNGASTIA WESTRALIENSE (Womersley, 1934) Gunther, 1939.

WOMERSLEY, H., 1934; *Rec. S. Aust. Mus.*, v, ii, 179; GUNTHER, C. E. M., 1939: *PROC. LINN. SOC. N.S.W.*, lxiv, i/ii, 73.

Schöngastia westraliense Womersley, 1934, 1937. Radford, 1942.

Neoschöngastia westraliense Gunther, 1939a. Womersley, 1939; Heaslip, 1941.

Neoschöngastia westraliensis Womersley & Heaslip, 1943 (*laps. cal.*).

Type, *Larva*: South Australian Museum.

Queensland: Rats and bandicoots.

NEOSCHÖNGASTIA BACKHOUSEI Gunther, 1939.

GUNTHER, C. E. M., 1939: *PROC. LINN. SOC. N.S.W.*, lxiv, i/ii, 73.

Neoschöngastia fournieri Gunther, 1938 (*nom. nud.*).

Neoschöngastia backhousei Gunther, 1939a, 1942. Wharton & Hardcastle, 1946.

Paraschöngastia megapodius Womersley, 1939 (*laps. mem.*). Womersley & Heaslip, 1943; Wharton & Hardcastle, 1946.

Paraschöngastia backhousei Gunther, 1940a, 1940d, 1941c.

Neoschöngastia backhousei Radford, 1942 (*laps. cal.*).

Type, *Larva*: School Public Health Tropical Medicine, Univ. Syd.

Paratype, *Larva*: Australian Museum.

New Guinea: Bush fowl (*Megapodius reinwardt*).

NEOSCHÖNGASTIA DUBIA Gunther, 1939.

GUNTHER, C. E. M., 1939: *PROC. LINN. SOC. N.S.W.*, lxiv, i/ii, 73.

Neoschöngastia incerta Gunther, 1938 (*nom. nud.*).

Neoschöngastia dubia Gunther, 1939a, 1942. Radford, 1942; Wharton & Hardcastle, 1946.

Paraschöngastia dubia Womersley, 1939. Gunther, 1940a, 1940d; Womersley & Heaslip, 1943; Kohls *et al.*, 1945.

Type, *Larva*: School Public Health Trop. Med., Univ. Sydney.

New Guinea: Bush fowl (*Megapodius reinwardt*), free.

NOTE.—The absence of sensillae was the reason for calling this species *dubia*; later specimens collected had clavate sensillae, and the genus is no longer in doubt.

NEOSCHÖNGASTIA EDWARDSI Gunther, 1939.

GUNTHER, C. E. M., 1939: *PROC. LINN. SOC. N.S.W.*, lxiv, i/ii, 73.

Neoschöngastia rioi Gunther, 1938 (*nom. nud.*).

Neoschöngastia edwardsi Gunther, 1939a, 1940d, 1942. Womersley, 1939; Radford, 1942;

Womersley & Heaslip, 1943; Finnegan, 1945.

Type, *Larva*: School Public Health Trop. Med., Univ. Sydney.

New Guinea: Bush fowl (*Megapodius reinwardt*), bandicoot (*Echymipera cockerelli*).

NEOSCHÖNGASTIA IMPAR Gunther, 1939.

GUNTHER, C. E. M., 1939: *PROC. LINN. SOC. N.S.W.*, lxiv, i/ii, 73.

Neoschöngastia clauda Gunther, 1938 (*nom. nud.*).

Neoschöngastia impar Gunther, 1939a, 1940a, 1940b, 1940d, 1941c, 1942. Womersley, 1939; Radford, 1942, 1946b; Womersley & Heaslip, 1943; Blake *et al.*, 1945a; Kohls *et al.*, Finnegan, 1945; Mohr, 1947.

Ascoshöngastia impar Griffiths, 1947.

Neoschöngastia bodensis Gunther, 1940b. Womersley & Heaslip, 1943; Finnegan, 1945.

Type, Larva: School Public Health Trop. Med., Univ. Sydney.

Paratypes, Larvae: British Mus., Australian Mus., S. Australian Mus., Natal Mus., P.H.D., Entebbe.

New Guinea: Rats (*R. browni*, *R. praetor*, *R. ringens*, *M. moncktoni*, *M. stalkerii*, *M. rubex*), bandicoots (*E. cockerelli*, *P. raffrayana*), rat.

British North Borneo: Mouse-deer (*Tragulus borneanus*).

NEOSCHÖNGASTIA LORIUS Gunther, 1939.

GUNTHER, C. E. M., 1939: PROC. LINN. SOC. N.S.W., lxiv, i/ii, 73.

Neoschöngastia jimungi Gunther, 1938 (*nom. nud.*).

Neoschöngastia lorius Gunther, 1939a, 1940d, 1942. Womersley, 1939; Radford, 1942; Womersley & Heaslip, 1943.

Type, Larva: School Public Health Trop. Med., Univ. Sydney.

Paratype, Larva: Australian Museum.

New Guinea: Lory (*Lorius rotatus*).

NEOSCHÖNGASTIA RETROCINCTA Gunther, 1939.

GUNTHER, C. E. M., 1939: PROC. LINN. SOC. N.S.W., lxiv, i/ii, 73.

Neoschöngastia retrocoronata Gunther, 1938 (*nom. nud.*).

Neoschöngastia retrocincta Gunther, 1939a, 1942. Radford, 1942; Wharton & Hardcastle, 1946.

Paraschöngastia retrocincta Womersley, 1939. Gunther, 1940a, 1940d; Womersley & Heaslip, 1943.

Type, Larva: School Public Health Trop. Med., Univ. Sydney.

Paratypes, Larvae: Australian Mus., S. Australian Mus.

New Guinea: Bush fowl (*Megapodius reinwardt*).

NEOSCHÖNGASTIA YEOMANSI Gunther, 1939.

GUNTHER, C. E. M., 1939: PROC. LINN. SOC. N.S.W., lxiv, i/ii, 73.

Neoschöngastia jamesi Gunther, 1938 (*nom. nud.*).

Neoschöngastia yeomansi Gunther, 1939a, 1942. Radford, 1942; Ewing, 1946b; Wharton & Hardcastle, 1946.

Paraschöngastia yeomansi Womersley, 1939. Gunther, 1940a, 1940d; Womersley & Heaslip, 1943.

Type, Larva: School Public Health Trop. Med., Univ. Sydney.

Paratypes, Larvae: British Mus., Australian Mus., S. Australian Mus., Rocky Mountain Lab., Natal Mus., P.H.D., Entebbe, Coll. Costa, Coll. Radford.

New Guinea: Bush fowl (*Megapodius reinwardt*).

Palau Is.: *Gallus gallus*, *Megapodius laperouse*.

NEOSCHÖNGASTIA DERRICKI Womersley, 1939.

WOMERSLEY, H., 1939: *Trans. Roy. Soc. S. Aust.*, lxiii, ii, 149.

Neoschöngastia derricki Womersley, 1939. Heaslip, 1941; Womersley & Heaslip, 1943.

Type, Larva: South Australian Museum.

Queensland: *R. lutreolus*, *R. assimilis*, rats and bandicoots.

NEOSCHÖNGASTIA PERAMELES Womersley, 1939.

WOMERSLEY, H., 1939: *Trans. Roy. Soc. S. Aust.*, lxiii, ii, 149.

Neoschöngastia isoodon Derrick *et al.*, 1939 (*nom. nud.*). Womersley, 1939.

Neoschöngastia perameles Womersley, 1939. Heaslip, 1941; Womersley & Heaslip, 1943; Fenner, 1946.

Type, Larva: South Australian Museum.

Queensland: Bandicoots (*Isoodon torosus*, *I. obesulus*).

NEOSCHÖNGASTIA QUEENSLANDICA Womersley, 1939.

WOMERSLEY, H., 1939: *Trans. Roy. Soc. S. Aust.*, lxiii, ii, 149.

Neoschöngastia queenslandica Womersley, 1939. Heaslip, 1941; Womersley & Heaslip, 1943.

Type, Larva: South Australian Museum.

Queensland: Rats (*R. assimilis*, *R. youngi*, *R. lutreolus*, *Melomys cervinipes*).

NEOSCHÖNGASTIA SMITHI Womersley, 1939.

WOMERSLEY, H., 1939: *Trans. Roy. Soc. S. Aust.*, lxiii, ii, 149.

Neoschöngastia smithi Womersley, 1939. Heaslip, 1941; Womersley & Heaslip, 1943.

Type, Larva: South Australian Museum.

Queensland: *R. assimilis*.

NEOSCHÖNGASTIA TRICHOSURI (Womersley, 1939), Womersley & Heaslip, 1943.

WOMERSLEY, H., 1939: *Trans. Roy. Soc. S. Aust.*, lxiii, ii, 149; WOMERSLEY, H., & HEASLIP, W. G., 1943: *Ibid.*, lxvii, i, 68.

Neoschöngastia westraliense Hirst (*laps. cal*) var. *trichosuri* Womersley, 1939.

Neoschöngastia westraliense v. *trichosuri* Womersley, 1939: Womersley & Heaslip, 1943.

Neoschöngastia trichosuri Womersley & Heaslip, 1943.

Type, Larva: South Australian Museum.

Queensland: Possum (*Trichosurus vulpecula*).

NEOSCHÖNGASTIA FOLIATA Gunther, 1940.

GUNTHER, C. E. M., 1940: *Proc. Linn. Soc. N.S.W.*, lxxv, iii/iv, 250.

Neoschöngastia foliata Gunther, 1940a, 1940d. Womersley & Heaslip, 1943.

Ascoshöngastia foliata Womersley & Kohls, 1947.

Type, Larva: School Public Health Trop. Med., Univ. Sydney.

Paratypes, Larvae: British Mus., Australian Mus., S. Australian Museum.

New Guinea: Wallaby (*Macropus coxeni*).

NEOSCHÖNGASTIA WOMERSLEYI Gunther, 1940.

GUNTHER, C. E. M., 1940: *Proc. Linn. Soc. N.S.W.*, lxxv, iii/iv, 250.

Neoschöngastia womersleyi Gunther, 1940a, 1940d. Womersley & Heaslip, 1943; Blake *et al.*, 1945a; Radford, 1946b.

Type, Larva: School Public Health Trop. Med., Univ. Sydney.

Paratypes, Larvae: British Museum, Australian Museum.

New Guinea: Wallaby (*Macropus coxeni*), rats (*R. browni*, *R. mordax*, *R. praetor*), bandicoot (*Echymipera cockerelli*).

NEOSCHÖNGASTIA (?) SHIELDSI Gunther, 1941.

GUNTHER, C. E. M., 1941: *Proc. Linn. Soc. N.S.W.*, lxxvi, iii/iv, 157.

Neoschöngastia shieldsi Gunther, 1941b. Womersley & Heaslip, 1943.

In the absence of sensillae, the placing here adopted is provisional.

Type, Larva: School Public Health Trop. Med., Univ. Sydney.

Paratypes, Larvae: British Museum, Australian Museum.

New Guinea: Rat (*Melomys rubex*).

NEOSCHÖNGASTIA CAIRNSSENSIS Womersley & Heaslip, 1943.

WOMERSLEY, H., & HEASLIP, W. G., 1943: *Trans. Roy. Soc. S. Aust.*, lxxvii, i, 68.

Neoschöngastia cairnsensis Womersley & Heaslip, 1943. Fenner, McCulloch, 1946.

Neoschöngastia cairnsensis var. *gateri* Womersley & Heaslip, 1943.

Type, Larva: South Australian Museum.

Queensland: Rats (*R. youngi*, *R. lutreolus*, *R. assimilis*), bandicoots (*Isoodon torosus*, *I. obesulus*, *Perameles nasuta*), *Uromys sherrini*, *Melomys cervinipes*.

NEOSCHÖNGASTIA (GUNTHERI) (Womersley & Heaslip, 1943).

WOMERSLEY, H., & HEASLIP, W. G., 1943: *Trans. Roy. Soc. S. Aust.*, lxxvii, i, 68.

Neoschöngastia guntheri Womersley & Heaslip, 1943 (*nom. praecoc.*). Fenner, 1946.

(*non*) *Neoschöngastia guntheri* Radford, 1942.

I have written to Mr. Womersley about the specific name of this species, and as it is his privilege to select a new name, I am leaving it listed as above in the meantime.

Type, *Larva*: South Australian Museum.

Queensland: Rats, *Hydromys longmani*.

NEOSCHÖNGASTIA HEASLIPI Womersley & Heaslip, 1943.

WOMERSLEY, H., & HEASLIP, W. G., 1943: *Trans. Roy. Soc. S. Aust.*, lxxvii, i, 68.
Neoschöngastia heaslipi Womersley & Heaslip, 1943.

Type, *Larva*: South Australian Museum.

Queensland: Rats.

NEOSCHÖNGASTIA (?) HIRSTI Womersley & Heaslip, 1943.

WOMERSLEY, H., & HEASLIP, W. G., 1943: *Trans. Roy. Soc. S. Aust.*, lxxvii, i, 68.
Neoschöngastia hirsti Womersley & Heaslip, 1943. McCulloch, Fenner, 1946.

In the absence of sensillae the placing of this species is regarded as provisional.

Type, *Larva*: South Australian Museum.

Queensland: *Uromys sherrini*, *Melomys cervinipes*, possum (*Trichosurus vulpecula*), bandicoot (*Isodon obesulus*), rats.

NEOSCHÖNGASTIA INNISFAILENSIS Womersley & Heaslip, 1943.

WOMERSLEY, H., & HEASLIP, W. G., 1943: *Trans. Roy. Soc. S. Aust.*, lxxvii, i, 68.
Neoschöngastia innisfailensis Womersley & Heaslip, 1943.

Ascoschöngastia innisfailensis Philip, 1947c. Womersley & Kohls, 1947.

Type, *Larva*: South Australian Museum.

Queensland: *Melomys littoralis*.

NEOSCHÖNGASTIA MELOMYS Womersley & Heaslip, 1943.

WOMERSLEY, H., & HEASLIP, W. G., 1943: *Trans. Roy. Soc. S. Aust.*, lxxvii, i, 68.
Neoschöngastia melomys Womersley & Heaslip, 1943. McCulloch, 1944.

Type, *Larva*: South Australian Museum.

Queensland: *Melomys littoralis*.

NEOSCHÖNGASTIA PHASCOGALE Womersley & Heaslip, 1943.

WOMERSLEY, H., & HEASLIP, W. G., 1943: *Trans. Roy. Soc. S. Aust.*, lxxvii, i, 68.
Neoschöngastia phascogale Womersley & Heaslip, 1943.

Type, *Larva*: South Australian Museum.

Queensland: *Phascogale* sp., bandicoots (*Isodon torosus*, *Perameles nasuta*).

NEOSCHÖNGASTIA RATTUS Womersley & Heaslip, 1943.

WOMERSLEY, H., & HEASLIP, W. G., 1943: *Trans. Roy. Soc. S. Aust.*, lxxvii, i, 68.
Neoschöngastia rattus Womersley & Heaslip, 1943. Mohr, 1947.

Type, *Larva*: South Australian Museum.

Queensland: *R. assimilis*.

New Guinea: Rats.

NEOSCHÖNGASTIA SIMILIS Womersley & Heaslip, 1943.

WOMERSLEY, H., & HEASLIP, W. G., 1943: *Trans. Roy. Soc. S. Aust.*, lxxvii, i, 68.
Neoschöngastia similis Womersley & Heaslip, 1943.

Type, *Larva*: South Australian Museum.

Queensland: Rats.

NEOSCHÖNGASTIA MCCULLOCHI Womersley, 1944.

WOMERSLEY, H., 1944: *Trans. Roy. Soc. S. Aust.*, lxxviii, i, 82.
Neoschöngastia mccullochi Womersley, 1944.

Ascoschöngastia mccullochi Womersley & Kohls, 1947.

Type, *Larva*: South Australian Museum.

New Guinea: Free.

NEOSCHÖNGASTIA SOEKABOEMIENSIS (Takekawa, 1945) Hayakawa & Hokari, 1947.

TAKEKAWA, S., 1945: *Nampogun Boekikyusui Bu*, cxvii; HAYAKAWA, K., & HOKARI, K., 1947: A Comparative Study of Japanese & Tropical Tsutsugamushi Diseases, Tokyo. *Trombicula soekaboemiensis* Takekawa, 1945.

Neoschöngastia soekaboemiensis Hayakawa & Hokari, 1947.

Type, Larva.

Java.

NEOSCHÖNGASTIA LANIUS Radford, 1946.

RADFORD, C. D., 1946: *Proc. Zool. Soc.*, cxvi, ii, 247.

Neoschöngastia lanius Radford, 1946c.

Ascoshöngastia lanius Sayers et al., 1947.

Type, Larva: British Museum.

Manipur: Shrike (*Lanius nasutus*).

NEOSCHÖNGASTIA MANIPURENSIS Radford, 1946.

RADFORD, C. D., 1946: *Proc. Zool. Soc.*, cxvi, ii, 247.

Neoschöngastia manipurensis Radford, 1946c.

Ascoshöngastia manipurensis Sayers et al., 1947.

Type, Larva: British Museum.

Manipur: *R. rufescens*.

NEOSCHÖNGASTIA THOMASI (Radford, 1946) Sayers et al., 1947.

RADFORD, C. D., 1946: *Proc. Zool. Soc.*, cxvi, ii, 247; SAYERS, M. H. P., et al., 1947: Report of Scrub Typhus Res. Lab., War Office.

Paraschöngastia thomasi Radford, 1946c.

Neoschöngastia thomasi Sayers et al., 1947.

Type, Larva: British Museum.

Manipur: Shrike (*Lanius nasutus*).

NEOSCHÖNGASTIA KOHLSI Philip & Woodward, 1946.

PHILIP, C. B., & WOODWARD, T. E., 1946: *Amer. J. Trop. Med.*, xxvi, ii, 157.

Neoschöngastia kohlsi Philip & Woodward, 1946a. Philip et al., 1946.

Ascoshöngastia kohlsi Philip & Woodward, 1946b. Ewing, 1946b; Audy, Sayers et al., 1947.

Holotype, Larva: U.S. National Museum.

Paratypes, Larvae: U.S. National Mus., S. Australian Mus., Rocky Mountain Lab., Coll. Philip, Coll. Woodward.

Philippine Is.: Rats (*R. mindanensis*, *R. vigoratus*).

NEOSCHÖNGASTIA PHILIPPENSIS Philip & Woodward, 1946.

PHILIP, C. B., and WOODWARD, T. E., 1946: *Amer. J. Trop. Med.*, xxvi, ii, 157.

Neoschöngastia philippensis Philip & Woodward, 1946a. Philip et al., 1946.

Ascoshöngastia philippensis Philip & Woodward, 1946b.

Holotype, Larva: U.S. National Museum.

Paratypes, Larvae: U.S. National Mus., S. Australian Mus., Rocky Mountain Lab., Coll. Philip, Coll. Woodward.

Philippine Is.: Rats (*R. mindanensis*, *R. vigoratus*, *R. alexandrinus*).

NEOSCHÖNGASTIA ATOLLENSIS Wharton & Hardcastle, 1946.

WHARTON, G. W., & HARDCASTLE, A. B., 1946: *J. Parasit.*, xxxii, iii, 286.

Neoschöngastia atollensis Wharton & Hardcastle, 1946.

Type, Larva: U.S. National Museum.

Okinawa, Ulithi: *Numenius phaeopus*, birds.

NEOSCHÖNGASTIA BOUGAINVILLENSIS Wharton & Hardcastle, 1946.

WHARTON, G. W., & HARDCASTLE, A. B., 1946: *J. Parasit.*, xxxii, iii, 286.

Neoschöngastia bougainvillensis Wharton & Hardcastle, 1946.

Type, Larva: U.S. National Museum.

Bougainville Is.: *H. tahitica*.

Guam: Noddy (*Anous stolidus*), tattler (*Heteroscelus incanus*).

NEOSCHÖNGASTIA CARVERI Wharton & Hardcastle, 1946.

- WHARTON, G. W., & HARDCASTLE, A. B., 1946: *J. Parasit.*, xxxii, iii, 286.
Neoschöngastia carveri Wharton & Hardcastle, 1946.
 Types, Larva: U.S. National Museum. Nymph: U.S. National Museum.
 Paratypes, Coll. Radford.
 Guam: *Numenius phaeopus*, *Demigretta sacra*, *Pluvialis dominica*, *Arenaria interpres*.
 Okinawa: *Gygis alba*, *Sterna douglasii*, *Monticola solitarius*.
 Ulithi: Plover (*Pluvialis dominica*).
 Peleliu Is.: Tattler (*Heteroscelus incanus*).

NEOSCHÖNGASTIA EGRETTE Wharton & Hardcastle, 1946.

- WHARTON, G. W., & HARDCASTLE, A. B., 1946: *J. Parasit.*, xxxii, iii, 286.
Neoschöngastia egretta Wharton & Hardcastle, 1946.
 Type, Larva: U.S. National Museum.
 Okinawa: Egret (*Egretta intermedia*).
 Ulithi: Egrets (*Egretta intermedia*, *Demigretta sacra*), noddy (*Anous stolidus*), plover (*Pluvialis dominica*).

NEOSCHÖNGASTIA EWINGI Wharton & Hardcastle, 1946.

- WHARTON, G. W., & HARDCASTLE, A. B., 1946: *J. Parasit.*, xxxii, iii, 286.
Neoschöngastia ewingi Wharton & Hardcastle, 1946.
 Type, Larva: U.S. National Museum.
 Ulithi: *Egretta intermedia*, *Pluvialis dominica*, *Gallus gallus*.
 Palau & Peleliu: *Gallus gallus*.
 Guam: *Heteroscelus incanus*.

NEOSCHÖNGASTIA MONTICOLA Wharton & Hardcastle, 1946.

- WHARTON, G. W., & HARDCASTLE, A. B., 1946: *J. Parasit.*, xxxii, iii, 286.
Neoschöngastia monticola Wharton & Hardcastle, 1946.
 Type, Larva: U.S. National Museum.
 Paratype, Coll. Radford.
 Okinawa: *Monticola solitarius*, birds.

NEOSCHÖNGASTIA NAMRUI Wharton & Hardcastle, 1946.

- WHARTON, G. W., & HARDCASTLE, A. B., 1946: *J. Parasit.*, xxxii, iii, 286.
Neoschöngastia namrui Wharton & Hardcastle, 1946.
 Type, Larva: U.S. National Museum.
 Paratype, Coll. Radford.
 Guam: *Numenius phaeopus*, *Heteroscelus incanus*, *Pluvialis dominica*.
 Okinawa: *Gygis alba*.
 Ulithi: Shore birds.

NEOSCHÖNGASTIA PAUENSIS Wharton & Hardcastle, 1946.

- WHARTON, G. W., & HARDCASTLE, A. B., 1946: *J. Parasit.*, xxxii, iii, 286.
Neoschöngastia pauensis Wharton & Hardcastle, 1946.
 Type, Larva: U.S. National Museum.
 Paratype, Coll. Radford.
 Ulithi: Plover (*Pluvialis dominica*).

NEOSCHÖNGASTIA POSEKANYI Wharton & Hardcastle, 1946.

- WHARTON, G. W., & HARDCASTLE, A. B., 1946: *J. Parasit.*, xxxii, iii, 286.
Neoschöngastia posekanyi Wharton & Hardcastle, 1946.
 Type, Larva: U.S. National Museum.
 Paratype, Coll. Radford.
 Okinawa: *Monticola solitarius*, *Streptopelia orientalis*.

NEOSCHÖNGASTIA RIVERSI Wharton & Hardcastle, 1946.

WHARTON, G. W., & HARDCASTLE, A. B., 1946: *J. Parasit.*, xxxii, iii, 286.
Neoschöngastia riversi Wharton & Hardcastle, 1946.

Type, *Larva*: U.S. National Museum.

Paratype, Coll. Radford.

Bougainville: *Eurystomus orientalis*, *Haliacetus sanfordi*, *Falco severus*.

Philippine Is.: *Halcyon chloris*, *Eurystomus orientalis*.

NEOSCHÖNGASTIA SOLOMONIS (Wharton & Hardcastle, 1946).

WHARTON, G. W., & HARDCASTLE, A. B., 1946: *J. Parasit.*, xxxii, iii, 286.
Neoschöngastia americana solomonis Wharton & Hardcastle, 1946. Wharton, 1946b.

Type, *Larva*: U.S. National Museum.

Paratype, Coll. Radford.

Bougainville: *Hirundo tahitica*.

Guam: *Anous stolidus*.

Iwo Jima: *Monticola solitarius*.

Okinawa: *Monticola solitarius*, *Streptopelia orientalis*, *Butorides striatus*, birds.

NEOSCHÖNGASTIA STRONGI Wharton & Hardcastle, 1946.

WHARTON, G. W., & HARDCASTLE, A. B., 1946: *J. Parasit.*, xxxii, iii, 286.
Neoschöngastia strongi Wharton & Hardcastle, 1946.

Type, *Larva*: U.S. National Museum.

Guam: *Numenius phaeopus*. Peleliu: *Arenaria interpres*.

NEOSCHÖNGASTIA BUSHLANDI (Philip, 1947).

PHILIP, C. B., 1947: *J. Parasit.*, xxxiii, v, 387.
Ascoschöngastia bushlandi Philip, 1947c.

Holotype, *Larva*: U.S. National Museum.

Paratypes, *Larvae*: U.S. National Mus., British Mus., S. Australian Mus., Rocky Mountain Lab., Coll. Wharton, Coll. Philip, Coll. Bushland.

Owi Is., N.G.: Bush turkey (*Megapodius* sp.).

NEOSCHÖNGASTIA ECHYMIPERA (Womersley & Kohls, 1947).

WOMERSLEY, H., & KOHLS, G. M., 1947: *Trans. Roy. Soc. S. Aust.*, lxxi, i, 3.
Ascoschöngastia echymipera Womersley & Kohls, 1947.

Type, *Larva*: South Australian Museum.

Paratypes, *Larvae*: S. Australian Mus., British Mus., U.S. National Mus., Rocky Mountain Lab.

New Guinea: Bandicoot (*Echymipera cockerelli*).

NEOSCHÖNGASTIA UROMYS (Womersley & Kohls, 1947).

WOMERSLEY, H., & KOHLS, G. M., 1947: *Trans. Roy. Soc. S. Aust.*, lxxi, i, 3.
Ascoschöngastia uromys Womersley & Kohls, 1947.

Type, *Larva*: South Australian Museum.

Paratypes, *Larvae*: S. Australian Mus., U.S. National Mus., British Mus., Rocky Mountain Lab.

New Guinea: *Uromys lamingtonensis*.

NEOSCHÖNGASTIA MASTA (Traub & Sundermeyer, 1950).

TRAUB, R., & SUNDERMEYER, E. W., 1950: *Proc. Helminth. Soc. Wash.*, xvii, i, 35.
Ascoschöngastia masta Traub & Sundermeyer, 1950.

Cotypes, *Larvae*: U.S. National Museum, Rocky Mountain Lab., British Mus., S. Australian Mus.

Burma: *R. rattus*, shrews (*Tupaia belangeri*, *Crocidura* sp.).

NOTE.—There is a misidentification (*Neoschöngastia minor* Bull. U.S. Army Med. Dept., 1944) which confuses this specific name for this genus.

PART XV.

Genus ASCOSCHÖNGASTIA Ewing, 1946.

- EWING, H. E., 1946: *Proc. Biol. Soc. Wash.*, lix, 69.
Neoschöngastia EWING, 1929 (*partim*). Ewing, 1946b.
Ascoschöngastia EWING, 1946b. Philip & Woodward, 1946b; Radford, 1946c; Wharton, 1946b, 1947c; Sayers *et al.*, Griffiths, Womersley & Kohls, Audy, 1947; Philip, 1947c; Traub & Sundermeyer, Audy & Harrison, 1950; WHARTON *et al.*, 1951.
 Genotype, *Ascoschöngastia malayensis* (Gater, 1932) Ewing, 1946.
 As *A. malayensis* has a special feature not shared by the many species labelled *Ascoschöngastia* in recent years, and as in any case it is not possible to assign many of the Asian and Australasian species correctly to this genus, I have left all the other similar species in *Neoschöngastia* until they can be properly sorted out.

ASCOSCHÖNGASTIA MALAYENSIS (Gater, 1932) Ewing, 1946.

- GATER, B. A. R., 1932: *Parasitology*, xxiv, ii, 143; EWING, H. E., 1946: *loc. cit. supra*.
Neoschöngastia malayensis Gater, 1932. Radford, 1942; Womersley & Heaslip, 1943.
Trombicula malayensis Hayakawa Tanaka *et al.*, 1945; Hayakawa & Hokari, 1947.
Ascoschöngastia malayensis Ewing, 1946b. Audy & Harrison, Traub & Sundermeyer, 1950; WHARTON *et al.*, 1951.
 Type, *Larva*: British Museum.
 Paratype, *Larva*: U.S. National Museum.
 Malaya: *R. malaisia*.

PART XVI.

Genus MYOTROMBICULA Womersley & Heaslip, 1943.

- WOMERSLEY, H., & HEASLIP, W. G., 1943: *Trans. Roy. Soc. S. Aust.*, lxxvii, i, 68.
Myotrombicula Womersley & Heaslip, 1943. Ewing, 1944b, 1946a; Lawrence, 1929; WHARTON *et al.*, 1951.
 Genotype, *Myotrombicula vespertilionis* Womersley & Heaslip, 1943.

MYOTROMBICULA VESPERTILIONIS Womersley & Heaslip, 1943.

- WOMERSLEY, H., & HEASLIP, W. G., 1943: *loc. cit. supra*.
Myotrombicula vespertilionis Womersley & Heaslip, 1943. Fischbach & Howell, 1945; Wharton *et al.*, 1951.
 The shape of the sensillae of this species is unknown.
 Type, *Larva*: South Australian Museum.
 South Australia (?): ? bats.

PART XVII.

Genus OENOSCHÖNGASTIA Womersley & Kohls, 1947.

- WOMERSLEY, H., & KOHLS, G. M., 1947: *Trans. Roy. Soc. S. Aust.*, lxxi, i, 3.
Oenoschöngastia Womersley & Kohls, 1947. WHARTON *et al.*, 1951.
 Genotype, *Oenoschöngastia cana* Womersley & Kohls, 1947.

OENOSCHÖNGASTIA CANA Womersley & Kohls, 1947.

- WOMERSLEY, H., & KOHLS, G. M., 1947: *loc. cit. supra*.
Oenoschöngastia cana Womersley & Kohls, 1947. Wharton *et al.*, 1951.
 Type, *Larva*: South Australian Museum.
 Paratypes, *Larvae*: South Australian Museum, Rocky Mountain Laboratory, U.S. National Museum, British Museum, Coll. Radford.
 New Guinea: Free (mound of brush turkey).

PART XVIII.

Genus HEASLIPIA (Womersley & Heaslip, 1943) Ewing, 1944.

- WOMERSLEY, H., & HEASLIP, W. G., 1943: *Trans. Roy. Soc. S. Aust.*, lxxvii, i, 68;
 EWING, H. E., 1944: *Proc. Biol. Soc. Wash.*, lvii, 101.
Trombiculoides Womersley & Heaslip, 1943 (*nom. praeocc.*: *non Trombiculoides* Jacot, 1938). Ewing, 1944a.

- Heaslipia* Ewing, 1944a, 1944b, 1946a. Lawrence, 1949; Wharton *et al.*, 1951.
Heaslipia (*Trombiculoides*) Philip *et al.*, 1946. Philip & Woodward, 1946a, 1946b.
 Genotype, *Heaslipia gateri* (Womersley & Heaslip, 1943) Ewing, 1944.

HEASLIPIA GATERI (Womersley & Heaslip, 1943) Ewing, 1944.

WOMERSLEY, H., & HEASLIP, W. G., 1943: *loc. cit. supra*: EWING, H. E., 1944: *loc. cit. supra*.

Trombiculoides gateri Womersley & Heaslip, 1943. Wharton *et al.*, 1951.

Heaslipia gateri Ewing, 1944a.

Heaslipia (*Trombiculoides*) *gateri* Philip *et al.*, 1946. Philip & Woodward, 1946a, 1946b.

Type, *Larva*: South Australian Museum.

Malaya: *R. argentiventer*.

PART XIX.

Genus NOVOTROMBICULA Womersley & Kohls, 1947.

WOMERSLEY, H., & KOHLS, G. M., 1947: *Trans. Roy. Soc. S. Aust.*, lxxi, i, 3.

Novotrombicula Womersley & Kohls, 1947. Wharton *et al.*, 1951.

Genotype, *Novotrombicula owiensis* Womersley & Kohls, 1947.

NOVOTROMBICULA OWIENSIS Womersley & Kohls, 1947.

WOMERSLEY, H., & KOHLS, G. M., 1947: *loc. cit. supra*.

Novotrombicula owiensis Womersley & Kohls, 1947. Wharton *et al.*, 1951.

Type, *Larva*: South Australian Museum.

Paratypes, *Larvae*: South Australian Museum, U.S. National Mus.

Owi Is., New Guinea: Free.

PART XX.

Genus MACKIENA Traub & Evans, 1950.

TRAUB, R., & EVANS, T. M., 1950: *J. Wash. Acad. Sci.*, xl, iv, 126.

Mackiena Traub & Evans, 1950a. Wharton *et al.*, 1951.

Genotype, *Mackiena empodiformis* Traub & Evans, 1950.

This genus should most likely be listed as a synonym of *Neoschöngastia* Ewing, 1929, but I am leaving it as distinct for the present.

MACKIENA EMPODIFORMIS Traub & Evans, 1950.

TRAUB, R., & EVANS, T. M., 1950: *loc. cit. supra*.

Mackiena empodiformis Traub & Evans, 1950a. Wharton *et al.*, 1951.

Holotype, *Larva*: U.S. National Museum.

Paratype, *Larva*: British Museum.

Burma: Weaver-finch (*Ploceus peguensis*).

PART XXI.

Genus TRISSETICA Traub & Evans, 1950.

TRAUB, R., & EVANS, T. M., 1950: *J. Parasit.*, xxxvi, iv, 356.

Trisetica Traub & Evans, 1950b. Wharton *et al.*, 1951.

Genotype, *Trisetica melvini* Traub & Evans, 1950.

This genus is fairly obviously a synonym of *Tecomatlana* Hoffmann, 1947, but it must be left here for the present.

TRISSETICA MELVINI Traub & Evans, 1950.

TRAUB, R., & EVANS, T. M., 1950: *loc. cit. supra*.

Trisetica melvini Traub & Evans, 1950b. Wharton *et al.*, 1951.

Holotype, *Larva*: U.S. National Museum.

Paratypes, *Larvae*: South Australian Museum, Rocky Mountain Lab., Chicago Natural History Museum.

Burma: Free in cave frequented by bats.

PART XXII.

Subfamily LEEUWENHOEKIINAE Womersley, 1944.

WOMERSLEY, H., 1944: *Trans. Roy. Soc. S. Aust.*, lxviii, i, 82.
 Trombiculinae Ewing, 1929 (*partim*).
 Leeuwenhoekinae Womersley, 1944. Ewing, 1946a; Wharton, 1947c; Lawrence, 1949;
 WHARTON *et al.*, 1951.

Leeuwenhoekinae Radford, 1946b (*laps. cal.*).

(*non*) Leeuwenhoekidae Womersley, 1945. Ewing, 1946a.

Type Genus, *Leeuwenhoekia* Oudemans, 1911.

Ewing (1942) split off *Comatacarus* and *Acomatacarus* from *Leeuwenhoekia*, and allied them with *Apolonia*; Womersley in 1944 raised *Leeuwenhoekia* to the status of a subfamily, but recognized only the one genus, *Leeuwenhoekia*. Then, in 1945, Womersley raised his subfamily to the status of a family, and included *Leeuwenhoekia*, *Comatacarus*, *Acomatacarus*, *Hannemania* Oudemans, 1911, and *Apolonia* Torres & Braga, 1939, together with a genus known only from the adult, *Neotrombidium* Leonardi, 1901. Womersley also transferred to *Acomatacarus* four adults previously assigned to other genera.

However, Ewing (1946a) and later authorities refused to agree that the Leeuwenhoekinae merited family status, and Wharton (1947c) redefined the subfamily and included the following genera:

Leeuwenhoekia Oudemans, 1911 (Type, *Heterothrombidium verduni* Oudemans, 1910).

Hannemania Oudemans, 1911 (Type, *Heterothrombidium hylodeus* Oudemans, 1910).

Odontacarus Ewing, 1929 (Type, *Trombicula dentata* Ewing, 1925).

Comatacarus Ewing, 1942 (Type, *C. americanus* Ewing, 1942).

Acomatacarus Ewing, 1942 (Type, *A. arizonensis* Ewing, 1942).

Whartonia Ewing, 1944 (Type, *Hannemania nudosetosa* Wharton, 1938).

Chatia Brennan, 1946 (Type, *C. setosa* Brennan, 1946).

Apolonia was transferred by Wharton to the Apoloniinae.

Finally, Wharton *et al.* (1951) made *Comatacarus* a subgenus of *Leeuwenhoekia* and made three new genera of Lawrence's (1949) into subgenera of *Acomatacarus* (these will be listed here as synonyms, since I am not dealing at present with subgenera).

An interesting point arises following the transfer by Womersley of four adults to *Acomatacarus*. They are one of the four Australian species of *Calothrombium* and three of the four species of *Microtrombidium* (*Dromeothrombium*), which were transferred because they are stated to be congeneric with Philip's nymph of *A. australiensis* and Kohls' nymphs of *A. nova-guinea* and *A. longipes*. Now the genus *Calothrombium* is by Berlese, 1918, and *Dromeothrombium* is a subgenus by Berlese dated 1912—and Article 27 of the International Rules of Zoological Nomenclature states:

"The Law of Priority obtains and consequently the oldest available name is retained:

"(b) When any stage in the life history is named before the animal itself;

"(d) When an animal represents a regular succession of dissimilar generations which have been considered as belonging to different species or even to different genera."

I am, however, deterred from adopting *Dromeothrombium* Berlese, 1912, as the prior name for *Acomatacarus* Ewing, 1942, because Womersley did not transfer all of the available members of the two genera concerned, but only some. This leaves a reasonable suspicion that Womersley's former placings of either the included or the excluded species were wrong, and since some have been left behind one must assume at present that they are still correctly placed and that the others were not.

The only other point is that Radford (1946b) described a new genus, *Womersleyia*, without mentioning how many segments its legs possessed (and so there is no way of deciding in what subfamily it belongs—this is an unfortunate weakness of Wharton *et al.* in their 1951 key); he placed it in the Leeuwenhoekinae, where it must stay for the present.

PART XXIII.

Genus HANNEMANIA Oudemans, 1911.

OUDEMANS, A. C., 1911: *Ent. Ber. Ned. Ent. Ver.*, iii, lviii, 137.

Heterothrombidium Verdun, 1909 (*partim*).

Hannemania Oudemans, 1911. Ewing, 1929, 1931, 1942, 1944*b*, 1946*a*; Thor, 1935, 1936; Fonseca, 1936; Womersley, 1937, 1945; Womersley & Heaslip, 1943; Thor & Willmann, 1947; Lawrence, 1949; WHARTON *et al.*, 1951.

(*non*) *Hannemania* Gunther, 1938.

Genotype, *Hannemania hylodeus* (Oudemans, 1910) Oudemans, 1911.

HANNEMANIA VELLAE Dumbleton, 1946.

DUMBLETON, L. J., 1946: *Trans. Roy. Soc. N.Z.*, lxxvi, iii, 409.

Hannemania vellae Dumbleton, 1946.

Type & Paratypes, *Larvae*: South Australian Museum.

Vella Lavella Is., B.S.I.: Bat.

PART XXIV.

Genus ACOMATACARUS Ewing, 1942 (*sensu lato*).

EWING, H. E., 1942: *J. Parasit.*, xxviii, 485.

Leeuwenhoekia Oudemans, 1911 (*partim*). Warburton, 1928; Ewing, 1929; Thor, 1935, 1936; Womersley, 1937, 1944; Gunther, 1939*a*, 1940*d*, 1941*c*, 1942; Womersley & Heaslip, 1943; Thor & Willmann, 1947.

Acomatacarus Ewing, 1942. Dumbleton, 1946; Radford, 1946*c*; Lawrence, Brennan, 1949; WHARTON *et al.*, 1951.

Hyracarus Lawrence, 1949.

Subgenus *Hyracarus* (Lawrence, 1949) Wharton *et al.*, 1951.

Austrombicula Lawrence, 1949.

Subgenus *Austrombicula* (Lawrence, 1949) Wharton *et al.*, 1951.

Austracarus Lawrence, 1949.

Subgenus *Austracarus* (Lawrence, 1949) Wharton *et al.*, 1951.

(*non*) *Trombicula* Berlese, 1905; Roy, 1946.

(*non*) *Hannemania* Oudemans, 1911; Gunther, 1938.

Genotype: *Acomatacarus arizonensis* Ewing, 1942.

ACOMATACARUS AUSTRALIENSIS (Hirst, 1925) Ewing, 1942.

HIRST, S., 1925: *Trans. Roy. Soc. Trop. Med. Hyg.*, xix, iii, 150; EWING, H. E., 1942: *loc. cit supra*.

Leeuwenhoekia australiensis Hirst, 1925*a*, 1928. Sambon, Walch, 1927; Warburton, 1928; Thor, 1936; Gunther, 1940*a*, 1940*d*, 1941*c*; Heaslip, 1941; Radford, 1942; Finnegan, Gill *et al.*, 1945; Philip & Woodward, 1946*b*; Thor & Willmann, 1947; Brumpt, 1949.

Leeuwenhoekia australiensis (Hirst, 1911). Womersley & Heaslip, 1943.

Leeuwenhoekia australiense Womersley, 1934, 1937 (*laps. cal.*). Gunther, 1929*a*, 1942.

Trombicula australiensis Patton & Evans, 1929. Roy, 1946.

Acomatacarus australiensis Ewing, 1942. McCulloch, 1946; Fuller, 1947*b*.

Acomatacarus (Leeuwenhoekia) australiensis. *Austral. Agric. Gaz.*, 1946.

Acomatacarus australiense McCulloch, 1947 (*laps. cal.*).

Hannemania blestowei Gunther, 1938.

Scrub-itch mite Jackson, 1908.

Types, *Larva*: British Museum. *Nymph*: South Australian Museum.

Paratypes, *Larvae*: Australian Museum, S. Australian Mus., School Public Health Trop. Med., Univ. Sydney.

Australia: Man, cat, rats, bandicoots.

New Guinea: Bush turkey (*Tallegalla jobiensis*), bush fowl (*Megapodius reinwardt*), thrushes (*Caleyia megarhyncha*, *Eupetes caerulescens*), pigeon (*Chalcophaps stephani*), whistler (*Pachycephala* sp.), cassowary (*Casuarus casuarinus*), catbird (*Ailuroedus melanocephalus*), pitta (*Pitta mackloti*), kingfisher (*Tanyiptera galeata*),

bower-bird (*Chlamydera cerviniventris*), *Pitohui kirrhocephalus*, birds of paradise (*Paradisca minor*, *P. raggiana*).

Celebes: Rat.

ACOMATACARUS NOVA-GUINEA (Womersley, 1944) Womersley, 1945.

WOMERSLEY, H., 1944: *Trans. Roy. Soc. S. Aust.*, lxxviii, i, 82; *Idem*, 1945: *Ibid.*, lxxix, i, 96.

Leeuwenhoekia nova-guinea Womersley, 1944. Blake *et al.*, 1945a; Radford, 1942.

Acomatacarus nova-guinea Womersley, 1945. McCulloch, Dumbleton, 1946.

Type, *Larva* & *Nymph*: South Australian Museum.

New Guinea: Magpie (*Gymnodactyla* sp.), kingfisher (*Tanysiptera galeata*), free. Nissan I.: Tree kangaroo.

ACOMATACARUS ADELAIDEAE (Womersley, 1944) Womersley, 1945.

WOMERSLEY, H., 1944: *Trans. Roy. Soc. S. Aust.*, lxxviii, i, 82; *Idem*, 1945; *Ibid.*, lxxix, i, 96.

Leeuwenhoekia adelaideae Womersley, 1944. Gill *et al.*, 1945; Fenner, 1946.

Acomatacarus adelaideae Womersley, 1945.

Type, *Larva*: South Australian Museum.

Australia: Cat, rats, *Uromys sherrini*, kangaroos (*Macropus major*, *M. rufa*), wild pig, sheep, apostle bird (*Struthidea cinerea*), honeyeater (*Entomyzon cyanotis*).

ACOMATACARUS HIRSTI (Womersley, 1944) Womersley, 1945.

WOMERSLEY, H., 1944: *Trans. Roy. Soc. S. Aust.*, lxxviii, i, 82; *Idem*, 1945: *Ibid.*, lxxix, i, 96.

Leeuwenhoekia hirsti Womersley, 1944. McCulloch, 1944.

Acomatacarus hirsti Womersley, 1945.

Type, *Larva*: South Australian Museum.

Queensland: Free.

ACOMATACARUS MCCULLOCHI (Womersley, 1944) Womersley, 1945.

WOMERSLEY, H., 1944: *Trans. Roy. Soc. S. Aust.*, lxxviii, i, 82; *Idem*, 1945: *Ibid.*, lxxix, i, 96.

Leeuwenhoekia mccullochi Womersley, 1944.

Acomatacarus mccullochi Womersley, 1945.

Type, *Larva*: South Australian Museum.

Queensland: Free.

ACOMATACARUS SOUTHCOTTI (Womersley, 1944) Womersley, 1945.

WOMERSLEY, H., 1944: *Trans. Roy. Soc. S. Aust.*, lxxviii, i, 82; *Idem*, 1945: *Ibid.*, lxxix, i, 96.

Leeuwenhoekia southcotti Womersley, 1944.

Acomatacarus southcotti Womersley, 1945.

Type, *Larva*: South Australian Museum.

Northern Territory of Australia: Skink (*Lygosoma* sp.).

ACOMATACARUS LONGIPES Womersley, 1945.

WOMERSLEY, H., 1945: *Trans. Roy. Soc. S. Aust.*, lxxix, i, 96.

Acomatacarus longipes Womersley, 1945.

Types, *Nymph* & *Larva*: South Australian Museum.

New Guinea: *Podargus* sp., honeyeater.

ACOMATACARUS ATHERTONENSIS Womersley, 1945.

WOMERSLEY, H., 1945: *Trans. Roy. Soc. S. Aust.*, lxxix, i, 96.

Acomatacarus athertonensis Womersley, 1945. McCulloch, 1946.

Type, *Larva*: South Australian Museum.

Queensland: Free.

ACOMATACARUS ECHIDNUS Womersley, 1945.

WOMERSLEY, H., 1945: *Trans. Roy. Soc. S. Aust.*, lxi, i, 96.*Acomatacarus echidnus* Womersley, 1945.

Type, Larva: South Australian Museum.

Queensland: *Echidna* sp.

ACOMATACARUS BARRINENSIS Womersley, 1945.

WOMERSLEY, H., 1945: *Trans. Roy. Soc. S. Aust.*, lxi, i, 96.*Acomatacarus barrinensis* Womersley, 1945.

Type, Larva: South Australian Museum.

Queensland: Man, free.

ACOMATACARUS RETENTUS (Banks, 1916) Womersley, 1945.

BANKS, N., 1916: *Trans. Roy. Soc. S. Aust.*, xl, 224; WOMERSLEY, H., 1945: *Ibid.*, lxi, i, 96.*Rhyncholophus retentus* Banks, 1916.*Microtrombidium (Enemthrombium [laps. cal.]) retentus* Womersley, 1934.*Calothrombium retentus* Womersley, 1937.*Acomatacarus retentus* Womersley, 1945.

Type, Adult: South Australian Museum.

Victoria: Free.

ACOMATACARUS ATTOLUS (Banks, 1916) Womersley, 1945.

BANKS, N., 1916: *Trans. Roy. Soc. S. Aust.*, xl, 224; WOMERSLEY, H., 1945: *Ibid.*, lxi, i, 96.*Rhyncholophus attolus* Banks, 1916.*Microtrombidium attolus* Womersley, 1934.*Microtrombidium (Dromeothrombium) attolus* Womersley, 1937.*Acomatacarus attolus* Womersley, 1945.

Type, Adult: South Australian Museum.

New South Wales: Free.

ACOMATACARUS DROMUS (Womersley, 1939) Womersley, 1945.

WOMERSLEY, H., 1939: *Trans. Roy. Soc. S. Aust.*, lxiii, ii, 149; *Idem*, 1945: *Ibid.*, lxi, i, 96.*Microtrombidium (Dromeothrombium) dromus* Womersley, 1939 (*partim*).*Dromeothrombium dromus* Womersley, 1945.*Acomatacarus dromus* Womersley, 1945.

Type, Adult: South Australian Museum.

South Australia: Free.

ACOMATACARUS PATRIUS Womersley, 1945.

WOMERSLEY, H., 1945: *Trans. Roy. Soc. S. Aust.*, lxi, i, 96.*Microtrombidium (Dromeothrombium) dromus* Womersley, 1945 (*partim*).*Acomatacarus patrius* Womersley, 1945.

Type, Adult: South Australian Museum.

South Australia: Free.

ACOMATACARUS AUDYI Radford, 1946.

RADFORD, C. D., 1946: *Proc. Zool. Soc.*, cxvi, ii, 247.*Acomatacarus audyi* Radford, 1946c. Sayers *et al.*, 1947.

Type, Larva: British Museum.

Paratypes: Coll. Radford, Coll. André, U.S. Nat. Mus.

Manipur: ? babbler.

ACOMATACARUS LYGOSOMÆ Dumbleton, 1946.

DUMBLETON, L. J., 1946: *Trans. Roy. Soc. N.Z.*, lxxvi, iii, 409.*Acomatacarus lygosomæ* Dumbleton, 1946.

Type & Paratypes, Larvae: Cawthron Institute, Nelson, N.Z.

New Zealand: Skink (*Lygosoma grande*).

PART XXV.

Genus NEOTROMBIDIUM (Leonardi, 1901) Berlese, 1912.

LEONARDI, G., 1901: *Zool. Anz.*, xxv, 18; BERLESE, A., 1912: *Redia*, viii, i, i.
Trombidium (*Neotrombidium*) Leonardi, 1901.

Neotrombidium Berlese, 1912. Hirst, 1928; Womersley, 1934, 1945.

Neotrombidium Leonardi, 1911 (*laps. cal.*). Womersley, 1937.

Genotype, *Neotrombidium furcigerum* (Leonardi, 1901) Berlese, 1912.

Womersley (1945) included this genus in the subfamily Leeuwenhoeekiinae because of the resemblance of adults of *Neotrombidium barringtonense* to the nymphs of *Acomatacarus*.

NEOTROMBIDIUM BARRINGTONENSE Hirst, 1928.

HIRST, S., 1928: *Proc. Zool. Soc., Lond.*, 1021.

Neotrombidium barringtonense Hirst, 1928b. Womersley, 1934, 1937, 1945.

Type, *Adult*: South Australian Museum.

New South Wales & South Australia: Free.

PART XXVI.

Genus WOMERSLEYIA Radford, 1946.

RADFORD, C. D., 1946: *Parasitology*, xxxvii, i/ii, 46.

Womersleyia Radford, 1946b. Lawrence, 1949.

Genotype, *Womersleyia minuta* Radford, 1946.

In Radford's description of *W. minuta* he did not give any indication of the numbers of leg segments, and without this information it is impossible to place any species in the key given by Wharton *et al.* (1951). However, Radford placed his genus in the Leeuwenhoeekiinae, and there it must stay for the present.*

WOMERSLEYIA MINUTA Radford, 1946.

RADFORD, C. D., 1946: *loc. cit. supra*.

Womersleyia minuta Radford, 1946b.

Type, *Larva*: British Museum.

Paratype, Coll. Radford, U.S. Nat. Mus., Coll. André.

Maldive Is.: Grasshoppers (Acrididae, Tetrigidae, Tettigoniidae spp.).

PART XXVII.

Subfamily HEMITROMBICULINAE Ewing, 1944.

EWING, H. E., 1944: *Proc. Biol. Soc. Wash.*, lvii, 101.

Trombiculinae Ewing, 1929 (*partim*).

Hemitrombiculinae Ewing, 1944a, 1944b, 1946a. Dumbleton, 1946; Wharton, 1947c.

Type Genus, *Hemitrombicula* Ewing, 1938.

I cannot see why Wharton (1947c) and Wharton *et al.* (1951) excluded this subfamily from the Trombiculidae, and I am retaining it here.

In 1946 Dumbleton erected the genus *Nothotrombicula* and placed it in this subfamily.

Genus NOTHOTROMBICULA Dumbleton, 1946.

DUMBLETON, L. J., 1946: *Trans. Roy. Soc. N.Z.*, lxxvi, iii, 409.

Nothotrombicula Dumbleton, 1946.

Genotype, *Nothotrombicula deinacridae* Dumbleton, 1946.

NOTHOTROMBICULA DEINACRIDAE Dumbleton, 1946.

DUMBLETON, L. J., 1946: *loc. cit. supra*.

Nothotrombicula deinacridae Dumbleton, 1946.

Type, *Larva*: Entomological Division, Nelson, New Zealand.

New Zealand: Giant weta (*Deinacrida rugosa* ?).

* Radford informs me (personal communication) that this species has six segments in all legs.

PART XXVIII.

Subfamily WALCHINAE Ewing, 1946.

EWING, H. E., 1946: *J. Parasit.*, xxxii, v, 435.

Trombiculinae Ewing, 1929 (*partim*).

Walchiinae Ewing, 1946a. WHARTON, 1947c; Lawrence, Fuller, 1949; WHARTON *et al.*, 1951.

Type Genus, *Walchia* (Walch, 1927) Ewing, 1931.

In this subfamily Wharton (1947c) modified Ewing's original definition by laying down that legs I have seven segments, legs II and III have six segments, with at least four sternal setae, and only one seta on coxae I. This is made more difficult in the key given by Wharton *et al.* (1951), in which it is impossible to place any subfamily or genus unless one knows the number of leg segments. Moreover, it places *Schöngastia oudemansi* (Walch, 1922) in an unnatural position within this subfamily. However, since Fuller's new genus to accommodate *S. oudemansi* here is not yet published, I have left that species in *Schöngastia* for the present.

In addition to two promised new genera, the subfamily now contains, according to Wharton *et al.* (1951):

Walchia Ewing, 1931 (Type, *Trombidium glabrum* Walch, 1927).

Schöngastiella Hirst, 1915 (Type, *Schöngastiella bengalensis* Hirst, 1915).

Gahrlepiea Oudemans, 1912 (Type, *Typhlothrombium nanus* Oudemans, 1910).

Gateria Ewing, 1938 (Type, *Gahrlepiea fletcheri* Gater, 1932).

It seems to me that Gater's original argument (1932) for re-including *Schöngastiella* in *Gahrlepiea* is still sound. *Gahrlepiea* was described by Oudemans (1912a) as having eight scutal setae, and so when Hirst found a species bearing six, he naturally founded a new genus to accommodate it—but when Gater found six species with from 4 to 20 scutal setae, it became obvious that all of these, and *Schöngastiella*, too, rightly belonged in the one genus. Otherwise, to be consistent, we should erect a new genus for each species with a different number of scutal setae. Furthermore, it is surely splitting hairs to make the presence or absence of non-marginal setae a generic character (I am speaking of species within the original conception of *Gahrlepiea*). I should like to see *Gateria* and *Schöngastiella* both re-included in *Gahrlepiea*, but for the present I shall follow Wharton *et al.* (1951) and list all four of their existing genera in this subfamily.

PART XXIX.

Genus WALCHIA (Walch, 1927) Ewing, 1931.

WALCH, E. W., 1927: *Geneesk. Tijdschr. v. Ned.-Ind.*, lxxvii, 922; EWING, H. E., 1931: *Proc. U.S. Nat. Mus.*, lxxx, viii, 1.

Trombidium Walch, 1927 (*nom. pracocc.*: = *Trombidium* Berlese, 1888 *nec* Fabricius, 1775). Fuller, 1949.

Walchia Ewing, 1931. Thor, 1935, 1936; Womersley, 1937, 1944; Radford, 1942, 1946c; Womersley & Heaslip, 1943; Thor & Willmann, 1947; Lawrence, 1949; WHARTON *et al.*, 1951.

Walchia Ewing, 1932: Womersley, 1937.

Genotype, *Walchia glabrum* (Walch, 1927) Ewing, 1931.

This genus is confined strictly to species with globose sensillae and only four scutal setae.

WALCHIA GLABRUM (Walch, 1927) Ewing, 1931.

WALCH, E. W., 1927: *loc. cit. supra*; EWING, H. E., 1931: *loc. cit. supra*.

Trombidium glabrum Walch, 1927 (*non Trombidium glabrum* Dugès, 1834). Womersley, 1944; Fuller, 1949; Wharton *et al.*, 1951.

Trombicula glabrum (Walch, 1927) Ewing, 1931. Fuller, 1949.

Walchia glabrum Ewing, 1931. Gater, 1932; Gunther, 1941c; Radford, 1942; Womersley & Heaslip, 1943; Womersley, 1944; Blake *et al.*, 1945a; Griffiths, Sayers *et al.*, Thor & Willmann, 1947; FULLER, 1949.

Trombidium (non *Trombidium* Berlese, 1888 nec Fabricius, 1775) *ewingi* Fuller, 1949 (nom. praecoc.). Wharton et al., 1951.

(non) *Walchia pingue* Gater, 1932; Womersley, 1944.

(non) *Walchia pingue* Gater, 1932; Womersley & Heaslip, 1943 (?) *vide* Fuller, 1949.

The situation here is rather complicated. *Trombidium glabrum* Walch, 1927 (referring to *Trombidium* Berlese, 1888) is preoccupied by *Trombidium glabrum* Dugès, 1834 (referring to *Trombidium* Fabricius, 1775). In 1905 Berlese renamed his *Trombidium* (he states that *Trombicula* is derived from *Trombidium*), and so when Ewing (1931) referred to *Trombicula glabrum* (Walch, 1927) he was quite in order, despite Fuller's objection (1949).

Now Article 35 of the International Rules for Zoological Nomenclature states: "A specific name is to be rejected as a homonym when it has previously been used for some other species or subspecies of the same genus."

Thus *Trombidium glabrum* Walch was not a homonym of *T. glabrum* Dugès; since it was accompanied by a valid description, it was merely a *nomen praecoccupatum*, and Ewing did all that was necessary when he called it *Trombicula glabrum* (Walch, 1927)—his subsequent transfer of it to *Walchia* has nothing to do with the status of the name *glabrum*.

However, Fuller (1949) rejected *Trombidium glabrum* Walch as a homonym, and renamed the species *Trombidium ewingi*; this is meaningless, since it cannot refer either to *Trombidium* Fabricius or to *Trombidium* Berlese, and cannot replace *Walchia*, which also precedes it. Actually, Walch's species can be correctly referred to as: "*Trombidium glabrum* Walch, 1927 (nec Dugès, 1834)"; its present name is *Walchia glabrum* (Walch, 1927) Ewing, 1931; and Fuller's name must be translated as: "*Walchia ewingi* (Fuller, 1949)"—a synonym of *W. glabrum*.

Type, Larva.

Celebes: Rat.

Malaya: *R. argentifer*.

Java & Sumatra: Hosts not specified.

India: *R. brunnesculus*.

Burma: Shrew (*Tupaia belangeri*).

New Guinea: *R. praetor*, *Melomys* sp., free.

WALCHIA DISPARUNGUIS (Oudemans, 1929) Womersley, 1944.

OUDEMANS, A. C., 1929: *Ent. Ber. Ned. Ent. Ver.*, vii, cxv, 398; WOMERSLEY, H., 1944: *Trans. Roy. Soc. S. Aust.*, lxviii, i, 82.

Schöngastiella disparunguis Oudemans, 1929.

Gahrlipeia disparunguis Gater, 1932.

Walchia disparunguis Womersley, 1944. Kohls et al., 1945; Mohr, Griffiths, 1947; Fuller, 1949.

Type, Larva.

Java: *Mus rattus*.

New Guinea: *R. browni*.

WALCHIA (?) ENODE Gater, 1932.

GATER, B. A. R., 1932: *Parasitology*, xxiv, ii, 143.

Walchia enode Gater, 1932. Radford, 1942; Hayakawa Tanaka et al., 1945; Hayakawa & Hokari, 1947; Fuller, 1949.

Walchia enodis Womersley & Heaslip, 1943 (*laps. cal.*). Radford, 1946c; Sayers et al., 1947.

In the absence of sensillae, the placing of this species is provisional.

Type, Larva: British Museum.

Paratypes, Larvae: U.S. National Museum, Molteno Institute.

Malaya: *R. mülleri*.

Burma: *R. brunnesculus*, bandicoot (*Bandicota bengalensis*).

WALCHIA LEWTHWAITEI Gater, 1932.

GATER, B. A. R., 1932: *Parasitology*, xxiv, ii, 143.

Walchia lewthwaitei Gater, 1932. Radford, Ewing, 1942; Womersley & Heaslip, 1943;

Hayakawa Tanaka *et al.*, 1945; Hayakawa & Hokari, 1947; Fuller, 1949.

Type, Larva: British Museum.

Paratypes, Larvae: U.S. National Museum, Moltano Institute.

Malaya: Rats (*R. diardi*, *R. surifer*), squirrel (*Sciuropterus belone*).

WALCHIA PINGUE Gater, 1932.

GATER, B. A. R., 1932: *Parasitology*, xxiv, ii, 143.

Walchia pingue Gater, 1932. Radford, 1942.

(non) *Walchia glabrum* Gater, 1932. Womersley, 1944; Fuller, 1949.

Type, Larva: British Museum.

Malaya: *R. ciliatus*.

New Guinea: Free.

WALCHIA RUSTICA (Gater, 1932) Womersley & Heaslip, 1943.

GATER, B. A. R., 1932: *Parasitology*, xxiv, ii, 143; WOMERSLEY, H., & HEASLIP, W. G., 1943: *Trans. Roy. Soc. S. Aust.*, lxvii, i, 68.

Gahrlipeia rustica Gater, 1932. Radford, 1942.

Walchia rustica Womersley & Heaslip, 1943. Fuller, 1949.

Type, Larva: British Museum.

Paratypes, Larvae: U.S. National Museum, Moltano Institute.

Malaya: *R. surifer*.

WALCHIA (?) TURMALIS (Gater, 1932) Womersley & Heaslip, 1943.

GATER, B. A. R., 1932: *Parasitology*, xxiv, ii, 143; WOMERSLEY, H., & HEASLIP, W. G., 1943: *Trans. Roy. Soc. S. Aust.*, lxvii, i, 68.

Gahrlipeia turmalis Gater, 1932. Gunther, 1940b; Ewing, Radford, 1942.

Walchia turmalis Womersley & Heaslip, 1943. Radford, 1946b; Fuller, 1949.

In the absence of sensillae, the placing of this species is provisional.

Type, Larva: British Museum.

Paratypes, Larvae: U.S. National Museum, Moltano Institute.

Malaya: *R. vociferans*.

Ceylon: Shrew (*Suncus giganteus*).

WALCHIA MOROBENSIS Gunther, 1939.

GUNTHER, C. E. M., 1939: *Proc. Linn. Soc. N.S.W.*, lxiv, i/ii, 73.

Walchia buloloensis Gunther, 1938 (*nom. nud.*).

Walchia morobensis Gunther, 1939a, 1940a, 1940d, 1942. Radford, 1942; Womersley & Heaslip, 1943; Fuller, 1949.

Type, Larva: School Public Health Trop. Med., Univ. Sydney.

Paratypes, Larvae: British Mus., Australian Mus., S. Australian Mus., Univ. California, Tulane Univ., Natal Mus., P. H. D. Entebbe.

New Guinea: *R. browni*, *R. ringens*.

WALCHIA (?) RIOI (Gunther, 1940).

GUNTHER, C. E. M., 1940: *Proc. Linn. Soc. N.S.W.*, lxv, iii/iv, 479.

Gahrlipeia rioi Gunther, 1940b. Womersley & Heaslip, 1943.

This is, of course, going too far—the shape of the scutum definitely places this species in *Gahrlipeia*, but since I am here following Wharton *et al.* (1951), the fact that this species has only four scutal setae leaves it nowhere else to go but in *Walchia*. However, since the sensillae are missing, any placing must be regarded as provisional.

Type, Larva: School Public Health Trop. Med., Univ. Sydney.

Paratypes, Larvae: British Museum, Australian Museum.

British North Borneo: Mouse deer (*Tragulid borneanus*).

PART XXX.

Genus GAHRLIEPIA (Oudemans, 1910) Oudemans, 1912.

OUDEMANS, A. C., 1910: *Ent. Ber. Ned. Ent. Ver.*, iii, liv, 86; *Idem*, 1912: *Ibid.*, lxvii, 272.

Typhlothrombium Oudemans, 1910a (*nom. praeocc.* : *non Typhlothrombium* Berlese, 1910).

Gahrlietia Oudemans, 1912a. Warburton, 1928; Gater, 1932; Thor, 1935, 1936; Womersley, 1937; EWING, 1938, 1942, 1946a; Gunther, 1940b; Womersley & Heaslip, 1943; RADFORD, 1946c; Thor & Willmann, 1947; Lawrence, 1949; WHARTON *et al.*, 1951.

(*non*) *Schöngastiella* Hirst, 1915b. Gater, 1932; Womersley & Heaslip, 1943.

(*non*) *Gateria* Ewing, 1938. Womersley & Heaslip, 1943.

Genotype, *Gahrlietia nanus* (Oudemans, 1910) Oudemans, 1912.

I am following Wharton *et al.*, 1951, in that I am regarding *Gahrlietia* as having more than six scutal setae, all of which are marginal.

GAHRLIEPIA CETRATA Gater, 1932.

GATER, B. A. R., 1932: *Parasitology*, xxiv, ii, 143.

Gahrlietia cetrata Gater, 1932. Radford, 1942; Womersley & Heaslip, 1943.

Type, *Larva*: British Museum.

Paratypes, *Larvae*: U.S. National Museum, Molteno Institute.

Malaya: *R. ciliatus*.

PART XXXI.

Genus SCHÖNGASTIELLA Hirst, 1915.

HIRST, S., 1915: *Bull. Ent. Res.*, vi, iii, 183.

Schöngastiella Hirst, 1915b. Thor, 1935, 1936; Womersley, 1937; EWING, 1938, 1942, 1944a, 1944b, 1946a; Radford, 1942, 1946c; Thor & Willmann, 1947; Lawrence, 1949; WHARTON *et al.*, 1951.

(*non*) *Schöngastiella* Oudemans, 1929.

(*non*) *Gahrlietia* (Oudemans, 1910). Gater, 1932; Gunther, 1940b; Womersley & Heaslip, 1943.

Genotype, *Schöngastiella bengalensis* Hirst, 1915.

I am following Wharton *et al.*, 1951, in that I include here those species with six scutal setae.

SCHÖNGASTIELLA BENGALENSIS Hirst, 1915.

HIRST, S., 1915: *loc. cit. supra*.

Schöngastiella bengalensis Hirst, 1915b. Radford, 1942; WHARTON *et al.*, 1951.

Gahrlietia bengalensis Gater, 1932. Womersley & Heaslip, 1943; Finnegan, 1945.

Gateria bengalensis Ewing, 1938, *vide* Womersley & Heaslip, 1943.

Type, *Larva*: British Museum.

Bengal: *Mus rattus*.

SCHÖNGASTIELLA BREVIS Radford, 1946.

RADFORD, C. D., 1946: *Proc. Zool. Soc.*, cxvi, ii, 247.

Schöngastiella brevis Radford, 1946c. Sayers *et al.*, 1947.

Type, *Larva*: British Museum.

Imphal: *R. brunnesculus*.

SCHÖNGASTIELLA LIGULA Radford, 1946.

RADFORD, C. D., 1946: *Proc. Zool. Soc.*, cxvi, ii, 247.

Schöngastiella ligula Radford, 1946c. Sayers *et al.*, 1947; Audy & Harrison, Traub *et al.*, 1950.

Type, *Larva* & *nymph*: British Museum.

Paratypes, *Larvae* & *nymphs*: Coll. Radford.

Imphal: Rat.

SCHÖNGASTIELLA PUNCTATA Radford, 1946.

RADFORD, C. D., 1946: *Proc. Zool. Soc.*, cxvi, ii, 247.*Schöngastiella punctata* Radford, 1946c. Sayers *et al.*, 1947.

Type, Larva: British Museum.

Imphal: *R. brunnesculus*, shrew (*Suncus fulvocinereus*).

PART XXXII.

Genus GATERIA Ewing, 1938.

EWING, H. E., 1938: *J. Wash. Acad. Sci.*, xxviii, 288.*Gahrlipeia* (Oudemans, 1910) Oudemans, 1912 (*partim*).*Gateria* EWING, 1938, 1942, 1944a, 1944b, 1946a. Radford, 1942, 1946c; Lawrence, 1949;WHARTON *et al.*, 1951.(non) *Gahrlipeia* (Oudemans, 1910). Womersley & Heaslip, 1943; Audy, 1947.Genotype, *Gateria fletcheri* (Gater, 1932) Ewing, 1938.I am here following Wharton *et al.*, 1951, in that I am including those species with more than six scutal setae, not all of which are marginal.

GATERIA FLETCHERI (Gater, 1932) Ewing, 1938.

GATER, B. A. R., 1932: *Parasitology*, xxiv, ii, 143; EWING, H. E., 1938: *J. Wash. Acad. Sci.*, xxviii, 288.*Gahrlipeia fletcheri* Gater, 1932. Audy, 1947.*Gahrlipeia fletcheri* Gater, 1938. Womersley & Heaslip, 1943.*Gateria fletcheri* Ewing, 1938. Radford, 1942.

Type, Larva: British Museum.

Paratypes, Larvae: U.S. National Museum, Molteno Institute.

Malaya: Rats (*R. diardi*, *R. vociferans*), squirrels (*Sciurus caniceps*, *Rhinosciurus tupaoides*), shrew (*Tupaia ferruginea*).

GATERIA (?) CILIATA (Gater, 1932) Radford, 1942.

GATER, B. A. R., 1932: *Parasitology*, xxiv, ii, 143; RADFORD, C. D., 1942: *Ibid.*, xxxiv, 55.*Gahrlipeia ciliata* Gater, 1932. Gunther, 1940b; Womersley & Heaslip, 1943.*Gateria ciliata* Radford, 1942.

In the absence of sensillae, the placing of this species is provisional.

Type, Larva: British Museum.

Malaya: *R. mülleri*.

GATERIA (?) RUTILA (Gater, 1932) Radford, 1942.

GATER, B. A. R., 1932: *Parasitology*, xxiv, ii, 143; RADFORD, C. D., 1942; *Ibid.*, xxxiv, 55.*Gahrlipeia rutila* Gater, 1932. Womersley & Heaslip, 1943.*Gateria rutila* Radford, 1942.

In the absence of sensillae, the placing of this species is provisional.

Type, Larva: British Museum.

Paratypes, Larvae: U.S. National Museum, Molteno Institute.

Malaya: *R. mülleri*.

GATERIA CROCIDURA Radford, 1946.

RADFORD, C. D., 1946: *Proc. Zool. Soc.*, cxvi, ii, 247.*Gateria crocidura* Radford, 1946c. Sayers *et al.*, 1947.

Type, Larva: British Museum.

Imphal: Shrew (*Suncus fulvocinereus*).

GATERIA HIRSUTA Radford, 1946.

RADFORD, C. D., 1946: *Proc. Zool. Soc.*, cxvi, ii, 247.*Gateria hirsuta* Radford, 1946c. Sayers *et al.*, 1947.

Type, Larva: British Museum.

Paratypes, Coll. Radford, Coll. André, U.S. Nat. Mus.

Imphal: Shrew (*Suncus fulvocinereus*).

GATERIA LONGIPILI Radford, 1946.

RADFORD, C. D., 1946: *Proc. Zool. Soc.*, cxvi, ii, 247.*Gateria longipili* Radford, 1946c. Sayers *et al.*, 1947.

Type, Larva: British Museum.

Imphal: Shrew (*Suncus fulvocinereus*).

GATERIA LANCIARIA Radford, 1946.

RADFORD, C. D., 1946: *Proc. Zool. Soc.*, cxvi, ii, 247.*Gateria lanciaria* Radford, 1946c. Sayers *et al.*, 1947.

Type, Larva: British Museum.

Imphal: Mole (*Talpa micrura*).

GATERIA SPINULOSA Radford, 1946.

RADFORD, C. D., 1946: *Proc. Zool. Soc.*, cxvi, ii, 247.*Gateria spinulosa* Radford, 1946c. Sayers *et al.*, 1947.

Type, Larva: British Museum.

Imphal: Shrew (*Suncus fulvocinereus*).

PART XXXIII.

INDEX OF GEOGRAPHICAL DISTRIBUTION.

(The Roman numerals indicate the Parts in which the species may be found.)

A: LARVAE ATTACKING MAN.

The following have been recorded as attacking man in the countries shown:

Acomatacarus australiensis, XXIV: Australia.*A. barrinensis*, XXIV: Queensland.*Schöngastia blestowei*, XIII: New Guinea.*S. katonis*, XIII: Parao Isles.*S. oudemansi*, XIII: Sumatra.*S. pseudo-schüffneri*, XIII: Sumatra.*S. pusilla*, XIII: New Guinea.*S. schüffneri*, XIII: Sumatra.*S. vandersandei*, XIII: British Solomon Is., Dutch New Guinea.*Trombicula acuscutellaris*, IX: Malaya.*T. akamushi*, VII: Japan, Malaya.*T. deliensis*, VIII: Malaya, Sumatra.*T. hirsti*, V: Formosa, Malaya, New Guinea, Queensland, Sumatra.*T. japonica*, VII: Japan.*T. keukenschrijveri*, IX: Sumatra.*T. rara*, IX: Sumatra.*T. samboni*, XII: South Australia.*T. sarcina*, XII: Queensland.*T. wichmanni*, VI: Celebes, Philippine Is.

B: GEOGRAPHICAL DISTRIBUTION.

Trombiculid mites have been reported in the following countries:

AUSTRALIA: *Acomatacarus adelaideae*, *A. athertonensis*, *A. attolus*, *A. australiensis*, *A. barrinensis*, *A. dromus*, *A. echidnus*, *A. hirsti*, *A. mccullochi*, *A. patrius*, *A. retentus*, *A. southcotti*, XXIV; *Guntherana bipygalis*, II; *Myotrombicula vespertilionis*, XVI; *Neoschöngastia antipodianum*, *N. cairnsensis*, *N. coorongensis*, *N. dasycerci*, *N. dcrricki*, *N. guntheri*, *N. heaslipi*, *N. hirsti*, *N. indica*, *N. innisfailensis*, *N. melomys*, *N. perameles*, *N. petrogale*, *N. phascogale*, *N. queenslandica*, *N. rattus*, *N. similis*, *N. smithi*, *N. trichosuri*, *N. westraliense*, XIV; *Neotrombidium barringtonense*, XXV; *Trombicula chiroptera*, XII; *T. deliensis*, VIII; *T. hirsti*, V; *T. novae-hollandiae*, *T. quadriense*, *T. samboni*, *T. sarcina*, *T. signata*, *T. tindalei*, *T. translucens*, XII.

BORNEO: *Neoschöngastia impar*, XIV; *Trombicula bodensis*, IX; *T. wichmanni*, V; *Walchia rioi*, XXIX.

- BRITISH SOLOMON IS.: *Hannemanina vellae*, XXIII; *Schöngastia vandersandei*, XIII.
- BRUNEI: *Trombicula wichmanni*, VI.
- BURMA: *Mackiena empodiformis*, XX; *Neoschöngastia indica*, *N. masta*, *N. mutabilis*, XIV; *Trisetica melvini*, XXI; *Trombicula akamushi*, VII; *T. burmensis*, *T. deliensis*, *T. fulleri*, VIII; *Walchia enode*, XXIX.
- CELEBES: *Acomatacarus australiensis*, XXIV; *Neoschöngastia globulare*, *N. indica*, XIV; *Trombicula hirsti*, V; *T. wichmanni*, VI; *Walchia glabrum*, XXIX.
- CYLON: *Neoschöngastia indica*, XIV; *Trombicula acuscutellaris*, IX; *T. akamushi*, VII; *T. deliensis*, VIII; *Walchia turmalis*, XXIX.
- CHINA: *Trombicula akamushi*, VII; *T. deliensis*, VIII.
- FORMOSA: *Neoschöngastia gallinarum*, XIV; *Trombicula akamushi*, *T. corvi*, VII; *T. deliensis*, VIII; *T. hirsti*, V; *T. issikii*, *T. pseudoakamushi*, VII.
- GUAM: *Neoschöngastia bougainvillensis*, *N. carveri*, *N. ewingi*, *N. indica*, *N. namrui*, *N. solomonis*, *N. strongi*, XIV; *Trombicula anous*, *T. pluvius*, XI.
- INDIA: *Acomatacarus audyi*, XXIV; *Gateria crocidura*, *G. hirsuta*, *G. lanciaria*, *G. longipili*, *G. spinulosa*, XXXII; *Neoschöngastia indica*, *N. lanius*, *N. manipurensis*, *N. thomasi*, XIV; *Schöngastiella bengalensis*, *S. brevis*, *S. ligula*, *S. punctata*, XXXI; *Trombicula cervulicola*, *T. coluberina*, X; *T. deliensis*, VIII; *T. gliricolens*, X; *T. hakei*, VI; *T. squamosus*, X.
- IWO JIMA: *Neoschöngastia solomonis*, XIV.
- JAPAN: *Trombicula akamushi*, *T. fuji*, *T. fujigmo*, *T. intermedia*, *T. japonica*, *T. pallida*, *T. palpalis*, *T. scutellaris*, *T. tamiyai*, VII.
- JAVA: *Neoschöngastia salmi*, *N. soekaboemiensis*, XIV; *Trombicula deliensis*, VIII; *T. mediocris*, *T. minor*, V; *Walchia disparunguis*, *W. glabrum*, XXIX.
- MALAYA: *Ascoschöngastia malayensis*, XV; *Gahrlepiea cetrata*, XXX; *Gateria ciliata*, *G. feitcheri*, *G. rutila*, XXXII; *Healipia gateri*, XVIII; *Neoschöngastia debilis*, *N. gallinarum*, *N. indica*, *N. lacunosa*, *N. mutabilis*, XIV; *Schöngastia oudemansi*, *S. vieta*, XIII; *Trombicula acuscutellaris*, IX; *T. akamushi*, VII; *T. batui*, IX; *T. deliensis*, VIII; *T. hastata*, IX; *T. hirsti*, V; *T. insolli*, *T. keukenschrijveri*, *T. munda*, *T. spicea*, IX; *Walchia enode*, *W. glabrum*, *W. leuthwaitei*, *W. pingue*, *W. rustica*, *W. turmalis*, XXIX.
- MALDIVE IS.: *Neoschöngastia indica*, XIV; *Schöngastia maldivensis*, XIII; *Trombicula acuscutellaris*, IX; *T. akamushi*, VII; *T. deliensis*, VIII; *Womersleyia minuta*, XXVI.
- MOROTAI: *Trombicula wichmanni*, VI.
- NEPAL: *Trombicula akamushi*, VII; *T. deliensis*, VIII.
- NEW GUINEA: *Acomatacarus australiensis*, *A. longipes*, *A. nova-guinea*, XXIV; *Guntherana bipygalis*, *G. parana*, II; *Neoschöngastia backhousei*, *N. bougainvillensis*, *N. bushlandi*, *N. dubia*, *N. echymipera*, *N. edwardsi*, *N. foliata*, *N. impar*, *N. lorius*, *N. mccullochi*, *N. rattus*, *N. retrocincta*, *N. riversi*, *N. shieldsi*, *N. solomonis*, *N. uromys*, *N. womersleyi*, *N. yeomansi*, XIV; *Novotrombicula owiensis*, XIX; *Oenoschöngastia cana*, XVII; *Schöngastia blestowei*, *S. jamesi*, *S. philipi*, *S. pusilla*, *S. taylori*, *S. vandersandei*, XIII; *Trombicula akamushi*, VII; *T. deliensis*, VIII; *T. densipiliata*, IX; *T. frittsi*, *T. gymnodactyla*, XI; *T. hirsti*, V; *T. kohlsi*, *T. nissani*, XI; *T. obscura*, VII; *T. pluvius*, XI; *T. rara*, IX; *T. rioi*, *T. robusta*, *T. scincoides*, XI; *T. wichmanni*, VI; *Walchia disparunguis*, *W. morobensis*, *W. pingue*, XXIX.
- NEW ZEALAND: *Acomatacarus lygosomae*, XXIV; *Nothotrombicula deinacridae*, XXVII; *Trombicula naultini*, XII.
- OKINAWA: *Neoschöngastia atollensis*, *N. carveri*, *N. egretta*, *N. monticola*, *N. namrui*, *N. posekanyi*, *N. solomonis*, XIV.
- PALAU IS.: *Neoschöngastia ewingi*, *N. yeomansi*, XIV.
- PARAO IS.: *Schöngastia katonis*, XIII.
- PELELU IS.: *Neoschöngastia carveri*, *N. ewingi*, *N. strongi*, XIV.
- PESCADORE IS.: *Trombicula akamushi*, VII.
- PHILIPPINE IS.: *Neoschöngastia indica*, *N. kohlsi*, *N. philippensis*, *N. riversi*, XIV; *Schöngastia blestowei*, *S. pusilla*, XIII; *Trombicula akamushi*, VII; *T. bodensis*, IX; *T. deliensis*, VIII; *T. piercei*, *T. scincoides*, XI; *T. wichmanni*, VI.

SUMATRA: *Neoschöngastia indica*, XIV; *Schöngastia oudemansi*, *S. pseudo-schüffneri*, *S. schüffneri*, XIII; *Trombicula acuscutellaris*, IX; *T. deliensis*, VIII; *T. densipiliata*, IX; *T. hirsti*, V; *T. keukenschrijveri*, IX; *T. pseudoakamushi*, VII; *T. rara*, IX; *Walchia glabrum*, XXIX.

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PART XXXIV.

INDICES OF PARTS AND OF SPECIES AND SYNONYMS.

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B: INDEX OF SPECIES AND SYNONYMS.

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- | | |
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| <i>gymnodactyla</i> , (<i>T. gymnodactyla</i>), xi. | <i>barrinensis</i> , xxiv. |
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I wish to take this opportunity to thank my many friends all over the world for their kindness in sending me reprints and references. The above list is not complete, and many errors will inevitably have crept into it. May I invite readers who locate omissions or errors to let me know of them, so that at a later date I may be able to publish a supplement containing additions and corrections?

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· ECOLOGICAL CLASSIFICATION AND NOMENCLATURE.

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Introduction.

The classification of vegetation in Australia is seriously hindered by a lack of general agreement on many basic principles concerning both classificatory units and terminology. This disagreement concerns not only the floristically determined units such as the association and alliance, but also the structural units, the formations and sub-formations. Perhaps the greatest confusion over classification has arisen because of the erroneous impression that climate is the controlling factor in determining vegetation. With this in mind many ecologists have named structural units in terms of the climate, or have introduced a term indicative of an ecosystem rather than of a plant community. Furthermore, different usages of the all-important but ill-defined term "association" have led to considerable confusion with regard to floristic units. Davis (1936, 1941a, 1941b), for example, uses this term in a much more restricted sense than do Pryor (1939), Pidgeon (1942) and Beadle (1948). One is tempted to suggest that the size of the association as used by different Australian ecologists has been governed in part by the extent of the area under investigation. An even more serious aspect of disagreement at present existing between ecologists in the southern and eastern Australian States is the concept of species dominance in relation to the classification of plant communities. South Australian ecologists (e.g., Crocker and Wood, 1947) are prepared to recognize as dominant species members of either the tallest stratum or of subordinate strata, or of both, while ecologists in New South Wales restrict the term to the tallest species, except in communities where the tallest stratum is very open.

In addition to the above difficulties which have arisen because of disagreement among ecologists themselves, there are the inherent difficulties which arise when an attempt is made to classify any natural system. Vegetation, soils, and animal communities usually vary continuously and in several directions; accordingly, any attempt to classify a continuously varying system into several categories must necessarily be somewhat arbitrary, in so far as at some points the system must be broken into distinct groups. The selection of these critical points for subdivision inevitably constitutes a controversial issue, since classification is essentially a compromise between the desire to preserve these natural groupings as continuously varying entities and the need to subdivide them for more utilitarian purposes.

Since Australian ecologists are at present embarking upon an intensive mapping programme, the writers feel that there is an immediate need for laying down a general classificatory scheme which will lead to some uniformity in ecological units within Australia. This scheme, which is a modification of the European and American systems, supplemented by certain miscellaneous terms, is outlined below; it replaces the monoclimal concept of Clements which dominated Australian ecologists in the past. Based on the principle that vegetation should be described objectively in terms of its floristics and structure without reference to the complex of factors governing it

(the interpretation of the status of the community is not part of this descriptive account), this scheme has resulted from experience in environments ranging from alpine to semi-arid and subtropical.

PRINCIPLES RELATING TO VEGETATION CLASSIFICATION.

1. Floristics and Structure.

Before attempting to classify plant communities, an understanding of the most important floristic and structural properties is essential. A knowledge solely of the species present in the community is insufficient; their qualitative and quantitative interrelationships and their interrelationships in space and time must also be considered.

The qualitative and quantitative data may be determined approximately by visual, semi-subjective methods which in themselves provide sufficient basic information at least to recognize the most abundant species, or by detailed statistical methods such as those employed by Scandinavian ecologists. The large areas of vegetation in Australia generally restrict observations to the former semi-subjective method. This method permits the recognition of the most abundant species, and if necessary can easily be extended to other species, leading to their classification as abundant, frequent, common, occasional, rare, or very rare, depending on their relative abundance in the community.

Except in simple single-layered communities the above-mentioned qualitative and quantitative data are inadequate for the precise description of the community. A more precise description is provided by a knowledge of the spatial relationships (structure) of the plants comprising the community. A still more complete picture of the community will result if the structural data are supplemented by data on the life-forms of the individual species according to the system proposed by Raunkiaer (1934). If the life-forms of all the species in the community are known, they may be expressed in quantitative, comparative terms on a percentage basis known as the life-form spectrum (= biological spectrum). However, it should be emphasized that the life-form system does not always reflect the climate alone of the community, as claimed by Raunkiaer. A more detailed scheme for describing and recording vegetation on a structural basis has been proposed recently by Dansereau (1951).

While the number of floristic groupings is virtually unlimited, the number of structural expressions of vegetation is relatively few. These can be classified into a definite number of structural forms and sub-forms which are listed in Table 1. Additional groups may be added if necessary. With regard to these structural forms, the following notes are relevant:

(i) Transitions from one form (or sub-form) to another frequently occur; for example, grassland commonly grades into savannah, and savannah into savannah woodland; tall woodland grades into dry sclerophyll forest, etc. To avoid the introduction of additional specific terms it is proposed that these transitions be accommodated by prefixing the designation by "tall", "low", "sparse", "dense", as the case may be. Similarly for the term "deciduous", when this is applicable.

(ii) The terms "wet" and "dry" in structural designations, such as wet and dry scrub, wet and dry sclerophyll forest, refer to the plant community itself and not necessarily to the habitat. "Wet", in contrast to "dry", is used to signify a higher degree of mesomorphism, or a higher incidence of helophytes.

2. Animal Communities.

The faunal associates of vegetation have generally been neglected by plant ecologists. However, they are closely integrated with the plants in a single biotic community and should therefore be described wherever possible. Since the role of animals in most terrestrial vegetation is that of coaction rather than dominance, animal communities should be described in terms of the stratum or strata which constitute their most important habitat and feeding niches (e.g., subterranean, floor, herbaceous, shrub, tree strata, etc.), together with relevant notes as to their role as predators, omnivores, or herbivores and with further qualification if required as to

their outstanding habits and mode of locomotion (e.g., nocturnal, saltatorial, cursorial, fossorial, arboreal, etc.). For more detailed treatment the works of Allee *et al.* (1949), and Clements and Shelford (1939) should be consulted.

3. Maturity Status.

It is customary to use different terminology for the naming of climax (mature) and seral (immature) communities. However, since ecologists vary so much in their concept of the climax (and stable equilibrium), no strict ruling for the assessment of maturity status is proposed at this stage. To the writers the decision is inconsequential as far as the objective classification is concerned, since any community must be described in terms of its floristics and structure. The appending of a unit name indicative of the status in no way alters this description; in fact the only possible disagreement that can arise from a difference in the interpretation of status is the use as a unit name of "association" for "associates" or vice versa.

One principle only need be mentioned: The writers reject the Clementian monocl原因 theory, which recognizes only one climax, the climatic climax, in a region, and regard all other types of vegetation as seral stages of the climatic climax. So also the term post-climax in the Clementian sense, used extensively by Davis, Pidgeon, and Beadle, must be rejected on the ground that the term connotes time, postulating a condition that would exist if the climate were to improve.

In the place of the Clementian interpretation of climax, any one of the following procedures may be adopted:

(i) All communities may be regarded as climax and described according to the terms, associations, alliances, etc., as outlined in the following pages.

(ii) The climax may be regarded as distinct from seral communities in so far as it is independent of the time factor. For practical purposes the climax may be regarded as a relatively permanent community which continues to regenerate and maintain itself for considerable periods of time which are long in comparison with the life span of the longest-lived individuals of the community. Communities which do not exist for much longer periods than the longest-lived individuals in them may be considered seral (Pryor, 1951). This time criterion is subjective, but field evidence such as that on the age of seedlings, saplings and mature trees, on the type of dispersion, and on the condition of the associated soils, lends support to this principle.

(iii) If a refinement of (ii) is required, the climax may be qualified in terms of the factor which limits it in a particular area. Thus we may recognize climatic, physiographic, edaphic, anthropogenic, and in special cases biological climax as communities which are limited respectively by climate, physiography, soil parent material, man, and the flora or fauna. By analogy a stage in a sere may be regarded as a temporal climax, in so far as it is limited by time; if a temporal climax represents the penultimate stage of a succession and is similar in structure to the ultimate stage (the climax), it may be designated as a subclimax in the Clementian sense.

In assessing the climax status of vegetation it should be borne in mind that the same community developed in different areas will not necessarily occur as the same type of climax: a particular savannah woodland community, for example, may occur as a climatic climax in sub-humid areas on a wide range of soil parent materials and slopes, whereas in humid environments its status is frequently that of an edaphic climax in so far as it is restricted to soils of heavy texture such as those derived from basalt. Similarly, the same community may occur as a climax in stable equilibrium with the environment in one area, and as a stage in a succession in another.

The assessment of maturity status is essentially a study of communities in relation to the limiting factors of their environments; it does not affect the description of the communities nor, to any appreciable extent, their ecological classification. Accordingly, disagreement among ecologists regarding the determination of maturity status, which is somewhat subjective particularly with regard to the time factor, should not influence their acceptance of a uniform scheme of ecological description and classification on the basis of the floristics and structure of the plant communities themselves.

TABLE I.

The structural forms and sub-forms, with synonyms (for authorities, see Glossary).

<i>Form.</i>	<i>Sub-form.</i>	<i>Synonyms.</i>
GRASSLAND	Hummock grassland	Sclerophyllous-, desert-, spinifex-, porcupine grassland
	Dry tussock grassland	Grassland, savannah, grass steppe, downs
	Wet tussock grassland	Meadow grassland
	Sod tussock grassland	Mountain-, alpine-, sub-alpine grassland
SAVANNAH	Shrub savannah	Savannah scrub
	Tree savannah	
ALPINE HERBFIELD	Tall alpine herbfield	Alpine meadow, herbfield, herb moor, mountain meadow
	Short alpine herbfield	
FEN		Low moor, Niedermoor,
		Flachmoor, marsh, swamp
BOG	Valley bog	Mixed mire, extreme acid fen, transition moor
	Raised bog	Raised moss, Hochmoor
FELDMARK		Fell-field, wind desert, fjaeldmark, Felsen-fluren, Fjæld-marker
HEATH		Heather
SALTBUSH		Shrub-steppe
SCRUB	Dry scrub	
	Wet scrub	
	Mangrove scrub	Tidal-, littoral scrub
MALLEE	Dry mallee	
	Wet mallee	
WOODLAND	Shrub woodland	
	Savannah woodland	
	Tall woodland	
	Sub-alpine woodland	Alpine woodland
SCLEROPHYLL FOREST	Swamp woodland	
	Dry sclerophyll forest	
	Wet sclerophyll forest	
RAINFOREST	Swamp sclerophyll forest	
	Temperate rainforest	Subantarctic rainforest, beech forest
	Subtropical rainforest	
	Tropical rainforest	
	Monsoon rainforest	Monsoon forest, deciduous rainforest

THE CLASSIFICATION OF CLIMAX VEGETATION.

A. THE FLORISTIC UNITS.

1. *The Association.*

The basic floristic unit for the classification of climax plant communities is the ASSOCIATION.

An Association is defined as a climax community of which the dominant stratum has a qualitatively uniform floristic composition and which exhibits a uniform structure as a whole.

Note:

(i) The dominant stratum is the stratum which, because of its physiognomy and relative continuity, dominates the rest of the community in the sense that it conditions the habitats of the other strata (Moore, 1951) (cf. "Dominant", as defined in Glossary).

(ii) Pryor (1951) justifiably points out that, in defining floristics, it is sometimes necessary to work at the level of the ecotype rather than at the level of the species, particularly with species of *Eucalyptus*.

(iii) The above definition of association does not insist upon quantitative uniformity of the dominants, which rarely occurs. Furthermore, it permits of the designation "association" being applied to communities with a single species dominant, which communities have been designated "consociations" by Clements and others. The latter term has no special value and could well be dropped from ecological literature.

For the naming of associations the following rules are proposed:

(a) In communities where the tallest stratum is continuous, the tallest stratum alone should be used to identify and designate the association (except in the special case of bogs discussed below). For example:

Eucalyptus hemiphloia (tall woodland) association.

E. pilularis-E. saligna (wet sclerophyll forest) association.

E. sieberiana-E. gummifera-E. piperita (dry sclerophyll forest) association.

This principle is generally accepted among ecologists, although there are some who use a combination of the tallest stratum and a subordinate stratum in the primary identification (e.g., Crocker and Wood, 1947). Furthermore, the English ecologists are tending to favour the use of the subordinate strata alone for the identification of an association (e.g., Watt, 1950). While the last-mentioned technique may be useful for certain ecological projects, it is not appropriate for community classification, because only subordinate strata are then classified, and frequently these are dependent on the taller stratum (or strata).

(b) For open communities two alternatives present themselves: When the community can be accurately identified by the tallest stratum alone, the procedure outlined above should be followed, e.g., for savannah woodlands. On the other hand, when a lower stratum is as important as, or more important than, the tallest stratum in identifying the community, then a combination of the dominants of the two strata should be used in the designation. ("Important" cannot be defined quantitatively; the term must remain subjective.) Such a procedure is recommended for very open communities such as savannahs; it is desirable also for the shrub woodlands, since the shrub layer of these communities is a conspicuous part of the community.

(c) The bogs, some of which have a shrub stratum with a closed canopy above the moss, are exceptional. The *Sphagnum* moss characterizes the community rather than the shrub layer even though the latter is the taller and closed. The moss stratum, therefore, is used in the designation in addition to the shrub stratum. Thus, *Epacris paludosa-Sphagnum cymbifolium* (raised bog) association.

For the purposes of detailed and applied ecology, especially forestry and agrostology, a purely qualitative designation of an association will not be adequate for the precise expression of percentage composition. This need can be satisfied by using numbers before the association title to indicate the relative proportion (or range of proportions) of the dominants. Thus we may designate $7/3$ *Eucalyptus pauciflora-E. rubida* association where the two dominant trees are in the proportion of 7 to 3. Where this designation is also supplemented by reference to the appropriate structural form or sub-form of the association, the most precise possible summary is obtained of the association itself and its properties. For example, the designation of the above community as the $7/3$ *Eucalyptus pauciflora-E. rubida* savannah woodland association summarizes the following data:

(a) The dominants and their relative frequency.

(b) The structure, in terms of life-form, habit, and arrangement.

(c) The climax status of the community.

(d) That the community is part of a larger structural group characterized by the savannah woodland sub-form.

In practice associations are almost invariably identified by eye. Many field workers have found that the amount of time required to sample a stand statistically with the view to determining uniformity or relative frequency of species is not commensurate

with the ultimate value of the result. As an aid to the identification of associations two of the more difficult problems frequently encountered may be discussed:

(a) The first problem concerns the recognition of the minimal area of an association, i.e., how large must a stand of vegetation be before it can be regarded as an association or a fragment of an association? When an association has a continuous area this question does not arise; it is significant, however, when associations are fragmented, which is usually the case.

The following definition of minimal area may serve as a guide: *The minimal area is the smallest sample which contains the characteristic species and which is large enough to exhibit the structure of the community.* Thus a single plant (e.g., a tree) with its underlying vegetation is not an association because it cannot show the structural relationships in the tallest stratum; in such a case the single plant is entered on the floristic list of the species of the surrounding association.

(b) In ecotonal regions floristic and structural gradations invariably cause difficulties. Floristic gradations are readily accommodated by the identification of additional associations or subassociations. Structural gradations provide a classificatory problem only at the limits of a structural form or sub-form, when one association may exhibit two different types of structure. This is common in scrubs and woodlands because of the fixing of the shrub-tree limits at 25 feet (the microphanerophyte limit). In such cases the association is best described under the heading of the structural form or sub-form into which most of its area falls; an appropriate note is inserted in the description.

A note on the synonymy of the association as defined and used above, with similar terms employed by other workers, is appropriate at this stage. It corresponds to the "type" used by most Australian foresters (e.g., Byles, 1932), and the "vegetation type" as used by ecologists such as Pryor (1939), Pidgeon (1942), and Beadle (1948). It sometimes corresponds to the "type" as defined by Crocker and Wood (1947), but need not necessarily do so since these workers apparently do not restrict their usage to qualitative variation only. Davis (1936, 1941a, 1941b) used the term "association" in much the same sense as the present writers. The nearest overseas equivalents are the "faciation" as used by Clements (1936), and the "association" as used by Braun-Blanquet (1932) and most other European ecologists (e.g., Du Rietz, 1936; Tansley, 1939).

2. The Sub-Association.

For more detailed purposes the subdivision of the association into sub-associations is recommended on a basis of qualitative variations of the subordinate species similar to that used for the association itself.

A Sub-Association is a subdivision of the association determined by a variation in the most important subordinate stratum of the association, without significant qualitative changes in the dominant stratum.

The widespread *Eucalyptus pauciflora-E. rubida* association, which occurs as a savannah woodland of scattered trees underlain by an herbaceous stratum, is used as an example. This association is divisible into three sub-associations on the basis of qualitative variations of the dominant grasses present in the herbaceous stratum:

The *E. pauciflora-E. rubida* : *Stipa scabra* sub-association;

the *E. pauciflora-E. rubida* : *S. scabra-Poa caespitosa* sub-association;

and the *E. pauciflora-E. rubida* : *P. caespitosa* sub-association.

For the most precise quantitative expression, the numerical system used for the association supplemented by reference to the appropriate structural form or sub-form, may be extended to the sub-association, as in the case of the 7/3 *E. pauciflora-E. rubida*: 3/2 *S. scabra-P. caespitosa* savannah woodland sub-association.

If it is necessary to subdivide these smallest units or to refer specifically to a stratum of the community not previously used in classifying the sub-association (e.g., in animal ecology), the term "society" may be used or direct reference may be made to the stratum concerned, as explained below.

3. *The Society.*

A *Society* is defined as a subordinate community contained within the structure of the association or sub-association. Stratum and aspect societies may be recognized. *Stratum societies* are subordinate communities which are conspicuous throughout the year. *Aspect societies* are conspicuous only in a particular season of the year, according to which they are referred to as spring (vernal), summer (aestival), autumn (autumnal), or winter (hiemal) societies. The plant community itself is designated floristically, as in the case of the *Polypodium diversifolium* (fern) stratum society of the *Eucalyptus fastigata*-*E. viminalis* association, or of the *Thelymitra venosa* (orchid) aestival society of the *Epacris paludosa*-*Sphagnum cymbifolium* association.

When designation of a specific subordinate stratum is necessary, direct reference is made to the growth form of the component species which may also be identified floristically if desired (e.g., the *Campylopus introflexus* moss stratum of the *Casuarina nana* association).

4. *The Alliance.*

Related associations are conveniently grouped into alliances. An *alliance* is defined as a group of floristically related associations of similar structure. This is the largest floristic unit recommended for use in Australia. The alliance takes its name from the most characteristic dominant species of its component associations. The characteristic species selected should be those which occur as dominants in as many of the component associations as possible, yet which occur relatively infrequently as the dominants of associations comprising other alliances. For example, in cool, humid, montane areas of New South Wales and Victoria the following associations form a natural group of wet sclerophyll forest communities of sufficiently close floristic affinity to constitute an alliance.

1. *Eucalyptus delegatensis* association.
2. *E. delegatensis*-*E. dalrympleana* association.
3. *E. delegatensis*-*E. viminalis* association.
4. *E. delegatensis*-*E. radiata* association.
5. *E. dalrympleana*-*E. radiata* association.
6. *E. pauciflora*-*E. radiata* association.
7. *E. dalrympleana* association.
8. *E. dalrympleana*-*E. pauciflora* association.
9. *E. pauciflora*-*E. viminalis* association.
10. *E. pauciflora* association.
11. *E. dalrympleana*-*E. dives* association.
12. *E. pauciflora*-*E. dives* association.

The most characteristic dominants of this group of associations are *E. delegatensis* and *E. dalrympleana*, by which the alliance is therefore designated as the *E. delegatensis*-*E. dalrympleana* alliance. In lists showing the component associations of an alliance, the associations should be arranged in the order which most closely demonstrates their floristic interrelationships. It may sometimes happen that an association occurs which has so little floristic and structural affinity with other associations, that it must also be regarded as an alliance of which it is the only component association.

Grouping of communities to form larger units is sometimes difficult because floristic composition and structure do not always appear to be correlated. For example, certain species with wide ecological tolerance may occur as the dominants or co-dominants in communities which differ greatly in structure. Consequently, in building synthetic units one is confronted with the question: when floristic composition and structure are not correlated, is floristic composition more important than structure, or *vice versa*, in the building up of larger units? This question is best answered by the consideration of two practical examples which illustrate the conditions that can

occur when species with wide ecological tolerances occur as dominants in communities of dissimilar structure:

(a) In Western New South Wales, *Eucalyptus woollsiana* dominates communities which may occur as shrub woodland, savannah woodland or tall woodland, depending on the nature of the soil. These communities are similar floristically and related by every structural gradation, so that their separation into three alliances of distinct sub-form would break a natural unit. These communities of *E. woollsiana* are therefore included in a single alliance, even though their range of structural variation exceeds the range of a sub-form.

(b) The reverse situation obtains for *Eucalyptus pauciflora* in the Monaro Region. This species shows even greater structural variation, occurring as the dominant in communities as distinct as savannah woodland, sub-alpine woodland, dry sclerophyll forest and wet sclerophyll forest. The grouping of all these communities in the same alliance would defeat the very purpose of classification, and if pursued to its illogical conclusion could lead to the recognition of only one alliance of *Eucalyptus* spp. for all southern and central tableland areas of the State. In the case of *E. pauciflora*, the alternative should be adopted of grouping the structurally distinct communities into different alliances composed respectively of associations showing the savannah woodland, sub-alpine woodland, dry sclerophyll forest, and wet sclerophyll forest sub-forms. This separation is also justified by the fact that the different sub-forms of *E. pauciflora* communities represent natural entities between which there are marked floristic differences in the subordinate strata, and by evidence that *E. pauciflora* itself represents a number of ecotypes. On closer analysis, therefore, the separation of the different sub-forms of *E. pauciflora* communities into different alliances is in accordance with the concept of floristic relationship (cf. Note ii, p. 64).

The alliance, as defined and used above, is synonymous with the "association" as used by ecologists such as Pryor (1939), Pidgeon (1942), and Beadle (1948). It may frequently correspond to the "association" of Crocker and Wood (1947), but need not do so since these ecologists do not restrict their definition of community dominant to the tallest species. Approximately equivalent terms used by overseas ecologists are the "alliance" or "Verband" (e.g., Braun-Blanquet, 1932; Du Rietz, 1936).

5. The Sub-Alliance.

A sub-alliance is defined as a subdivision of an alliance, obtained by arranging the component associations into groups of maximum affinity.

A sub-alliance is designated according to the most characteristic dominant species of its component associations. For example, the *Epacris paludosa*-*Sphagnum cymbifolium* alliance of raised bog communities contains the following ten associations:

1. *Callistemon sieberti*-*Sphagnum cymbifolium* association.
2. *Epacris paludosa*-*S. cymbifolium* association.
3. *E. serpyllifolia*-*S. cymbifolium* association.
4. *Richea continentis*-*S. cymbifolium* association.
5. *Restio australis*-*S. cymbifolium* association.
6. *R. australis* association.
7. *R. australis*-*Carex gaudichaudiana* association
8. *C. gaudichaudiana* association.
9. *Carpha nivicola* association.
10. *Astelia alpina* var. *novae-hollandiae* association.

The first five and last five associations form two groups which not only possess floristic unity in themselves but also differ appreciably from each other. Consequently, it is valid to recognize these groups as sub-alliances of the *E. paludosa*-*S. cymbifolium* alliance, and to refer to them as the *E. paludosa*-*S. cymbifolium* and *R. australis*-*Carex gaudichaudiana* sub-alliances.

The floristic relationships of the component associations of an alliance do not always permit their grouping into sub-alliances. Such a subdivision, moreover, is not always necessary since the same information concerning floristic affinities within the alliance is usually apparent from the order in which the component associations are listed.

B. THE STRUCTURAL UNITS.

The Formations and Sub-Formations.

The synthetic structural units recommended for use in classifying the Australian vegetation are the formation and sub-formation.

A formation is defined as the structural unit to which are referred all climax communities exhibiting the same structural form, irrespective of floristic composition.

A sub-formation is defined as a subordinate synthetic structural unit within the general pattern of a formation, to which are referred all climax communities exhibiting the same structural sub-form, irrespective of floristic composition.

These formations and sub-formations are analogous to the forms and sub-forms listed in Table 1 and defined in the Glossary.

The grouping together of communities of similar structure as formations and sub-formations presents no theoretical difficulties. Also the grouping together of alliances into formations and sub-formations is usually straightforward, since structural uniformity is a secondary criterion of the alliance. As explained previously in connection with such ecologically versatile species as *Eucalyptus woollisiana*, however, it is sometimes necessary to constitute a large alliance which transgresses the defined limits of structure, in order to preserve the floristic affinities and natural unity of the communities in which the versatile species occurs as dominant. In cases such as these it may not be possible to refer the structurally variable alliance to a sub-formation, though it is usually possible to refer it to a formation.

The essential difference between the concept of formation outlined in this paper and the older concept of Clements should be emphasized. According to the viewpoint adopted in this paper, the formation is not an ecological entity reflecting climate alone, but a synthetic group of communities expressing a similar set of ecological conditions of which climate is only one. If formations and sub-formations were determined by climate to the exclusion of other factors, they would occur in broad zones correlated with climate. This sometimes happens if the climatic factor overshadows the other factors (physiography, soil parent material, the flora and fauna), but is rarely the case in regions of environmental diversity where one of the other factors may be limiting. The validity of the latter statement is shown by the often fragmentary and discontinuous distribution of formations and sub-formations in Australia.

C. SUMMARY OF THE SYSTEM RECOMMENDED FOR THE CLASSIFICATION OF AUSTRALIAN VEGETATION, WITH NOTES ON ALTERNATIVE SYSTEMS AND MAPPING PROCEDURE.

1. *Classification.*

In the system described in the previous pages, the classification of climax vegetation is based both on floristic and structural criteria. The procedure to be adopted may be summarized as follows:

(a) The primary floristic units, the associations, are first determined and designated in terms of the dominant species.

(b) The most closely related associations are then grouped into synthetic floristic units, the alliances, which are designated in terms of the most characteristic dominant species.

(c) Finally, the alliances are grouped according to structural affinity into structurally defined formations and sub-formations.

According to this classification, community floristics are more important than structure in recognizing the associations and grouping the latter into the alliance, while community structure alone is used to group the alliances into the formations and sub-formations.

While the writers recommend this combined floristic and structural system as being the most suitable for the Australian vegetation, other workers may prefer to use an almost entirely floristic system at the one extreme or a purely structural system at the other. In the former instance the classification will be based on the recognition and designation of the associations (or smaller units) and alliances, as described above. In the purely structural classification, on the other hand, community

floristics are ignored and only the formations and sub-formations are recognized. Since the latter system is by far the most rapid and requires least botanical knowledge, it is usually preferred by workers engaged in reconnaissance ecological surveys or in surveys which require a knowledge of the vegetation merely as a background for the study of some other feature of the environment.

2. Mapping.

The choice of mapping units will be governed mainly by the degree of detail of the survey and the purposes for which it is required. For most ecological work in Australia the alliance will be found to constitute the most suitable unit. If greater detail is required, sub-alliances, associations, or even sub-associations or smaller communities may be mapped. For broader reconnaissances, and for other types of survey, the plant communities may be mapped in terms of formations and sub-formations.

In areas of considerable environmental diversity where such a relatively large number of plant communities occurs that their boundaries cannot all be shown on the vegetation map, the communities may be mapped as a composite unit or *complex*. In these cases an appended note is necessary as to the communities which constitute the complex, and if possible their relative importance and individual distribution.

THE CLASSIFICATION OF SERAL VEGETATION.

(1) Succession: Primary and Secondary.

Plant succession is defined as the process by which the same area is occupied by different plant communities, when all factors except time remain constant.* Successions are also referred to as seres.

A primary succession (prisere) is defined as one which occurs on a naturally bare area not previously occupied by vegetation.

A secondary succession (subsere) is defined as one which occurs on a denuded area on which the original vegetation has been completely or partly destroyed by some external influence (e.g., fire, flood, grazing).

Types of Succession.—Successions are termed *hydroseres* or *xeroseres*, according as they commence in permanent water or on land. The hydroseres may be distinguished as *haloseres* when they commence in salt or brackish water, and *limnoseres* when they commence in fresh water. The xeroseres may be distinguished as *lithoseres* when they commence on rock surfaces, *psammoseres* when they commence on sand, and *pedoseres* when they commence on previously formed soil.

Qualifying terms may also be used in reference to the various types of sere, as for example acid or alkaline limnosere and moist or dry lithosere.

(2) Seral Units: Stages in Succession.

A stage is defined as any clearly marked step in succession. The stages of a succession may be designated in several ways: by the sequence of plant communities according to *time*, to *floristic composition*, to *structure*, to *growth form*, to *life-form*, and to *space*.

(a) *Stages in Time.*—Seral stages may be designated *pioneer*, *transitional*, or *terminal*, depending on their time of appearance in the succession. The terminal stage corresponds to the end point or climax of the sere.

* The factors of the environment in all successions unaffected by civilized man are: climate, physiography, soil parent material, the flora and fauna, and time. In successions affected by man, a sixth factor, the human or anthropogenic factor, must also be considered.

To avoid confusion among ecologists, the important distinction should be emphasized between the independent variable or factor, soil parent material, and the dependent variable, soil. In a given succession soil parent material, like all other factors, except time, does not change. The soil, however, like the plant and animal communities, is not independent and undergoes development through seral stages until the climax soil for the particular area is attained.

(b) *Floristic Stages*.—The basic seral floristic unit is the associates. Its derivatives are sub-associates and societies.

An associates A sub-associates A societies	} is defined as the floristic unit } of seral vegetation, corresponding to	{ an association, { a sub-association. { a society.
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In any complete sere, the climax association is the final floristic stage which replaces the final associates or the penultimate stage of the succession.

The designation of the seral floristic units is similar to the designation of the climax units (e.g., the *Ranunculus millani* associates of the *Poa caespitosa*—*Danthonia nudiflora* sod tussock grassland association).

There are no seral equivalents to the alliance and sub-alliance.

(c) *Structural Stages*.—Most of the structural expressions of vegetation previously described as structural forms and sub-forms may also occur as seral structural stages under certain conditions. Thus, in a given sere to a climax structural form, for example, a hydrosere to sclerophyll forest, we may designate the successive seral communities as the fen stage, the grassland stage, the heath stage and the scrub stage, etc., as the case may be. In addition to the structural stages which correspond to the climax forms and sub-forms, other structural terms may be coined if the sere is sufficiently complex to warrant it, as, for example, swamp heath, scrub forest, etc.

(d) *Stages in Growth Form*.—The designation of seral stages according to growth form resembles the designation according to structure. Thus, in a particular succession, we may recognize algal, lichen, moss, herb, shrub and tree stages.

(e) *Stages in Life-Form*.—The designation of seral stages according to life-form is a refinement of the designation by growth form. The same life-forms are used as in Raunkiaer's system (cf. Glossary). Accordingly, we may refer to the successive stages of a sere, for example, a limnosere to sclerophyll forest, as the hydrophyte stage, the xerophyte stage, the hemicryptophyte stage, the chamaephyte stage, the nanophanerophyte stage, the microphanerophyte stage and the meso- and megaphanerophyte stage.

(f) *Stages in Space*.—The designation of seral stages according to their position in space is largely confined to hydroseres. In the latter successions it is sometimes convenient to make reference to a stage as a submerged stage, a floating stage, or a terrestrial stage, as the case may be.

(3) *The Choice of Units for the Classification of Seral Vegetation.*

According to the above discussion, seral communities may be classified in terms of stages which may be designated variously in terms of time, floristics, structure, growth-form, life-form and space. The designations used in classifying the seral communities will depend on the degree of detail required and on the type of succession itself. For the most general purposes a classification on the basis of time and growth form will probably be adequate (e.g., the pioneer lichen and moss stages, the transitional shrub stages, the terminal tree stage). Where slightly more detail is required the classification should also incorporate the sequence of stages according to structure (e.g., the pioneer algal stage, the transitional fen, bog, heath and scrub stages, the terminal forest stage).

When more accuracy is necessary the classification should incorporate all criteria, of which the floristic criterion is the most important. Accordingly, the pioneer and transitional stages of the sere are designated as associates and the terminal stage or climax as an association. Within a particular associates, sub-associates and societies may also be identified if necessary. Appropriate designations indicating structure, growth-form or life-form, and sometimes spatial position are then appended. In a given limnosere terminating in savannah woodland, for example, the successive stages will be designated in a manner resembling the following:

Pioneer Stages:

Submerged *Spirogyra* algal associates,

Floating *Azolla filiculoides* fern associates;

Transitional Stages:

- Cladium junceum* fen associates,
Epacris breviflora-*Blindia robusta* raised bog associates,
Epacris serpyllifolia-*Kunzea muelleri* swamp heath associates,
Kunzea peduncularis-*Leptospermum flavescens* wet scrub associates;

Terminal Stage (Climax):

- Eucalyptus pauciflora*-*E. stellulata* savannah woodland association.

For the quantitative designation of particular associates, sub-associates, or societies, the numerical system described for the association and its derivatives may be used (e.g., the 7/3 *E. serpyllifolia*-*K. muelleri* : 4/1 *Carex hebes*-*Luzula campestris* heath sub-associates).

(4) *The Importance of Seral Units in the Classification of Vegetation in Australia.*

The definitions of seral units and their application to seral communities, outlined above, do not differ greatly in themselves from earlier definitions and usages, either in Australia (e.g., Pidgeon, 1942) or overseas (e.g., Clements, 1928). There is a basic difference, however, between the writers' interpretation of climax status and the older Clementian interpretation. Since the Clementian system permits only one climax, the number of communities classified as seral (i.e., as associates or structural stages, etc., instead of associations or formations and subformations) is correspondingly large, so much so that in many cases the climatic climax of the region is never attained in practice but exists in theory only. The authors, on the other hand, recognize several types of climax (climatic, physiographic, edaphic, anthropogenic, biological); from which it follows that many of Clements' so-called seral stages are to be regarded as climaxes limited by some factor other than climate.

While the need to designate and classify that small fraction of the Australian vegetation which is seral is fully recognized and provided for in the previous discussion, it is emphasized that primary plant succession appears to be occurring only on a minor scale under present conditions in Australia. The interrelationships of most Australian plant communities have frequently been oversimplified by undue emphasis on the importance of primary succession (e.g., Pidgeon, 1942) and by the failure to recognize the fact that physiography, soil parent material, or even the flora and fauna, frequently overshadow climate in determining the type of vegetation. Accordingly, much of the vegetation referred to as seral by Clementian ecologists is quite stable and mature; so that many of the so-called priseres constructed for present-day vegetation represent sequences in space only, which are rarely paralleled by corresponding sequences in time. Furthermore, it is now certain that many present-day plant communities have not developed according to the priseres which have been constructed from the spatial relationships of existing communities, but that they ante-date the present climatic regime as relics of earlier geological and climatic periods. This is shown by the frequent association of these communities with fossil land-forms and soils which are known to have persisted through several climatic periods. It is therefore evident that much of the present-day Australian vegetation has evolved by a process of climatically-induced replacement of the climax communities of one climatic period by the climax communities of the succeeding period. This process was probably also accompanied by the more or less complete extinction of older communities as climatic conditions changed, and by the appearance of new elements both from the interaction of existing elements and the immigration of new ones from other regions.

THE DISCLIMAX AND PASTURES.

During the process of land settlement and development by civilized man the vegetation is subjected to influences which are usually quite distinct from those of the aboriginal (cf. Andrews, 1920); the latter should always be regarded as part of the biotic factor of the original climax. Under the former so-called anthropogenic influences the original climax may remain virtually unchanged, may be destroyed, or may be more or less modified from its original condition to a new position of equilibrium. If in

the last instance a considerable degree of modification occurs, a disclimax (= anthro-pogenic climax) may be produced; a *Disclimax* is defined as a modification of the original climax, involving a qualitative change of dominants or of structural form or subform of the community as a whole, which is maintained in a relatively stable condition by the activities of civilized man or domestic animals.

In pastoral regions all conditions mentioned above may be found. The extent to which the original communities have been changed or modified depends on a number of variables, of which the most important are the nature of the original community, the type of stock grazed and the intensity of grazing (including grazing by rabbits), the introduction of new species, the extent of ringbarking and clearing, the frequency of cultivation and burning, and the length of time during which the community has been exposed to these influences. Some communities (e.g., alpine, herbfield, fen, bog, feld-mark) may at times show virtually no modification in species composition or structure, but in general, communities in areas which have been grazed for considerable periods differ appreciably from the original vegetation.

In communities such as grassland, saltbush, scrub, and savannah, the shrub and herbaceous strata are modified chiefly by the grazing animal and by fire, and sometimes both species composition and structure are completely altered (e.g., the change from saltbush to grassland). In forest and woodland burning may also be practised; furthermore, the trees are either thinned or entirely removed to encourage the better development of the herbaceous stratum, which in turn has been modified by the suppression or destruction of the original dominants with the development of subordinate species capable of withstanding the effects of grazing and trampling by stock, and in some cases fires. For example, in many areas of woodland in eastern New South Wales *Themeda australis*, once the dominant or codominant in the herbaceous stratum, has now been virtually eliminated, and the pasture dominants are now species of *Stipa* and *Danthonia*.

Where all species of the community as a whole are accessible to stock, the entire community constitutes the pasture. On the other hand, when trees and shrubs are present and their edible portions are not eaten by stock, the pasture is part only of the whole community; in such cases mention should be made of the original vegetation from which the pasture has developed.

From the foregoing it is evident that the terms association and alliance (and their derivatives) are not generally applicable to a pasture community, except in those relatively rare instances where the latter community includes all the strata of the original community and resembles it in floristic composition and structure. In purely agrostological work, therefore, the vegetation being subjected to grazing should be referred to simply as *pasture*, which may be defined as *all plants in an area accessible to domestic livestock*, and may include trees, shrubs and herbs. The component communities of pastures are referred to as *pasture types* (cf. Roe, 1947), and are designated by the dominant species (usually the tallest and most abundant). For example, the *Stipa-Danthonia* pastures of woodland areas of New South Wales include a number of pasture types such as *Danthonia pilosa*; *D. pilosa-Enneapogon nigricans*; *E. nigricans*; *Stipa scabra-D. auriculata*, etc. The relative frequency of the dominant species may be designated by numerals, e.g., the 5/1 *Stipa scabra-Danthonia auriculata* pasture type. For quantitative methods of pasture measurement the works of Donald (1946) and others should be consulted.

Pastures and pasture types may be further qualified by various terms according to the extent to which the floristic and/or structure of the original communities have been modified. When the dominant species in the pasture are native perennials and there are few or no exotics, the term *native pasture* may be applied. *Natural pastures* are those which have been developed under the influence of man and the grazing animal but without artificial seeding of exotic species; they are commonly characterized by the dominance of exotic annuals, especially in those areas where the rainfall is almost wholly winter in its incidence (e.g., the agricultural areas of Western Australia and South Australia). *Improved pastures* are those into which one or more species has

been introduced, either on cultivated ground or into native or natural pasture; when such a pasture is established on cultivated ground it is called a *sown pasture*, and if perennial forage species are used it is a *permanent pasture*.

GLOSSARY.*

- ABUNDANCE (relative).—The relative frequency of a species in a sample of vegetation. Usually estimated subjectively by eye and referred to one of the following classes: abundant, frequent, common, occasional, rare, very rare.
- ACIDOPHILOUS.—Growing in or preferring acid soils.
- AESTIVAL.—Pertaining to summer, e.g., aestival society (q.v.).
- ALLIANCE.—A group of floristically related associations of similar structure.
- ALPINE.—Referring to elevated environments above the tree line where the ground is snow-covered continuously for about six to twelve months of the year.
- ALPINE HERBFIELD.—A closed alpine community dominated by perennial herbs, including forbs and grasses. Subforms: Tall Alpine Herbfield; Short Alpine Herbfield.
Tall Alpine Herbfield. An alpine herbfield community dominated by relatively tall herbs below which subordinate herbaceous strata are usually present.
Short Alpine Herbfield. An alpine herbfield community dominated by short carpet-forming herbs, usually so closely appressed to the ground that subordinate strata do not develop.
- ALPINE MEADOW (Wood, 1950) = Alpine herbfield.
- ALPINE WOODLAND (Pryor, 1939) = Subalpine woodland.
- ANTHROPOGENIC CLIMAX.—A climax community limited by some part of the anthropogenic factor. = Disclimax.
- ANTHROPOGENIC FACTOR.—The influence of man, in the broadest sense, including, for example, the influences of domestic stock, plant introduction, burning and clearing.
- ARBOREAL.—Pertaining to or living in trees.
- AREA.—The geographic area over which a taxonomic group (species, genus, etc.) or plant community occurs.
- ASPECT.—(i) The direction to which a slope faces, as determined by the points of the compass.
 (ii) Seasonal changes in the community. Used particularly in referring to societies (q.v.).
 (iii) General appearance.
- ASPECT SOCIETY.—A society conspicuous only during a particular season of the year.
- ASSOCIATION.—A climax community of which the dominant stratum has a qualitatively uniform floristic composition, and which exhibits a uniform structure as a whole.
- ASSOCIES.—A seral community of which the dominant stratum has a qualitatively uniform floristic composition, and which exhibits a uniform structure as a whole. The seral analogue of the association.
- AUTUMNAL.—Pertaining to autumn, e.g., autumnal society (q.v.).
- BEECH FOREST = Temperate rainforest.
- BIOLOGICAL CLIMAX.—A climax community limited by some part of the native flora or fauna. (The application of this concept is generally limited to comparisons between geographically discontinuous areas.)
- BIOLOGICAL SPECTRUM (Raunkiaer, 1934) = Life-form spectrum.
- BIOME.—The whole living community, including both plants and animals.
- BOG.—An hygrophilous community dominated by hummock-forming mosses and acidophilous shrubs or helophytes and hydrophytes. Subforms: Valley Bog; Raised Bog.
Valley Bog. A bog community composed of a continuous network of low moss hummock banks with associated acidophilous plants, enclosing impoverished fen vegetation; the bog surface as a whole is flat or slightly concave in appearance.
Raised Bog. A bog community composed of a regular succession of alternating moss hummocks and hollows with associated acidophilous shrubs and helophytes and hydrophytes; the bog surface as a whole is convex in appearance.
- BOLE.—The trunk of a tree up to the first main branching. (See crown.)
- CANOPY.—A cover of foliage, formed either by the community as a whole or by one of its component layers. It may be continuous or discontinuous.
- CHAMAPHYTE.—A plant with renewal buds lying on the ground or not more than 25 cm. above it.
- CHARACTERISTIC SPECIES.—The species which distinguish the community, not necessarily those in the tallest stratum.
- CLIMATIC CLIMAX.—A climax community limited by some part of the climatic factor.
- CLIMAX.—The final stage in a succession. A community in stable equilibrium with its environment. (Both definitions are subjective, depending on the individual's concept of the time factor.)
- COACTION.—The interaction of organisms, e.g., the reciprocal effects of plants and animals.
- CODOMINANT.—Of more or less equal importance as dominants; applicable to two or more species in the same stand.

* In compiling this section Carpenter's "An Ecological Glossary" (1938) has been freely used.

- COMMUNITY.**—Any assemblage of plants and their dependent fauna.
- COMPLEX.**—Two or more distinct communities (with or without regular arrangement), which are so irregular or small that they cannot be conveniently mapped individually, and are therefore considered together.
- CONSOCIATION.**—An association with a single dominant species. (The term is regarded as unnecessary.)
- CONTINUOUS.**—Touching, or almost so, as applied to the canopy of any stratum.
- CROWN.**—The part of the tree above the first branching, as distinct from the bole.
- CRYPTOPHYTIC.**—Pertaining to cryptophytes—i.e., plants whose renewal buds are below the surface of the soil; includes geophytes, helophytes, most hydrophytes, and many hemi-cryptophytes.
- CURSorial.**—Pertaining to animals with limbs adapted to running.
- DECIDUOUS.**—Losing its foliage completely for part of the year; hence summer deciduous, winter deciduous.
- DECIDUOUS RAINFOREST** = Monsoon rainforest.
- DISCLIMAX.**—A modification of the original climax, involving a qualitative change of dominants or of structural form or subform of the community as a whole, which is maintained in a relatively stable condition by the activities of civilized man or domestic animals. = Anthropogenic climax.
- DISCONTINUOUS.**—Open or broken, as applied to the canopy of any stratum.
- DOMINANT.**—A species which, because of its life-form and frequency, dominates the other members of the community (except for other dominants) in the sense that it conditions the habitats of its associates. (Moore, 1951.)
- DOMINANT STRATUM.**—The stratum which, because of its physiognomy and relative continuity, dominates the rest of the community in the sense that it conditions the habitats of the other strata. (Moore, 1951.)
- DOWNS** (Prescott, 1931; Blake, 1938) = Dry tussock grassland.
- ECOLOGICAL AMPLITUDE** = Ecological tolerance.
- ECOSYSTEM.**—A system in which the inorganic and organic components of the environment are integrated to form a natural unit. The components of the ecosystem include physiography, soil parent material, climate, the flora and fauna, time, man (in ecosystems affected by the anthropogenic factor), the soil, and plant and animal communities.
- ECOTONE.**—Transitional communities, characterized either by transitions (mixing) in floristic composition (= floristic ecotones) or transitions in structure (= structural ecotones).
- ECOTYPE.**—A genotypical variant of a species, which arises as a response to a particular type of habitat.
- EDAPHIC.**—Pertaining to the soil (cf. primary edaphic).
- EDAPHIC CLIMAX.**—A climax community limited by an edaphic property determined by the soil parent material.
- ENVIRONMENT.**—The resultant of all variables which affect an organism or community. These variables include climate, physiography, geology, flora and fauna, man, time, soil, and plant and animal communities.
- EPHEMERAL.**—Transient, not permanent.
- EPIPHYTE.**—A plant which grows perched on another plant or object without being parasitic on the supporting plant.
- ERICOID.**—Applied to leaves which are small, xeromorphic, terete or elongate, and frequently with sharp points.
- EXOTIC.**—Introduced, not native.
- FACIATION** (Clements, 1936) = Association.
- FAUNA.**—The animal species occurring in an area.
- FEEDING NICHE.**—The habitat from which an animal obtains its food.
- FELDMARK.**—An open subglacial community of dwarf flowering plants, mosses and lichens, usually dominated physiognomically by chamaephytes.
- FELL-FIELD** (Warming, 1909) = Feldmark.
- FELSEN-FLUREN** (Warming, 1909) = Feldmark.
- FEN.**—An hygrophilous community dominated by helophytes and hydrophytes (usually monocotyledons), from which hummock-forming mosses are absent.
- FEN, extreme acid** (Du Rietz, 1949) = Valley bog.
- FJÆLDMARK** = Feldmark.
- FJÄLD-MARKER** (Warming, 1909) = Feldmark.
- FLOATING STAGE.**—The stage in an aquatic succession characterized by floating plants.
- FLOOR.**—The ground layer of a community, including dead vegetable matter, litter and the upper humus.
- FLORA.**—The plant species within an area, determined partly by the disseminules available to the area and partly by the ability of these species to survive in the area (cf. vegetation).
- FLORISTIC COMPOSITION.**—The species present in a community expressed as a floristic list.
- FLORISTIC UNIT.**—A man-made grouping of plants recognized on the basis of community floristics.
- FORB.**—An herbaceous plant, not a grass.

- FOREST**—A closed community dominated by meso- or mega-phanerophytes, characterized by flat-topped crowns which usually form an interlacing canopy, and by boles of which the length is equal to or greater than the depth of the crowns.
- FOREST TYPE** (Byles, 1932) = Association.
- FORMATION**—A synthetic structural unit to which are referred all climax communities exhibiting the same structural form, irrespective of floristic composition.
- FOSSEDAL**—Pertaining to digging or burrowing animals.
- FREQUENCY**—A measure of the occurrence of a plant in a community, estimated quantitatively either in absolute figures or as a percentage) or semi-quantitatively (see abundance).
- FRINGING FOREST**—A forest community (sometimes woodland) fringing a watercourse. The structure varies (see Table I).
- GEOPHYTE**—A plant with renewal buds buried in the soil (> 5 cm. below the soil surface).
- GRASSLAND**—A community dominated by perennial grasses. Subforms: Hummock Grassland; Dry Tussock Grassland; Wet Tussock Grassland; Sod Tussock Grassland.
- GRASSLAND**—An open grassland community dominated by coarse, xeromorphic grasses forming isolated hummocks (aggregations of tussocks), between which seasonal therophyte societies may be present.
- Dry Tussock Grassland**—A closed grassland community dominated by xeromorphic grasses forming discrete but open and poorly developed tussocks usually isolated at their base but uniting as a loosely interlacing leaf canopy above, below which smaller perennial and annual herbs are present.
- Wet Tussock Grassland**—A closed grassland community dominated by tall, hygrophilous grasses, sometimes codominant with other monocotyledonous herbs, forming large, compact tussocks isolated at their base but uniting as a densely interlacing leaf canopy above, below which smaller perennial mesomorphic herbs are present.
- Sod Tussock Grassland**—A closed grassland community dominated by grasses of short to medium height forming compact tussocks in close contact at their base and uniting as a densely interlacing leaf canopy above, below which smaller perennial mesomorphic herbs are present.
- GRASSLAND**—Alpine grassland (Joint Scientific Committee, 1946) = Sod tussock grassland.
Desert grassland (Prescott, 1931) = Hummock grassland.
Meadow grassland (Tansley, 1939) = Wet tussock grassland.
Mountain grassland (Prescott, 1931) = Sod tussock grassland.
Porcupine grassland (Prescott, 1931) = Hummock grassland.
Sclerophyllous grassland (Prescott, 1931) = Hummock grassland.
Subalpine grassland (Joint Scientific Committee, 1946) = Sod tussock grassland.
- GRASS STEPPE** (Prescott, 1931) = Dry tussock grassland.
- GROWTH FORM** = Habit.
- GROWTH FORM STAGE**—The stage in a succession identified by the predominant growth form.
- HABIT**—General appearance of an organism, e.g., erect, climbing, etc.
- HABITAT**—The environment in which an organism or community exists.
- HALOPHYTIC**—Pertaining to plants growing on saline soil.
- HALOSERE**—A succession which commences in salt water or in salty places.
- HEATH**—A typically closed community dominated by nanophanerophytes or chamaephytes (commonly with ericoid leaves), from which hummock-forming bog mosses are absent.
- HEATHER**—(i) *sens. strict.* = A heath dominated by Ericaceous plants (Tansley, 1939). (ii) *sens. lat.* = Heath, not necessarily Ericaceous.
- HELIOPHYTE**—A plant with renewal buds submersed in water or buried in water-saturated soil, but with vegetative shoots projecting into the air.
- HEMICRYPTOPHYTE**—A plant with renewal buds in the soil surface (approx. 0-5 cm.) protected by the surrounding soil or litter.
- HERB**—A non-woody plant.
- HERBAGE**—Herbs taken collectively: grasses and forbs.
- HERBFIELD** (Cockayne, 1921) = Alpine herbfield.
- HERBIVORE**—An animal living entirely on vegetable matter.
- HERB MOOR** (Cockayne, 1921) = Alpine herbfield.
- HYEMAL**—Pertaining to winter, e.g., biennial society (q.v.).
- HYDROPHYTE**—A plant with renewal-buds submersed in water or buried in water-saturated soil and with the vegetative shoots submersed in water also.
- HYDROSERE**—A succession in water or moist places.
- HYDROPHILOUS**—Inhabiting wet land or water.
- HYPERCLIMAX**—A community which, in the process of succession, will change with time = seral community.
- LAYER** = Stratum.
- LIANE**—A climbing or twining plant.
- LIFE-FORM**—Name of a plant based on the position of its perennating buds. (See Raunkiaer's life-forms.)
- LIFE-FORMS** (Raunkiaer, 1934).—Megaphanerophyte, mesophanerophyte, microphanerophyte, nanophanerophyte, chamaephyte, hemipterophyte, geophyte, heliophyte, hydrophyte, therophyte, succulent-stemmed phanerophyte, epiphyte. (See definitions of each life-form.)

LIFE-FORM SPECTRUM (Raunklaer, 1934).—A means of expressing the relative percentages of species belonging to the various life-forms of plants in a given area. The normal spectrum for the world is shown in the following table.

Percentage Distribution of the Species among the Life-forms.

No. of Species	Mega- and Meso-phanerophytes (MM)	Micro-phanerophytes (M)	Nano-phanerophytes (N)	Chamomphytes (Ch)	Hem-criptophytes (H)	Geophytes (G)	Holophytes and Hydrophytes (HH)	Therophytes (Th)	Staccant (S)	Epiphytes (E)	Paraphytes (P) (C) (G)
400	6	17	20	9	27	3	1	13	1	4	1.0

LIFE-FORM STAGE.—A stage in a succession identified by the dominance of plants with the same life-form.

LIGNOTUBER.—A (large) woody swelling, chiefly or entirely subterranean at the base of the stem of certain plants and containing numerous cortical buds.

LIMNOSERE.—A succession which commences in fresh water.

LITHOSERE.—A succession which commences on rock.

MACROCLIMATE.—The climate external to the community.

MACROENVIRONMENT.—The environmental conditions under which the community developed, measured outside the community.

MALLEE.—A community dominated by multi-stemmed microphanerophytes (mallees) with lignotubers. Subforms: Dry Mallee; Wet Mallee.

Dry Mallee.—A xeromorphic mallee community characterized by a densely interlacing or discontinuous dominant stratum, and discontinuous lower shrub and herbaceous strata.

Wet Mallee.—A mallee community characterized by usually densely interlacing dominant and lower shrub strata, and a discontinuous herbaceous stratum which frequently contains helophytes.

MALLEE.—A microphanerophyte with many stems arising from a large underground lignotuber. Applied to species of *Eucalyptus* only, although many other plants (e.g. *Melaleuca*) exhibit a mallee habit.

MANGROVE.—A shrub (less commonly a tree) growing in a substratum saturated by brackish or salt water, and characteristically producing apogeotropic roots (pneumatophores) which become aerial.

MARSH.—A waterlogged area in which the level of the water table is near (but usually not far above) the soil surface, and in which the soil has an inorganic basis. (Frequently used also in reference to fen.)

MATURE.—Climax.

MEGAPHANEROPLITE.—A tree with renewal buds on aerial shoots more than 30 metres above soil level.

MESOMORPHIC.—Exhibiting morphological characters indicative of moderate water supply, such as soft thin leaves, thin cuticle, etc.

MESOPHANEROPLITE.—A tree with renewal buds on aerial shoots 5-30 metres above soil level.

MICROCLIMATE.—The climate within a community or within a microhabitat (see macroclimate, microhabitat).

MICROHABITAT.—The habitat within a community, or within a small area or any special place.

MICROPHANEROPLITE.—A tall shrub with renewal buds on aerial shoots 2-5 metres above soil level.

MINIMAL AREA.—The smallest sample of a community which contains the characteristic species and which is large enough to exhibit the structure of the community.

MIRE (Sjörs, 1948; Du Rietz, 1949).—A general term which includes both bog and fen.

MIXED MIRE (Du Rietz, 1949) = Valley bog.

MONOCLIMAX THEORY (Weaver and Clements, 1929).—The theory that maintains that in any area all communities, by the process of succession, will ultimately develop into the same community which is designated the climatic climax.

MONSOON FOREST (Blake, 1948) = Monsoon rainforest.

MONTANE.—Pertaining to mountainous environments, below subalpine.

MOOR.—Flachmoor (Tansley, 1939) = Fen; Herb moor (Cockayne, 1921) = Alpine herbfield; Hochmoor (Tansley, 1939) = Raised bog; Low moor (Tansley, 1939) = Fen; Niedermoer (Tansley, 1939) = Fen; Transition moor (Tansley, 1939) = Valley bog.

MOSAIC = Complex.

MOUNTAIN MEADOW (Prescott, 1931) = Alpine herbfield.

NANOPHANEROPLITE.—A shrub with renewal buds on aerial shoots 25 cm.-2 metres above soil level.

NOCTURNAL.—Pertaining to night.

OMNIVORE.—An animal which feeds on a wide range of food, as distinct from those which are predominantly herbivorous or predaceous.

PASTURE.—Any plant community grazed by domestic livestock.

Improved Pasture.—A pasture into which one or more species has been introduced, either on cultivated ground or into native or natural pastures.

Native Pasture.—A pasture in which endemic perennial species are dominant, in which there are few or no exotic species.

Natural Pasture.—A pasture developed under the influence of man and the grazing animal but without artificial seeding, in which the original dominants have been partly or entirely replaced by exotic species.

Permanent Pasture.—A sown pasture of perennial forage species (with or without annuals), established artificially on cultivated ground.

Sown Pasture.—A pasture established artificially on cultivated ground.

PASTURE TYPE.—A disclimax or natural community of qualitatively uniform dominants grazed by domestic animals; it is designated by its dominant species.

PEDOSERE.—A succession which commences on previously formed soil; the term is applicable usually to secondary successions.

PHYSIOGRAPHIC CLIMAX.—A climax community limited by physiography.

PREDATOR.—An animal which preys upon and eats other animals.

PRIMARY EDAPHIC.—Pertaining to the soil parent material (cf. edaphic).

PRISERE.—Primary succession.

PSAMMOSERE.—A succession which commences on sand.

PTERIDOPHYTE QUOTIENT (Raunkiaer, 1934).—The proportion of pteridophytes in a flora compared with the proportion in the total flora of the world (1/25). The Pt.-Qt. of a flora

$$\text{thus} = \frac{\text{no. of pteridophytes} \times 25}{\text{no. of phanerogams.}}$$

(Similarly Moss, Liverwort, and Lichen Quotients, of which the proportions to phanerogams in the total flora of the world are 1/11, 1/35, and 1/22 respectively.)

RAINFOREST.—A closed community dominated by usually mesomorphic meso- or megaphanerophytes forming a deep, densely interlacing canopy in which lianes and epiphytes are invariably present, with mesomorphic subordinate strata of smaller trees, shrubs, and ferns and herbs. Subforms: Temperate Rainforest; Subtropical Rainforest; Tropical Rainforest; Monsoon Rainforest.

Temperate Rainforest.—A rainforest community characterized by the usually poor development of lianes and epiphytes, the sparseness of the subordinate strata of smaller trees, shrubs, and ferns and herbs (except in damp places), and the abundance of hygrophilous mosses and liverworts on the ground and boles of the trees.

Subtropical Rainforest.—A rainforest community characterized by an abundance of lianes and epiphytes, well developed subordinate strata of smaller trees and shrubs, a poorly developed ground stratum of ferns and herbs (except in light breaks), and the comparative sparseness of hygrophilous mosses and liverworts on the ground and boles of the trees.

Tropical Rainforest.—Similar to Subtropical Rainforest, but containing an additional uppermost stratum of tall trees (frequently palms) whose canopy is discontinuous; lianes usually more prolific.

Monsoon Rainforest.—A rainforest community characterized by the dominance of deciduous species in the tree strata in which lianes and epiphytes are usually fairly common, moderately well developed shrub and herbaceous strata, and the sparseness of hygrophilous mosses and liverworts on the ground and boles of the trees.

RAINFOREST, SUBANTARCTIC (Fraser and Vickery, 1937) = Temperate rainforest.

RAUNKIAER.—See life-form.

SALTATORIAL.—Leaping, jumping.

SALTBUSH.—An open shrub community dominated by halophytic nanophanerophytes or chamaephytes (typically Chenopodiaceae).

SAMPLE.—A randomly selected plot of arbitrarily pre-determined dimensions within a stand of vegetation (Pryor, 1951).

SAVANNAH.—A community dominated by perennial xeromorphic grasses together with widely scattered woody phanerophytes. Subforms: Shrub Savannah; Tree Savannah; Mallee Savannah.

Shrub Savannah.—A savannah community containing micro- or nanophanerophytes, other than mallees.

Tree Savannah.—A savannah community containing meso- or megaphanerophytes.

Mallee Savannah.—A savannah community containing mallees.

Note.—Some of the so-called savannahs do not constitute true vegetation units, but consist essentially of a mosaic of grassland and of scrub, mallee, or woodland; the grassland communities occur on generally more uniform tracts, and the scattered shrubs or trees on sites of locally greater soil moisture availability or aeration. This situation is known definitely to obtain in some of the apparent savannahs in certain areas of New South Wales, for example, on chernozemic soils of the north-west.

SAVANNAH.—Also previously used for grassland (Pryor, 1939).

SAVANNAH MALLEE (Key, 1951) = Open mallee.

SAVANNAH SCRUB = Open scrub.

SCLEROPHYLL.—Hard-leaved, usually xeromorphic.

SCLEROPHYLL FOREST.—A closed community dominated by sclerophyllous meso- or megaphanerophytes characterized by flat-topped crowns which form a usually interlacing canopy, and by boles of which the length is equal to or greater than the depth of the crowns. Subforms: Dry Sclerophyll Forest; Wet Sclerophyll forest; Swamp Sclerophyll Forest.

Dry Sclerophyll Forest.—A sclerophyll forest community characterized by a usually interlacing dominant stratum, well developed but usually discontinuous strata of xeromorphic shrubs, and a usually discontinuous herbaceous stratum.

Wet Sclerophyll Forest.—A sclerophyll forest community characterized by a tall, densely interlacing dominant stratum below which a discontinuous stratum of smaller, shade-tolerant trees may sometimes develop, well developed continuous or discontinuous strata of mesomorphic shrubs, and a dense or sparse herbaceous stratum.

Swamp Sclerophyll Forest.—A sclerophyll forest community characterized by an herbaceous stratum of helophytes.

SCRUB.—A community dominated by single-stemmed microphanerophytes branching near ground level. Subforms: Dry Scrub; Wet Scrub; Mangrove Scrub.

Dry Scrub.—A xeromorphic scrub community characterized by a discontinuous or loosely interlacing dominant stratum, a discontinuous lower shrub stratum, and a sparsely continuous herbaceous stratum.

Wet Scrub.—A scrub community characterized by a densely interlacing dominant stratum, a continuous or discontinuous lower shrub stratum, and a continuous or discontinuous herbaceous stratum containing helophytes.

Mangrove Scrub.—A tidal scrub community characterized by a densely interlacing dominant stratum of species of mangrove with pneumatophores, a discontinuous lower shrub stratum usually of young mangroves, and a ground stratum of algae on the pneumatophores and mud.

SCRUB, LITTORAL = Mangrove scrub.

SCRUB, TIDAL = Mangrove scrub.

SCRUB, SAVANNAH = Shrub savannah.

SERAL.—Successional.

SERE.—Succession.

SHRUB.—A woody plant less than about 8 metres in height (the upper limit of the microphanerophyte life-form), frequently with many stems.

SOCIES.—The seral equivalent of the society.

SOCIETY.—A subordinate community contained within the structure of the association or sub-association.

STAGE.—A single clearly marked step in succession.

STAND.—A continuous piece of vegetation within which there is a definite degree of homogeneity (Pryor, 1951) (cf. sample).

STATUS (maturity).—The stage in development of a community relative to the climax, i.e., seral or climax.

STEPPE.—Shrub steppe (Prescott, 1931; Wood, 1937) = Saltbush. Tree steppe (Wood, 1937) = Open scrub.

STRATIFICATION.—The condition brought about by the occurrence of strata (layers) within a community.

STRATUM.—A layer in a community produced by the occurrence at approximately the same level of an aggregation of plants of the same habit; thus tree stratum, herbaceous stratum, etc.

STRATUM SOCIETY.—A society which is present throughout the whole year (see aspect society).

STRUCTURAL FORM.—The structural characteristics exhibited by a community which at present are classified according to the following well-defined types: grassland, savannah, alpine herbfield, fen, bog, feldmark, heath, saltbush, scrub, mallee, woodland, sclerophyll forest, rainforest. (See Table I in text and under the appropriate titles in Glossary.)

STRUCTURAL STAGE.—A stage in a succession identified by a community conforming to one of the defined structural forms (q.v.), e.g., shrub stage.

STRUCTURAL SUBFORM.—A division of a structural form identified by a minor variation in structure, e.g., savannah woodland is a subform of the woodland form.

STRUCTURAL UNIT.—A synthetic unit to which all communities of the same structure are referred, irrespective of their floristic composition (see formation, subformation).

STRUCTURE.—The spatial arrangement of plants within a community (see structural form, stratification).

SUBALLIANCE.—A subdivision of an alliance obtained by arranging the component associations into groups of maximum affinity.

SUBALPINE.—Referring to elevated environments where the ground is snow covered continuously for at least one month and up to about six months of the year.

SUBASSOCIATION.—A subdivision of an association determined by a variation in the most important subordinate stratum of the association, without significant qualitative changes in the dominant stratum.

- SUBASSOCIATION.**—The seral equivalent of the subassociation.
- SUBCLIMAX.**—The penultimate stage of a succession, resembling the climax in structure.
- SUBFORMATION.**—A subordinate synthetic structural unit within the general pattern of a formation, to which are referred all climax communities exhibiting the same structural subform, irrespective of floristic composition.
- SUBLACIAL.**—Pertaining to (exposed) environments in close proximity to glaciers, ice sheets, or permanent snow.
- SUBMERGED STAGE.**—The stage in a hydrosere identified by the dominance of submerged aquatic plants.
- SUBORDINATE SPECIES.**—A species of a community which is not the dominant (or codominant).
- SUBSERE.**—Secondary succession.
- SUCCESSION.**—The process by which the same area is occupied by different plant communities when all factors except time remain constant.
- Primary succession.*—A succession which occurs on a naturally bare area, not previously occupied by vegetation.
- Secondary succession.*—A succession which occurs on a denuded area on which the original vegetation has been completely or partly destroyed by some external influence (e.g., fire, flood, grazing).
- SUCCULENT-STEMMED PHANEROPLANT.**—A succulent-stemmed plant with renewal buds more than 25 cm. above soil level.
- SWAMP.**—A waterlogged area in which the level of the water table is above the soil surface for most of the year. (Also used loosely in reference to fen or marsh.)
- SYNSIUM** = Stratum.
- RAISED MOSS** (Tansley, 1939) = Raised bog.
- TERRESTRIAL STAGE.**—A seral stage on land.
- THEROPHYTE.**—An annual plant surviving the unfavourable season only as seeds.
- TOLERANCE** (ecological).—The ranges of variation of factors of the environment within which an organism or community can function.
- TEMPORAL CLIMAX.**—A community limited by time. A stage in succession.
- TREE.**—A woody plant more than about 8 metres in height (the lower limit of the meso-phanerophyte life-form), usually with a single stem.
- TYPE** (Pryor, 1939) = Association.
- VEGETATION.**—The total aggregation of plant communities in an area (cf. flora).
- VEGETATION TYPE** (Pryor, 1939) = Association.
- VERBAND** (Du Rietz, 1936) = Alliance.
- VERNAL.**—Pertaining to spring, e.g., vernal society (q.v.).
- VERSATILE SPECIES.**—A species with a wide ecological tolerance.
- WIND DESERT** (Hamilton, 1926) = Feldmark.
- WOODLAND.**—A community dominated by meso-phanerophytes characterized by rounded crowns which form an open or loosely interlacing canopy, and by boles of which the length is usually less than the depth of the crowns. Subforms: Shrub Woodland; Savannah Woodland; Tall Woodland; Subalpine Woodland.
- Shrub Woodland.*—An open woodland community characterized by a discontinuous dominant stratum in which the crowns of the dominants are separated by a distance greater than the diameter of the crown, a discontinuous but well developed stratum of microphanerophytes, discontinuous smaller shrub strata of nanophanerophytes and chamaephytes, and a continuous or discontinuous herbaceous stratum.
- Savannah Woodland.*—A usually open woodland community characterized by a discontinuous dominant stratum in which the crowns are separated by a distance equal to or slightly greater than the diameter of the crown, and a usually continuous herbaceous stratum without well-developed strata of micro-phanerophytes and smaller shrubs.
- Tall Woodland.*—A closed woodland community characterized by a tall sparsely continuous dominant stratum in which the crown depth of the dominants equals or only slightly exceeds the length of the bole, and by the poor development or lack of subordinate strata of microphanerophytes, smaller shrubs and herbs.
- Subalpine Woodland.*—A closed subalpine woodland community (sometimes reduced to the dimensions of scrub) characterized by a usually continuous dominant stratum in which the crown depth of the dominants greatly exceeds the length of the bole, discontinuous but well-developed shrub strata of nanophanerophytes and chamaephytes, and not microphanerophytes, and a dense, continuous herbaceous stratum.
- Swamp Woodland.*—A woodland community characterized by an herbaceous stratum of helophytes.
- XEROMORPHIC.**—Exhibiting the morphological characters supposedly induced by a scanty water supply, e.g., hard (small) leaves, thick cuticle, etc.
- XEROSERE.**—A succession which commences in a dry place (see lithosere, psammosere, pedosere).

SUMMARY.

A scheme for the objective classification of plant communities is outlined.

Classification on a structural basis is discussed and structural forms and subforms suitable for the description of the known Australian plant communities are defined.

Units for the floristic classification of climax communities are defined and their usages discussed. These units are the *Association*, the *Alliance*, and the *Society*. Sub-units are also proposed.

Structural units for the classification of the floristic units are proposed. These units are the *Subformation* and *Formation*.

Seral communities are dealt with in the same detail and suitable units are defined.

A glossary of ecological terms is included.

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A NOTE ON THE STRATIGRAPHY AND STRUCTURE OF THE WELLINGTON-MOLONG-ORANGE-CANOWINDRA REGION.

By GERMAINE JOPLIN, B.A., D.Sc., Ph.D., AND OTHERS.

(Plate i and two Text-figures.)

[Read 30th April, 1952.]

Synopsis.

Reconnaissance mapping has been carried out over an area of about 2,000 square miles, and it has been shown that Silurian strata have been folded into a great anticlinorium upon which later folding has been superimposed. The first movement is attributed to the Bowring Orogeny, and the second to the Kanimblan.

The Silurian strata have been mapped as the Gamboola, Nanima and Manildra Formations, and there is evidence that the first is of Lower Silurian age.

Ordovician, Devonian and Jurassic strata also occur in the area, as well as Tertiary lavas and related intrusions. Granites may be of Kanimbla age.

Introduction.

The region covered by the map (Plate i) has an area of about 2,000 square miles. Joplin and Culey (1938) published a reconnaissance map of a small part of the area, and subsequent, more detailed mapping has necessitated some modifications, which are incorporated in the present map. The map is a compilation of the work of sixteen people. Six of these workers—Misses E. M. Basnett, M. J. Colditz and E. M. Phillips and Messrs. R. Brewer, D. G. Moye and N. C. Stevens—mapped certain areas (see inset) as part of their honours course in the Department of Geology, University of Sydney, and their work has been carried out mainly by compass traverses on parish maps. The work of Basnett and Colditz (1946) and Stevens (1950) is published. Reconnaissance mapping between areas of more detailed mapping has been carried out by Misses M. Breckenridge, A. G. Culey, J. Johnston and G. A. Joplin, and Messrs. T. G. Vallance and K. Sharp, and a part of the work of L. J. Jones (1935), C. A. Sussmilch (1906) and C. A. Sussmilch and H. I. Jensen (1909) has been used to tie the area to already-published work.

Although parts of the map are published, it is presented for three reasons: (i) it indicates the regional structure which is not apparent in the maps of isolated areas; (ii) it incorporates work which may not otherwise be published and which may save much time for those undertaking more detailed work in the future; and (iii) the map shows the relation between the Silurian rocks of the Wellington-Molong area and the Ordovician strata to the south (Stevens, 1951).

As the general geology of the area is fairly well known from published work, it is proposed only to make amendments and additions to the stratigraphy and to indicate broadly the structure of the area.

STRATIGRAPHY.

Ordovician.

Basnett and Colditz (1946) recorded graptolite-bearing slates surrounded by Silurian andesites at Wellington and at Apsley, and suggested that the Silurian strata were deposited around Ordovician islands. Later Moye found graptolites in slates near Borenore, not far from Lower Silurian limestones (Fletcher, 1950), and recently G. H. Packham* has found Ordovician graptolites near the Nandillyan limestone. Stevens found graptolite slates associated with limestones and andesites faulted against Upper Devonian strata near Cargo and has more recently found Ordovician limestones interbedded with andesite on the Belubula River (Stevens, 1951). This discovery raises the question of the age of the andesites and limestones within the area of the present map.

* Personal communication.

Section A-B (Text-fig. 2) indicates a possible relation between Lower Silurian and Ordovician strata near Amaroo and Borenore, though it must be emphasized that much work remains to be done in this part of the area, which at present is the subject only of rough reconnaissance.

Although the possibility of an Ordovician age of some of the andesites adjacent to black slates in the Wellington District cannot be overlooked, there is reason to believe that the Silurian strata were deposited on an uneven basement of Ordovician rocks, and the explanation offered by Basnett and Colditz (1946) seems to be the most likely one.

Silurian.

There appears to be a threefold division of the Silurian in this region, but until further palaeontological work is undertaken, it is impossible to say what part of the succession is represented.

Gamboola Formation.

Basnett and Colditz (1946) mapped a Lower Sedimentary Series, underlying andesites, in the Wellington District, and these rocks, which consist mainly of low-grade slates, tuffaceous slates, cherts and limestones, have been traced south to the main road between Molong and Orange in the Parish of Gamboola. *Halysites* from this area was described by Etheridge (1904). On the present map the Borenore limestone, from which Fletcher (1951) has recently described Lower Silurian trilobites, is shown to be continuous with this formation, though this interpolation may not be correct, because, as indicated above, much detailed work remains to be done in the Borenore-Amaroo area. Etheridge (1909) recorded trilobites in a limestone near Borenore, but the relation of this limestone to the Lower Silurian limestone is not clear.

This Formation unconformably overlies the Ordovician and is conformably overlain by andesites and related pyroclastic rocks. Unfortunately it is not possible to measure the thickness as it occupies the core of an anticlinorium which is pitching to the north, and the base is possibly covered by the volcanic pile of the Canoblas. In section A-B only the apparent base is exposed on an uneven Ordovician surface.

Limestone members within this Formation possibly include the Borenore and Spring Creek Limestones, the Nandillyan Limestone and the Narragal Limestone. The Molong Limestone (see C-D, Text-fig. 2) may be regarded as a member at the top of this Formation or as one at the base of the Nanima Formation. Rhyolites occur on Spring and Oakey Creeks, but these may be (?) Lower Devonian.

It is proposed to name this unit the Gamboola Formation and to include the above lenses of limestone as members.

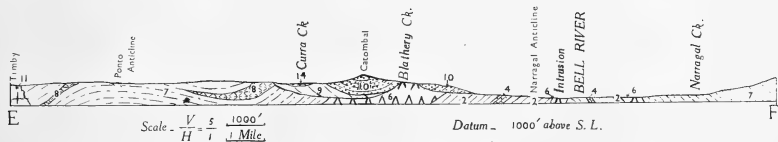
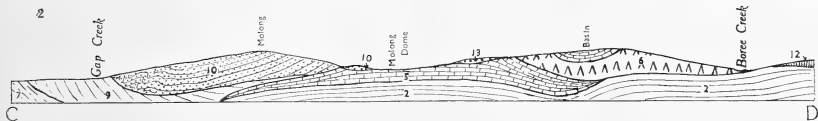
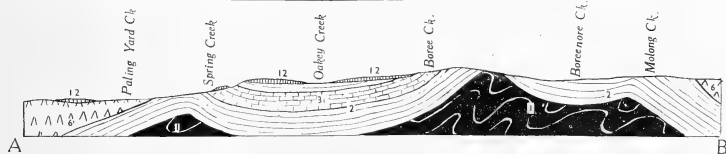
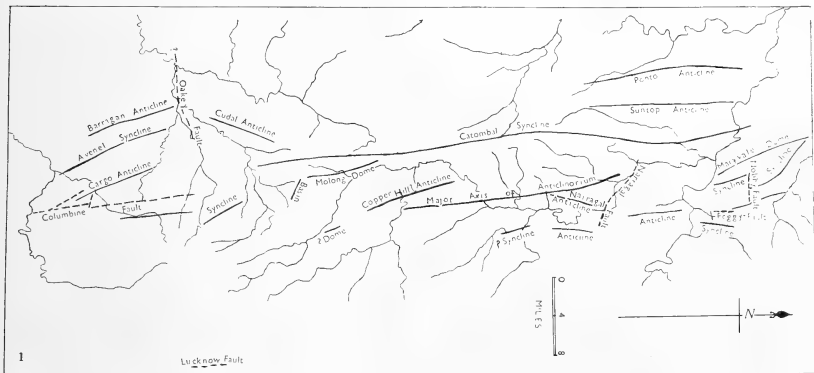
The Molong and Narragal Limestones are invaded by porphyrites which are possibly feeders to the overlying flows in the Nanima Formation.

Nanima Formation.

Basnett and Colditz (1946) described a Volcanic Series between a Lower and Upper Sedimentary Series in the Wellington District, and Colditz (1948) showed that it consisted of hornblende and pyroxene andesites, trachyandesites, trachybasalts, basalts, tuffs and agglomerates associated with sills of hornblende lamprophyre. Basnett (1942) described a lamprophyre sill on Pogygy Creek that had suffered serpentinization in a fault-zone.

Basnett and Colditz also recorded lenses of limestone interbedded with the lavas and tuffs. Work further south has indicated that the Molong Limestone may be a member low in this Formation, and it is obvious from section C-D (Text-fig. 2) that the limestone in the basin south of the Molong Dome is on a higher horizon in this Formation. Stevens (1951) has correlated the Cargo Limestone with that of Molong. Basnett and Colditz consider that the limestone at Wellington Caves is possibly Devonian, but the present writer considers that a fault, visible in the Cathedral Cave, which brings rhythmically banded limestones against massive limestone, is possibly a fault bringing the Devonian against the Silurian. Thus, there is reason to believe that the limestone exposed east of the river on the Caves Reserve is a member of this Formation.

The Nanima Formation is named after the Parish of Nanima, from which much of the material described by Colditz was collected, and may thus be regarded as the type-area for this Formation. It is underlain by the Gamboola Formation and overlain by the Manildra Formation.



Text-fig. 1.—Sketch map showing trends of the major structures in the Wellington-Molong-Orange-Canowindra Region.

Text-fig. 2.—Sketch sections across the Wellington-Molong-Orange-Canowindra Region. 1, Ordovician strata; 2, Gamboola Formation; 3, Boremore-Spring Creek Limestone; 4, Narragal Limestone; 5, Molong Limestone; 6, Nanima Formation; 7, Manildra Formation; 8, Garnetiferous Porphyry and Tuff; 9, Garra Beds; 10, Catombal Formation; 11, Granite; 12, Basalt; 13, Tertiary Gravels; 14, Alluvium.

Manildra Formation.

This sequence of tuffs, cherts and indurated shales was described by Joplin and Culey (1938) as the Manildra Beds. More detailed work has subsequently revealed (Basnett and Colditz, 1946; Stevens, 1950) that garnetiferous tuffs and porphyries occur near the top of the Formation, and Moye* has suggested the possibility of the felspathic

* Personal communication.

tuffs near Stuart Town being the equivalents of these. North of Cumnock, and also near Wuuluman, rhyolites occur near the top of the Formation, and it now appears fairly certain that the Burrawong Limestone, the Nubrigyn Limestone and the Canomodine Limestone form lenses in this succession and are therefore members. The Formation is underlain by the Nanima Formation and overlain by rhyolites of probable Lower Devonian age.

Devonian.

Rhyolites.

M. E. Phillips has been able to map several separate flows of rhyolite, which crop out over a considerable area west of Gumble and extend south of Manildra. They overlie the Manildra Formation and may be of Upper Silurian age, though it seems more likely that they are Lower Devonian.

Garra Beds.

The reconnaissance term "Garra Beds" is retained for this sequence of rocks as no further detailed mapping has been done within them, and it is not known whether they should rank as a formation or as a group. Hill (1942) considers that both Lower and Middle Devonian limestones are represented in these beds, but as yet no line of demarcation can be plotted and only a further extension of the beds is shown on the present map. At the southern end of the belt, near Walker's Creek, the Garra Beds have been shown to be more extensive than was at first supposed by Joplin and Culey (1938), and they appear on the eastern edge of the overlying Upper Devonian strata. On the other hand, the easterly extension on the north, in the area of the Wellington Caves, has been reduced for reasons explained above.

Although Basnett and Colditz suggested a slight unconformity between the Devonian and Silurian strata, their sections show no break in the sequence, and Joplin and Culey found no suggestion of unconformity in the Molong-Manildra region. The present compilation, however, shows a well-marked regional overlap, particularly well shown in the area mapped by Brewer and Moye, and an attempt has been made in sections C-D and E-F to show an unconformity between the Garra Beds and the underlying Silurian as well as between these beds and the overlying Upper Devonian strata. More detailed work may reveal faults which may necessitate a somewhat different interpretation.

Catombal Formation.

Matheson (1930) placed the upper part of the Upper Devonian of the Catombal Range in the Catombal Series, and the lower part containing *Spirifer disjunctus* in the "Transition Stage", but Basnett and Colditz have pointed out that both are of Upper Devonian age, and suggest that "Catombal Series" be applied to the whole sequence. As the term "series" can be applied only to a time-stratigraphical unit, it is necessary to apply a suitable name for the rock unit. Furthermore, Brown (1931) has already designated the time-stratigraphical unit as Lambie Stage, thus indicating that it belongs to the upper part of the Upper Devonian sequence.

It is suggested that Catombal Formation be applied to this unit, which consists mainly of conglomerates, quartzites and red shales in this area.

STRUCTURE.

It has been shown that the Silurian of this district may be divided into three units—the Manildra, Nanima and Gamboola Formations, and that the lowest is the Gamboola Formation.

The major structure is an anticlinorium with a pitch slightly west of north, but it is somewhat masked by the development of numerous smaller pitching folds. The largest of these is the Catombal Syncline which trends north-south for about 60 miles and slightly transgresses the axis of the anticlinorium.

In many places cross-warping has caused reversal of pitch and caused anticlines to form domes, and synclines basins.

The trends of the larger folds have been plotted in Text-figure 1, where it can be clearly seen that the major axis of the anticlinorium is inclined to that of the Catombal Syncline. As the syncline, which is occupied by rocks of Lower, Middle and Upper Devonian age, transgresses the larger fold, the latter must have formed in pre-Devonian time and must be related to the Bowning Orogeny (Browne, 1947). The Catombal fold, on the other hand, is post-Devonian and probably formed during the Kanimbla Orogeny. Although it is impossible to interpret the structure when the configuration and nature of the basement are unknown, reference to Text-figure 1 will show that the Cudal Anticline, the Borenore Syncline and the small basin south of the Molong Dome radiate inwards towards the southern end of the Catombal Syncline, and it is tentatively suggested that this gathering of the folds is due to the downwarping of the Catombal Syncline. It is also possible that the Barragan, Avenel and Cargo folds are also related, though their axes have been disturbed by subsequent faulting. The Molong Dome and Copper Hill Anticline also trend towards the Catombal axis and may have been caused by the same movement. A gathering of the folds at the northern end of the axis is not so apparent although the Pogy Fault, and a small syncline about one mile east of it, show such a trend. The Maryvale Dome is possibly on the main axis of the Silurian fold and the Ponto and Suntop Anticlines, as well as a small anticline north of the Narragat Fault, are nearly parallel to the Bowning axis of folding and are possibly related to it.

Faults.

Basnett and Colditz recorded four faults in the Wellington area and Stevens mapped two major faults in the southern area. With the possible exception of the Pogy Fault all appear to be pre-Devonian, and to have transgressed probable Kanimbla folds, thus they may be late Kanimbla.

On account of the similarity between the serpentized lamprophyre in the Pogy Fault, and the serpentine associated with augite-andesite at Lucknow, it is suggested that a fault occurs at this locality though it has not been mapped and the trend indicated is hypothetical. Detailed mapping will probably reveal other faults in the area, particularly in the region between Boree and Oakey Creeks, which has so far received little attention.

Unconformities.

In dealing with the stratigraphy it was indicated that two slight unconformities are shown—one between Silurian and Lower Devonian rocks and the other between rocks of Middle and Upper Devonian age (Brown, 1932).

SUMMARY.

It has been indicated that the map is a compilation based on the work of sixteen people. Though some parts have been mapped in detail, it is mainly a piece of reconnaissance mapping. Nevertheless, it serves a useful purpose in giving a regional picture of the area and reveals slight unconformities between Silurian and Devonian rocks and between Middle and Upper Devonian strata. Furthermore, the general structure of the area is revealed, and it seems fairly evident that Kanimbla folding and faulting have been superimposed on an anticlinorium which was folded during the Bowning Orogeny.

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STUDIES OF N-FIXING BACTERIA. I.

A NOTE ON THE ESTIMATION OF AZOTOBACTER IN THE SOIL.

By Y. T. TCHAN, Macleay Bacteriologist to the Society.

[Read 30th April, 1952.]

Synopsis.

The controversy on the use of liquid and solid media for the estimation of *Azotobacter* is critically examined. Experiences show that both techniques have some advantages and difficulties. A combined technique is proposed.

In 1926 Winogradsky published an account of his silico-gel method for the estimation of *Azotobacter* in the soil. He mistrusted the old liquid medium and based his objections on the fact that, in a liquid medium, if *Clostridium* develops in the lower layers a certain amount of N can be fixed which destroys the electivity of the medium. If abundant CO₂ is given off the medium becomes unsuitable for the growth of *Azotobacter*. The presence of protozoa may also affect the test and prevent the formation of a characteristic pellicle on the surface of the liquid. Because of these difficulties, Winogradsky considered that a positive test for *Azotobacter* is possible only when a large number of *Azotobacter* cells is present.

Jensen (1940) first pointed out that the liquid medium is better for detecting the sporadic presence of *Azotobacter* in the soil, although he thought that the plate method could be as accurate as the liquid medium if a comparable amount of soil inoculum were used.

More recently McKnight (1949) confirmed Jensen's observation and considered that the liquid medium is more accurate than the plate method.

Derx (1950) considered Winogradsky's silico-gel method as a very efficient procedure for isolation of N-fixing organisms: "As will presently be seen, this method has led to an important deepening of our knowledge of N-fixing organisms."

For the study of free N-fixing organisms in soil, it seems to us important to make a choice between different techniques.

The difference between the plate method and the liquid medium is not only dependent on the physico-chemical constitution, but there is a big difference in the quantity of inoculum used. Apparently we cannot decide on the accuracy of each technique when the quantity of inoculum used is not the same: (0.02 gr. p. plate (10 cm. of diameter) and 1 gr. p. liquid medium).

Experiments were carried out to determine the accuracy of each technique.

Azotobacter chroococcum recently isolated from the soil (Sydney University) was used. This culture was first incubated at 30°C. for 24 hours. A small quantity of it was then inoculated on a glucose-Agar for 18 hours. A suspension of this young culture was made in sterilized distilled water. A microscopic examination shows that all cells were mobile and we may therefore assume that all the cells were living, although it is not safe to assume that they can all reproduce. A direct estimation with a haemocytometer gives the number of cells contained in 1 c.c. The suspension was then diluted successively, by a factor of 10, until the last dilution contained the required number of cells.

The medium used was Winogradsky's standard medium with 1.0% of glucose. For the plate count technique, 2% of washed Agar is added.

Five parallel sets of the two media were inoculated with 0.2 c.c. of each dilution, and incubated at 30°. The cultures were examined after one week; if no growth was then visible they were incubated for a further week.

Number of cells calculated/0.2 c.c.	200	20	2	0
Plate: Mean number of colonies (5 plates)	52	0	0	0
Liquid medium: Number of tubes positive	5	5	3	0

It is clear that the liquid medium is capable of giving a positive growth with a few *Azotobacter* cells, if not with a single cell. If soil were present, it is possible that one would not obtain such reliable results, as Winogradsky suggested.

In order to test this, a soil is needed which does not contain *Azotobacter*, but which has all the physico-chemical-biological qualities necessary for its growth. Fortunately, the Gilgai soil from Curlewis in New South Wales has the qualities required. A similar experiment carried out with 0.5 gr. of soil (5 parallel sets in each case).

Number of cells calculated/0.2 c.c.	1200	120	12	1.2	0
Plate count: Mean of 5 sets	Excess of colonies.	40.3	0	0	0
Liquid medium: Number of tubes positive	5	5	5	1	0
Liquid medium + soil: Number of tubes positive	5	5	5	3	0

In all tubes containing soil, there was an abundant development of *Clostridium*. A microscopic examination shows the presence also of protozoa which in our case do not affect the formation of a characteristic pellicle of *Azotobacter*.

This experiment seems to eliminate all Winogradsky's objections and the presence of soil seems favourable for the growth of *Azotobacter*.

In order to determine the effect of humus, an extract of humus was made from the Gilgai soil and added to the test solution. The addition of this humus to the medium did not seem to alter the growth of *Azotobacter* significantly.

Number of cells calculated	1000	100	10	1	0
Plate counts 5 sets	Excess of colonies	26	0	0	0
Liquid humus: Number of tubes positive	5	5	5	0	0
Liquid + soil: Number of tubes positive	5	5	5	1	0

DISCUSSION.

In the tests carried out the liquid medium was more satisfactory than the 2% Agar medium for detecting the presence of *Azotobacter* in the soil. The Agar medium gives generally 25-33% of the theoretical number of colonies. Jensen (1940) found that the relationships between the plate count of *Azotobacter* and the corresponding direct counts of *Azotobacter*-like cells varied from 0.25% to 47%, with only 3 at 30-47% out of a total of 15 cases. Even if we accept that the *Azotobacter*-like cells in the soil are not all *Azotobacter*, our results agree quite well with Jensen's.

Using the statistical table given by McCrady (in Calmette et al., 1948) we can easily estimate the number of *Azotobacter* by the liquid medium.

Number of Cells Calculated	Plate Counts.	Liquid Count. Number Characteristic.	Number of <i>Azotobacter</i> .	Liquid Count + Soil. Number Characteristic.	Number of <i>Azotobacter</i>
200	52.0	553	90		
120	40.3	551	35	553	90
100	25.5	{ 550 551	{ 25 35	551	35

Although the liquid medium gave a better estimate of the total number of *Azotobacter* it does not give a proper estimate of the different species present.

CONCLUSION.

The above tests suggest that the liquid medium is more accurate than the 2% Agar plate for detecting the *Azotobacter* in soil. If we desire to have an idea of the different species composing the soil population (of *Azotobacter*) it is better to use the plate count technique.

Five gr. of soil is added to 45 c.c. of liquid medium (dilution 1/10). 0.5 c.c. of this suspension is diluted in 4.5 c.c. of sterilized water (1/100) 1 c.c. by fraction of 0.2 c.c. to 5 plates 5 liquid medium. The operation is repeated until a satisfactory dilution is obtained.

The dilution tubes from which we take off 2.5 c.c. of suspension receive 7.5 c.c. of liquid medium to make a volume of 10 c.c.

For routine work, therefore, it is desirable to use both techniques, and the following method has been adopted:

Quantity of Inoculum Used in Different Dilutions.

Dilution.	Liquid Medium for Detecting Sporadic Presence of <i>Azotobacter</i> on Dilution Tubes.	Liquid Medium in Test Tubes. Five Tubes for Each Dilution.	Agar Medium. Five Sets.
1/10	4.75 gr.	0.02 × 5 = 0.1 gr.	0.02 × 5 = 0.1 gr.
1/100	0.025 gr.	0.002 × 5 = 0.01 gr.	0.002 × 5 = 0.01 gr.
1/1000	0.0025 gr.	0.0002 × 5 = 0.001 gr.	0.0002 × 5 = 0.001 gr.

In the case of routine work, the number of plates and test-tubes can be reduced to two or three parallel sets only. The simultaneous estimation with liquid and agar medium, a kind of self control, gives a better result.

The dilution 1/10 is used to detect a sporadic presence of *Azotobacter*.

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STUDIES OF NITROGEN-FIXING BACTERIA. II.

THE PRESENCE OF AEROBIC NON-SYMBIOTIC NITROGEN-FIXING BACTERIA IN SOILS
OF THE SYDNEY DISTRICT.

By Y. T. TCHAN, Macleay Bacteriologist to the Society.

(Two Text-figures.)

[Read 30th April, 1952.]

Synopsis.

Many authors had noticed that in Australia *Azotobacter* can be isolated from acid soils. No detailed description of these *Azotobacter* has been published. In the present work an acid-tolerant nitrogen-fixing bacterium is isolated and its distribution in the Sydney district is studied.

It is generally accepted that the genus *Azotobacter* grows only at a pH above 5.9-6.0 and workers, e.g., Derx (1950), used an acid medium to prevent the growth of *Azotobacter*. However, several species of non-symbiotic acid-tolerant nitrogen-fixing bacteria are known. Starkey and De (1939) first isolated an organism which they called *Azotobacter indicum* from rice fields. The systematic position of this organism is doubtful and Burk (1939) thought "it may not be *Azotobacter*". Derx *et al.* (1950) found this same organism in Indonesian soils and later (1950) placed it in a new genus which they called *Beijerinckia*, separated from *Azotobacter* by certain morphological and physiological characters.

This new genus was defined as follows: "Straight or slightly curved or irregular, locally swollen to buckled, rods, characterized by the presence, at the extremities, of highly refractive spherical bodies, presumably consisting of lipoids. No endospores, motility present, at least in certain stage of the development. Flagellation peritrichous.

"Aerobic; developing in media with pH 3.5-9 and fixing atmospheric N in the absence of N compounds. Growth is accompanied by the formation of acid and in some species, by the formation of large amount of a tough to elastic slime. No surface pellicle is formed on liquid media, no development on peptone-broth agar. Gram negative."

Derx (1950) successfully isolated two other new species of *Beijerinckia*, including one species in which motility is rare or absent.

Another non-symbiotic N-fixing bacterium has been isolated by Stapp (1939). His organism shows some resemblance to *Azotobacter agilis*, but differs from the latter by its tolerance of acid conditions. This organism is classified as *Azotomonas insolita*.

Kauffmann and Toussaint (1951) have isolated a new *Azotobacter lacticogenes* which has an optimum pH at 5.5.

In Australia, the aerobic non-symbiotic N-fixing bacteria reported by Swaby (1939), Jensen (1940) and McKnight (1949), are *Azotobacter chroococcum* and occasionally *Azotobacter vinelandii* and *Azotobacter beijerinckii*. McKnight, however, following Bergey, considered *Azotobacter beijerinckii* and *Azotobacter chroococcum* to be conspecific.

In soils with a pH of 5 or less, two out of 32 samples contained *Azotobacter* and 17 out of 148 samples with a pH between 5 and 6 were positive.

During work in the Botany Department of Sydney University planned to determine the nitrogen requirements of *Hakea*, nutrient solutions were added to a washed river sand (Nepean River) used for growth studies. According to Miss P. J. Bradhurst (1951), there was a gain of N if the sand had received little or no combined N. If enough N was added there was a loss of N, but the quantity of N in the sand after the experiment seemed to be fixed at a certain level independent of the amount of N pre-existing. If this were true it suggested the possibility of N fixation by non-symbiotic N-fixing bacteria.

A glucose agar, N-free, and a similar liquid medium were inoculated with a sample of the sand. After a week some white colonies appeared on the surface of the agar. At the end of three weeks, the colonies became yellow. The inoculated liquid medium became turbid after the same incubating period; there was no pellicle formation. The medium also became slightly acid; Bromothymol Blue gave a yellow colour but the acidity was not enough to give a red colour with Methyl Red, thus indicating a pH between 5 and 6. The microscopic examinations showed the presence of nearly pure cultures of large coccoid cells containing prominent refractive bodies. When stained with Methylene Blue the cytoplasm of these cells showed blue with large colourless globules.

As the mineral solution used in the pot experiments had an acid pH slightly above 5.5, it was natural to consider the possibility of the acid-tolerant *Beijerinckia* being present. However, a close examination of cells showed that the morphology of this organism differed from that of *Beijerinckia*.* They were not rods, but coccoid cells like those of *Azotobacter*, differing from *Azotobacter chroococcum*, *Azotobacter vinelandii*, and *Azotobacter agilis* in the presence of fatty bodies and in cultural characters, especially the absence of pellicle formation in liquid medium. Winogradsky (1938) has noted transitory lipid bodies in the precystic stage of *Azotobacter vinelandii*, but in our organism the bodies are permanent. Lipman (1903) has already recorded lipid bodies in *Azotobacter beijerinckii* from which our organism differs by its tolerance to acid conditions.

It is premature to discuss the taxonomic position of this organism and further cytological and physiological studies are necessary. The occurrence of the acid-tolerant organism was of considerable interest and a survey of soils in the Sydney District was undertaken to determine the natural occurrence of the organism.

METHODS.

Medium: The original medium used by Starkey and De (1939) to isolate their organism, was a mineral basic medium with sucrose as organic matter. Derx (1950) suggested using an acid medium at pH 5 to prevent the growth of *Azotobacter*. This medium, however, hydrolyses the agar during sterilization. The medium finally adopted is Winogradsky's standard medium with 1 part in 10,000 of humus and 1% of glucose at pH 7.2. Humus was extracted by NaOH and dialysed first against tap water for twenty-four hours and then against distilled water for twenty-four hours. When the solid medium is used 2% of washed agar is added.

Qualitative detection. 0.1 g. fresh soil is first sprinkled on the surface of the agar medium and 5 g. is inoculated in 45 c.c. of liquid medium. The incubation is at 30°C. After a few days, the colonies or liquid cultures are examined. Cultures are kept in the incubator for one month before being considered negative.

MACROSCOPIC CHARACTER OF CULTURE.

Agar medium: Colonies are large (2 mm. in diameter. After three or four weeks their diameter may be 10 mm.). They are first white, becoming slightly yellow or grey. Some strains develop a dark chocolate colour different from the almost black colour of *Azotobacter chroococcum*. Microscopic examination is necessary in doubtful cases.

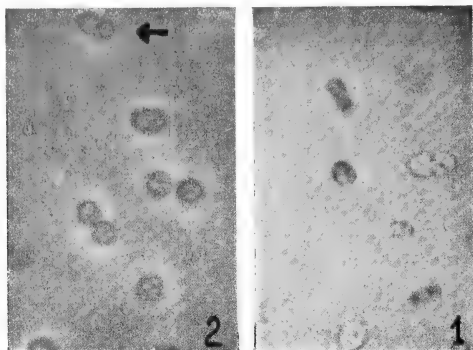
Liquid medium: The cultures start with a uniform turbidity of the medium. A close examination shows that the suspension of cells is rough and agglutinated. In old cultures there is no pellicle formation on the surface of the liquid medium. Sometimes a ring is formed. The ring may be wide enough to cover the centre (in a test tube), but even in this case, after gentle shaking, the mass of bacterial cells falls slowly to the bottom of the medium which becomes cloudy. This development is quite different from the characteristic pellicle formation of *Azotobacter*. In a mixed culture with *Azotobacter* the liquid medium is much more difficult to use because the whole picture is dominated by *Azotobacter*. In a mixed culture microscopic examination

* *Beijerinckia* strains were kindly supplied by Professor Derx and Miss J. T. de Vries, to whom we are much indebted.

shows the presence of our organism. When the liquid culture alone gives a positive test it is always considered as a doubtful case. The liquid culture is only considered positive when a transfer to a solid medium gives a characteristic culture.

MICROSCOPIC CHARACTER OF CELLS.

The typical difference between our organism and other *Azotobacter* is the presence of large fatty bodies, not stainable by the aniline dyes or iodine. When a culture is examined in the presence of Methylene Blue (aqueous solution) under the high-power lens, large colourless globules can be seen very clearly in the cells against the blue cytoplasm. One drop of culture was suspended in one drop of 2 parts per 1,000 of



Text-figures 1, 2.

1.—Photomicrograph ($\times 1,900$). Living cells in Methylene Blue aq. solution. White spots are lipid bodies.

2.—Photomicrograph ($\times 1,900$). Photograph taken with phase contrast microscope. Arrow indicates one *Beijerinckia*-like cell.

Methylene Blue. When the culture showed a positive test, the slide was dried, washed with alcohol to remove the Methylene Blue and stained with Gram stain.* Our organism (Gram negative) shows red cytoplasm, including large colourless fatty bodies which differentiated it from other species of *Azotobacter*.

Quantitative Estimation: The technique used has been described previously (Tchan, 1952). The combination of a liquid and a solid medium for the estimation of our organism gives good results when it is the only non-symbiotic aerobic N-fixing bacterium present. In a mixed culture, when *Azotobacter* is present, it is not very difficult to distinguish the colonies of our organism from *Azotobacter* colonies on the agar medium, but in the liquid medium, as already mentioned, the estimation is not always as reliable as in agar medium. The liquid medium is therefore only used as a control of the agar medium.

pH Determination: Samples are first tested colorimetrically to determine their approximate pH. If the soil gives a positive growth of our organism an electrometric pH determination is carried out with a glass electrode.

* (1) Crystal violet 10 g. Ammonium oxalate 4 g. 95% alcohol 100 c.c. Water 400 c.c.

(2) Iodine 1 g. KI 2 g. 95% alcohol 25 c.c. Water 100 c.c.

(3) Iodine solution as above 5 c.c. Alcohol 95% 95 c.c.

(4) Erythrosin 1 g. Phenol 5 g. Water 100 cc.

Stain 1 minute with crystal violet. Wash with tap water. Stain 1 minute with iodine (2) solution. Wash with iodine solution (3) until no more violet colour can be removed. (If the slide is still violet or blue, the destaining operation may be continued 20 or 30 minutes.) Wash with water. Counterstain with Erythrosin. Gram positive organisms are violet or blue and Gram negative organisms are red. Soil particles are colourless.

Humus Determination: The estimation of humus content is only made with samples giving a positive growth of our organism. The technique adopted is Demolon's method (1944). This permits comparative studies of the relationship between humus content and *Azotobacter* population of soils, and enables us to make a comparison with the results of Chalaust (1948) in France.

RESULTS.

The results of the survey are summarized in Tables I and II. Table I gives all soils tested, arranged in order of pH. Table II describes in more detail the soils giving a positive growth of our organism or of *Azotobacter*.

TABLE I.

Sample Positive or Negative.	Date.	Collected By.	pH.	Soil Type.	Locality.
-	16.5.51	Crommelin.	3.5	Sand.	Warrah Reserve, near Woy Woy.
-	16.5.51	Crommelin.	4.3	Sand (orchard).	Warrah Reserve, near Woy Woy.
-	16.5.51	Crommelin.	4.5	Sand.	Warrah Reserve, near Woy Woy.
-	23.4.51	McKee.	4.5	Sand, virgin soil.	Northbridge.
-	20.4.51	Beadle.	5.0		New England.
-	25.4.51	Tchan.	5.0	Sandstone in cultivated soil.	Mosman.
-	25.4.51	Tchan.	5.0	Sandstone in cultivated soil.	Mosman.
-	30.4.51	Beadle.	5.0	Laterite.	French's Forest.
-	2.5.51	McLuckie.	5.0	Sandstone.	Leura.
-	2.5.51	McLuckie.	5.0	Sandstone.	Leura.
-	10.7.51	Baas-Becking.	5.0	Sandstone.	National Park.
-	10.7.51	Baas-Becking.	5.0	Sandstone.	National Park.
-	20.4.51	Edenborough.	5.0	Podsol sand.	Lindfield.
-	20.4.51	Edenborough.	5.5	Podsol sand.	Lindfield.
-	20.4.51	Beadle.	5.5	Shale podsol.	Chatswood.
-	23.4.51	McKee.	5.5	Garden.	Northbridge.
-	25.4.51	Tchan.	5.5	Garden soil.	Mosman.
-	25.4.51	Tchan.	5.5	Garden soil.	Mosman.
-	25.4.51	Swaby.	5.5		Hurstville.
-	16.5.51	Crommelin.	5.5		Warrah.
-	16.5.51	Beadle.	5.5	Peat.	Guyra, New England.
-	16.5.51	Beadle.	5.5	Beech forest.	Guyra.
+	2.5.51	Bruck.	5.5	Sand.	Rose Bay.
+	7.3.51	Botany School.	5.5	River sand.	Nepean River.
+	20.4.51	Edenborough.	5.62	Podsol sand.	Lindfield.
+	25.4.51	Chalmers.	5.6	Clayey garden.	Eastwood.
+	10.7.51	Rivera.	5.65	Rainforest podsol.	Mt. Keira.
+	20.4.51	Edenborough.	5.9	Podsol (sand).	Lindfield.
-	23.4.51	Mercer.	6.0	Sandstone.	Fitzroy Hills.
-	16.5.51	Beadle.	6.0	Alluvial soil.	New England.
-	16.5.51	Beadle.	6.0		New England.
-	30.7.51	Tchan.	6.0	Residual laterite.	Newport.
-	16.5.51	Beadle.	6.0	Chocolate soil.	New England.
+	30.4.51	Fraser.	6.2	Sand.	Wollstonecraft.
-	30.7.51	Tchan.	6.2	Garden.	Newport.
+	20.4.51	Hindmarsh.	6.4	Sand.	Rose Bay.
+	25.4.51	Robertson.	6.4	Shale.	Haberfield.
-	30.7.51	Tchan.	6.7	Podsol.	Newport.
-	6.6.51	Beadle.	7.0		
+	23.4.51	Thornton.	7.0	Sand.	Homebush.
+	23.4.51	Thornton.	7.0	Sand.	Homebush.
-	16.5.51	Beadle.	7.0		New England.
+	7.5.51	Everson.	7.0	Garden.	Goulburn.
-	20.4.51	Edenborough.	7.0	Podsol sand.	Lindfield.
-	26.4.51	Burges.	8.0	Clayey garden.	Ryde.

TABLE I.—Continued.

Sample Positive or Negative.	Date.	Collected By.	pH.	Soil Type.	Locality.
	17.4.51	Hannon.			Jannali.
	17.4.51	Tehan.		Sand.	Woy Woy.
	17.4.51	Tehan.		Sand.	Woy Woy.
	17.4.51	Hannon.			Jannali.
	17.4.51	Hannon.		Sand.	Jannali.

TABLE II.

Date.	pH.	Soil Type.	Milligrammes of Humus per Gramme of Soil.	Number of Our Organism per Gramme of Soil.	Number of <i>Azotobacter</i> per Gramme of Soil.	Locality.
	5.5	River sand.	Nil.	Sporadic.	Nil.	Nepean River.
2.5.51	5.5	Sandy.	9.0	Sporadic.	Nil.	Rose Bay.
25.4.51	5.6	Clay.	14.0	100	Nil.	Eastwood.
20.4.51	5.62	Podsol sand.	8.6	500	Nil.	Lindfield.
10.7.51	5.65	Podsol rainforest.	80.0	100	50	Lindfield.
20.4.51	5.9	Sand.	11.4	Sporadic.	Nil.	Mt. Keira.
30.4.51	6.2	Sand.	9.0	100	Nil.	Wollstonecraft.
25.4.51	6.4	Shale.	96.0	Sporadic.	—	Haberfield.
20.4.51	6.4	Sand.	10.4	1700	1000	Rose Bay.
23.4.51	7.0	Sand.	7.2	Sporadic.	Nil.	Homebush.
23.4.51	7.0	Sand.	56.0	50	Nil.	Homebush.
7.5.51	7.0	Garden.	40.0	Nil.	830	Goulburn.

DISCUSSION AND CONCLUSION.

It is generally supposed that in the acid soils of New South Wales non-symbiotic aerobic N-fixing bacteria are absent. The fixation of N is thought to be due principally to symbiotic N fixation and anaerobic N fixation. The presence of our organism in Sydney, perhaps in other parts of New South Wales, may modify our idea of the N economy of acid soils. It is too early to generalize; only a survey of this kind on a large scale can define the distribution of this group of organisms in Australia, and assess their importance in the nitrogen economy of the soil.

In New South Wales soils, especially in the Sydney district, the organism is fairly frequent. Over 50 samples were examined and 22% gave a positive test. Comparing the results with the frequency of *Azotobacter* in Australian soils we obtain:

Author.	N.S.W.			Queensland.			Victoria.		
	Positive Soil Samples Examined.	Total Soil Samples Examined.	%	Positive Soil Samples Examined.	Total Soil Samples Examined.	%	Positive Soil Samples Examined.	Total Soil Samples Examined.	%
Jensen (1940), <i>Azotobacter</i>	37	143	25.8						
McKnight (1949), <i>Azotobacter</i>				63	143	43.15			
Swaby (1939), <i>Azotobacter</i>							21	80	26.15
Tehan	11	50	22.0						

There is no obvious correlation between the humus content of the soil and the presence or absence of our organism. In the 11 samples of soils giving a positive test the humus content ranges from nil to 96 mg. per g. Chalaust (1948) in France has pointed out that the numbers of *Azotobacter* vary with the humus content of the soil. Our results show no such relationship but they include only a small number of soils.

Other aspects of the problem may be raised. It seems possible that our organism lives mainly in sandy soils, but here, too, the number of samples is too small to give a definite conclusion. Our organism is found in soils whose pH ranges from 5.5 to 7.0.

These preliminary investigations show that acid tolerant N-fixing organisms are present in Australia, especially in the Sydney district. Their general ecology in Australia is still unknown except that the pH and humus content of soils seem to be without effect. It will be interesting to investigate the physiology of this group of organisms in relation to their ecology.

Acknowledgements.

The author is indebted to Professor N. A. Burges, Hon. Professor Baas-Becking, Dr. N. C. W. Beadle and Dr. H. S. McKee for their criticism and help. Also to all the staff of the University of Sydney who collected soil samples for this work.

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ERNEST CLAYTON ANDREWS.
1870-1948.

(*Memorial Series, No. 13.*)

(With Portrait, Plate ii.)

By the death on July 1, 1948, of Ernest Clayton Andrews, geological science in Australia lost one of its outstanding figures. Modest and self-effacing, a man in whom was no guile, friendly, helpful, lovable, he left behind such a record of geological research and of unselfish service in the cause of science generally as would be hard to match. By training and experience a field-geologist, with little first-hand knowledge of laboratory methods or techniques, he sought to correlate and integrate individual facts of his own and others' observing and to establish basic principles of wide application. In this way, like David before him, he helped to break down the barriers of State boundaries that tended to keep Australian geology and geologists within unnatural water-tight compartments. His contributions to geological science were not only intrinsically valuable, but original and stimulating, and his brilliant and far-reaching generalizations provided sound foundations whereon his successors have built. He was in truth one of the pioneers.

The youngest but one of a family of seven, Andrews was born of English parents on October 18, 1870, in the Sydney suburb of Balmain, but his childhood and youth were spent at what is now Rockdale, then largely bush with scattered houses, where his father, a rather dour man of puritanical outlook and with a strong bias in favour of the so-called practical things of life, conducted a small school. So rapidly did Ernest imbibe the three R's, that at the age of seven he was set to teaching the younger pupils. Out of school hours he was kept busily employed in strictly utilitarian domestic pursuits. Happily this stern and Spartan régime did not embitter or warp his naturally sweet and sensitive nature, possibly because an instinctive love of beauty found an outlet in the largely enforced reading of the Bible and the entirely surreptitious perusal of such literature as he could come by. As opportunity offered he assimilated "The Canterbury Tales", "The Faery Queene", "Paradise Lost", "The Pilgrim's Progress", Macaulay's "History of England", and other classics. The literature of Greece and Rome (mainly in translation) also attracted him, and in his geological papers one occasionally comes on apt classical allusions, as when he likens the geologist to "Antaeus of old, who must draw strength from continual contact with the Earth".

The books he read were not merely to become a part of his knowledge; long passages of them he learnt by rote, to the development of a memory that was phenomenally retentive naturally. In later life when lecturing he would recite without notes dates and details of events, relying only on his memory. On the occasion of his Presidential Address to the Royal Society of New South Wales in 1922 the lights failed without warning, but Andrews, who happened at the moment to be giving biographical details of recently deceased members, calmly continued his recital without interruption in the dark.

He was almost entirely self-taught for, apart from the early years spent under his father's tuition, he had only six months at a primary school at the age of 14. During this time, however, he rose to be dux of the school and was deemed a fit candidate for the Junior Public Examination. Two years later he was appointed a pupil teacher at Hurstville, and sat for the Senior Public (roughly equivalent to the present Leaving Certificate) Examination. For this he chose geology as a tenth subject (solely, it is said, because his pen refused to scratch out the name on the Application Form), started to study it three weeks before the examination, and gained an A pass. Finishing his period as a pupil teacher, he entered the Teachers' Training College in 1891, matriculated in the same year to the University of Sydney and graduated Bachelor of Arts in 1894, geology and mathematics being among his subjects.

He was appointed to a city school, but at his own request was transferred to Bathurst, where he taught for four years. The schoolmasterly habits, early and deeply ingrained in him, persisted through life; his conversation with junior, and indeed contemporary, geologists was wont to be somewhat didactic, in the manner of one instructing the young, and in his talks before scientific gatherings he made free and frequent use of simple illustration and homely analogy.

But school-teaching was not to be his serious life-work. At the University he had fallen under the spell of Edgeworth David, the newly-appointed Professor of Geology, and his inherent love of nature was quickened by rambles with a few kindred spirits in the country around Bathurst; as a result he presented his first geological paper, "On the Geology of the Cow Flat district, near Bathurst", to the Australasian Association for the Advancement of Science at its Sydney meeting in January, 1898. About this time Professor David was asked by Professor Agassiz of the Harvard Museum of Comparative Zoology to find a young graduate capable of undertaking the collection of coral-reef material in Fiji. He chose Andrews, who, obtaining leave of absence from teaching duties, spent six months without remuneration in Fiji and Tonga with an assistant, measuring (with the aid of a coil of rope 1,100 feet long) cliff sections of coral limestone and noting the phenomena of vertical uplift so well exhibited in those islands; his report on this work was later published as a Bulletin of the Museum of Comparative Zoology. He conceived a great admiration for the kindness, honesty and navigational skill of the Fijian natives. He lived like them, ate the same food, learnt their language and accumulated much of their folklore. It was probably during this time that he acquired that interest in problems of Pacific structure which became almost a ruling passion with him in later life, and on which he was an acknowledged authority.

But the Fijian trip also opened up for him vistas of work in other geological fields. Conscious of his scientific shortcomings, he obtained leave to attend University courses in geology and chemistry, and was appointed a geologist on the Geological Survey of New South Wales on 1st July, 1899. In the Survey he remained for 32 years, filling successively higher posts till he was appointed to the position of Government Geologist in 1920. This office he held till his retirement at the end of 1931.

These years in the Geological Survey were profitable for Andrews and for geological science in Australia. Opportunities for field study came thick and fast and varied, and the young geologist, his true *métier* discovered and his ambitions in process of realization, found new avenues of investigation ever opening before him, some economic some not. The traditions of the Survey were, naturally enough, for the most part utilitarian, and though the young Edgeworth David had imported an element of "academic" geology, he had some nine years before left for the wider sphere of the University. Andrews perceived that in investigating an ore-deposit something more was needed than mere description, and he sought to discover causes and to establish basic principles. His first task, a difficult one for a tyro, was an examination of the Hillgrove mining field in southern New England. Quite ignorant of mining terms but loth to display his ignorance, he set himself to master these while studying the intricacies of the ore-deposit and its enclosing rocks. This was the first of a series of studies of active and decadent mining fields in many parts of the State, such as Yalwal, Kiandra, Drake, Forbes-Parkes, Cobar and Canbelego, the results of which were published in the Mineral Resources series of the Geological Survey. These detailed examinations and others into the occurrence of tin, molybdenum, bismuth, wolfram and other ores in the Northern, Central and Southern Highlands, gave Andrews a thorough insight into ore-deposits, and to his restless and inquiring mind provided much food for thought on such questions as igneous petrogenesis, the origin and mode of emplacement of ore-bodies, and the conditions attending the formation of deep leads. The section on auriferous leads contained in his Forbes-Parkes report is regarded as one of the clearest and most illuminating expositions of the subject. The great New England bathyliths, with their lithological variations and evidences of successive injection, provided vivid and spectacular lessons in petrogenesis, and from an examination of them Andrews independently developed views on magmatic injection through overhead stoping virtually identical with those propounded about the same time by Professor R. A. Daly.

His last and greatest contribution to the study of the State's mineral wealth was the report on the Broken Hill silver-lead-zinc field. Despatched from Sydney to make a brief inspection of what was in official quarters regarded as a moribund field, he worked for some time single-handed, essaying the impossible task of mapping not merely the lodes themselves and their immediate environs but also the igneous and metamorphic complex in which they were emplaced. Later the mining companies subsidised the work and enabled it to be done in greater detail, so that though the responsibility remained with Andrews he had the help of a number of subordinates. Investigations were spread out over several years and eventually the results were embodied in a monumental memoir with numerous maps and sections, the most imposing of its kind ever issued by the New South Wales Department of Mines. Andrews himself had complete confidence in the future of the field, a confidence justified by the fact that now, thirty years after the issue of the Memoir, the ore-reserves in sight are at least as great as they were then.

The greatness of the report is apt to be obscured by the wealth of detail, but it is significant that twenty-five years after its publication geophysicists and geologists making intensive studies of the lodes were agreed that Andrews's views on the structures were still substantially correct. Incidentally, the lesson of the value of geological work in mining was so brought home to the mining fraternity of Broken Hill that each of the chief mines now has its own geological staff, a thing unheard of in the days before the survey.

A study that quite early attracted the interest of Andrews was that of Physiography. In the great New England plateau with its level skyline, and its peneplain surface cut into by mature valleys trenched by profound gorges, he found abundant illustrations of the principles enunciated by Gilbert, W. M. Davis and other American pioneers of geomorphology, whose writings had fired his imagination. But to his colleagues his opinions were unorthodox, heretical. On returning to Sydney after a New England trip he disclosed to a conservative senior his conviction that the great gorges there were youthful, only to meet with the chilling reply: "Oh, no, Mr. Andrews, you are quite wrong; they are very old." But Andrews, talking in terms of development rather than years, knew he was right, and his views on the history of the New England plateau, presented in a series of papers, have, with remarkably little modification, stood the test of nearly half a century. True he was unable to decide definitely whether differential erosion or faulting was responsible for the differing levels of adjacent peneplain surfaces, and for his natural enough vacillation on this point he was severely taken to task by less enterprising colleagues.

A little physiographic handbook for schools from his pen, "An Introduction to the Physical Geography of New South Wales", appeared in 1905. This expounded the main physiographic principles, with illustrations from various parts of the State, but chiefly from around Sydney. While some of its interpretations are now known to be in error, the book shows an amazing grasp of many of the physiographical features of New South Wales, though it is to be feared that some of its contents were rather above the heads of the budding geographers who had to study it.

Andrews was really the pioneer of modern physiographic studies in this State, if not in Australia. Like all pioneers, he made mistakes, but in all essentials his work forms the basis of most of the present-day conceptions of the physiographic evolution of the continent. Perhaps his crowning contribution to physiographic thought was his paper, published in 1910, on the Geographical Unity of Eastern Australia in Tertiary and post-Tertiary Time, a masterly integration and interpretation of the results of observations by himself and others. His conception of a great epoch of differential uplift—the Kosciusko Uplift—beginning about the end of the Pliocene, is now generally accepted, and has been extended to include the whole of the Australian continent. Probably many of those to whom the concept is a commonplace have forgotten who was its originator and are unaware that it was formulated less than fifty years ago.

Having lived and worked for a number of years amid river-made landscapes, he was much impressed during a visit to New Zealand by the evidences of glacial erosion

in the Flordland region. As a result he became an ardent champion of the efficacy of glacier corrasion at a time when this was seriously questioned and even forthrightly denied and decried by eminent authorities. In the *Journal of Geology* in 1906 he exposed the fallacy of judging the efficiency of Pleistocene glaciers during glacial maxima or ice-floods by the feebleness and inertness of their degenerate successors of the present day. This paper, in which he crossed swords with opponents like Fairchild, attracted favourable notice overseas, and was probably responsible for an invitation to visit the United States of America in 1908. For Andrews this trip, later extended to Britain and Europe, was full of inspiration; it afforded priceless opportunities of seeing and discussing with the foremost authorities many of the great physiographic phenomena, particularly in the Californian Sierras, where several weeks were spent in the company of Dr. G. K. Gilbert, W. D. Johnston and others. Opportunity was also afforded for meeting and discussing problems with workers in Economic Geology, Petrology and Structural Geology. Andrews always retained a warm affection for those with whom he had fongathered on the trip, and in particular often spoke of Gilbert with admiration amounting almost to hero-worship. Undoubtedly this communion with kindred spirits in other lands had a profound effect on his subsequent work.

American experiences served to confirm his belief in the efficacy of glacial erosion, and his views were embodied in three papers published between 1909 and 1912—"Corrasion by Gravity-Streams", "An Excursion to the Yosemite", and "Erosion and its Significance". The papers attracted comparatively little notice in Australia, but were warmly received in the United States of America as important and significant contributions to erosional theory. The first of them was regarded by Andrews as one of his best papers. It is perhaps unfortunate that in this, as in others of his longer papers, he was somewhat discursive, and this fact and the very close and detailed reasoning which characterizes them are apt to discourage all but the most earnest readers.

Andrews's early investigations in Fiji gave him a lasting interest in coral reefs. With his friend Charles Hedley he examined the Queensland coast and the Great Barrier Reef in 1901 in a small sailing boat, and in 1917 with W. M. Davis of Harvard he made a tour of the reefs of New Caledonia and the New Hebrides. The general question of coral reefs he discussed in his presidential address to the Royal Society of New South Wales in 1922, particularly stressing their sensitiveness and accuracy as criteria of Cainozoic earth movements within the Pacific region.

The importance of tectonic structure was strongly borne in on him during his economic investigations, particularly in the Cobar and Broken Hill fields, and structural geology, leading naturally on to palaeogeography and geological history, came to be regarded by him as of paramount importance. A number of his papers are concerned with the structural features and tectonic history of Australia and the Pacific and with the origin of mountain ranges. An undulatory theory of earth movements, often assumed but never expounded in detail, seems to have dominated his tectonic thoughts.

Preoccupation with many branches of geology by no means exhausted the intellectual activities of Andrews. To them he added a lively and knowledgeable interest in botany, particularly that of Australian native plants. Gilbert had initiated him into the botany of the Californian Sierras, and from his friends J. H. Maiden and R. H. Cabbage he had imbibed a knowledge of systematic botany and an interest in Australian plant ecology and geographical distribution. Thus in some of his geological reports and notably in his Broken Hill Memoir, we find lists and illustrations of the local trees, shrubs and other plants. Nor was he content to be a systematist; he must needs be thinking of the origins and development of the plants and their bearing on geological history. So we find papers by him on the development of the Natural Order Myrtaceae (1913), and the Natural Order Leguminosae (1915), the geological history of the Australian flowering plants (1916), and the origin of the Pacific insular floras (1940). The geological importance of plant distribution he was fond of stressing. On one occasion he was giving a series of special lectures to University students on the former land-connexions of Australia. The students, long accustomed to regard a display of

rock specimens as the natural concomitant of a geology lecture, were rather non-plussed at finding the lecture bench covered with an array of botanical specimens instead, but soon learnt the significance of this attempt to "say it with flowers".

These "intellectual excursions" into domains beyond the ordinary limits of geology did not impair, but rather enhanced the value of his geological work.

To the problems that confronted him day by day as Government Geologist he brought the same concentration of thought and effort that marked all his scientific research. An unfamiliar phase of work involving chemistry, physics or technology was carefully and diligently studied until he had a reasonable grasp of it. In departmental policy he took the long view, and planned for the future as well as for the needs of the immediate present. His term of office was marked by the issue in 1926 of *The Mineral Industry of New South Wales*, an up-to-date compendium of information on the known mineral resources of the State, superseding Pittman's *Mineral Resources* published nearly thirty years before. The revision and extension of the surveys of some of the coalfields were also undertaken, as well as investigations of artesian water resources. Andrews himself, in addition to general direction and supervision of the work, took an active part in it.

Absorption with research and administrative routine did not prevent him from doing much to advance the cause of Science in Australia. In the realm of Economic Geology he acted as Australian delegate to the Second Empire Mining Congress in 1927 and was president of the Australasian Institute of Mining and Metallurgy in 1929. He served for several years on the Council of the Royal Society of New South Wales and was president in 1921. Our own Society, on the Council of which he served for twenty-five years, till the time of his death, and of which he was president in 1937, benefited from his knowledge and experience. At the time of his death he had completed twenty-four years as a Trustee of the Australian Museum.

As Honorary General Secretary of the Australasian Association for the Advancement of Science from 1922 to 1926 he devoted much thought to the revision of the constitution, and his work formed the basis of the present constitution. He presided over the Brisbane meeting of the Association in 1930. He was a foundation member of the Australian National Research Council and a member of the Executive Committee from 1922 to 1942, including the critical period of reconstruction.

A natural result of his American geological connexions was an invitation to attend the first Pacific Science Congress at Honolulu in 1920. Three years later he was one of the four general secretaries organizing the Australian meeting, and he was on delegations to succeeding meetings in 1926, 1929, 1933 and 1939.

In 1927 he was accorded the high honour, unique indeed for an Australian, of an invitation to deliver the Silliman Lectures at the University of Yale, U.S.A. The lectures were never published, but the last of them, a philosophical survey of the world's history through geological time and of mankind's achievements, was given in revised and modified form as his presidential address to the Australasian Association for the Advancement of Science in 1930.

For many years he was Australian associate editor of *Economic Geology*, and a number of articles came from his pen. In 1942 he was Clarke Memorial Lecturer of the Royal Society of New South Wales.

Honours conferred on him in recognition of his eminence in research and his efforts in the cause of Science were: the David Syme Prize and Medal of the University of Melbourne (1915); the Clarke Memorial Medal of the Royal Society of New South Wales (1928); the Lyell Medal of the Geological Society of London (1931), and the Mueller Medal of the Australian and New Zealand Association for the Advancement of Science (1946). He had the rare distinction of Honorary Membership of the Washington Academy of Science. Strangely enough no governmental recognition of the important contributions he had made to Science and to the welfare of his native State ever came his way.

His retirement from the Geological Survey in 1931 afforded him leisure for reading, writing and reflection; to the succeeding period belong some of his more comprehensive

papers such as "The Origin of Modern Mountain Ranges" (1934), "The Structural History of Australia During the Palaeozoic" (1938), and "The Structure of the Pacific Basin" (1940). The philosophic outlook, begotten or quickened by his association with G. K. Gilbert, which had long been evident in his scientific papers and had found expression in his presidential address to the Australasian Association for the Advancement of Science, was now intensified, and among his latest writings were two small books, *The Increasing Purpose* (1938) and *The Eternal Goodness* (1948), the latter published a few days before his death. These were designed to reassure earnest souls, distressed by signs of moral retrogression in mankind, by reviewing the evidences of general advance and upward, albeit pulsatory, movement in the organic world since the earliest geological times.

A man of anything but robust physique, and suffering for most of his life from acute gastric or intestinal trouble, Andrews confounded the gloomy predictions of his medical advisers by pinning his faith to methods of treatment of his own fashioning. His diet was rigid and sparse, even when he was working hardest, and on occasion was limited to one meal a day. Yet his physical energy was amazing; most of his geological field work was accomplished on foot, whether it meant floundering toilsomely through the snows of Kiandra or traversing the bare, sun-baked plains of the Broken Hill region. While in America in 1908 he, with a companion, was the first to climb Mt. Darwin (14,000 ft.). No less remarkable were his mental energy and powers of concentration.

One of his most prominent characteristics was a profound admiration for the qualities and achievements of the pioneers, particularly the early explorers of the inhospitable interior of Australia who battled constantly against peril and hardship. He was steeped in the stories of their adventures, and during his American trip would narrate some of these at night round the campfire, to the obvious astonishment of his audience, who were hearing for the first time of feats of daring and endurance "down under" that matched those of their own pioneers. In his Clarke Memorial Lecture to the Royal Society of New South Wales on "The Heroic Period of Geological Work in Australia", he paid unstinted tribute to those who had laid the foundations of our geological knowledge.

He was twice married, first to Florence Wynn Byron, who died in 1923, and later to Mabel Agnes Smith, who survives him.

A bibliography of his published scientific papers will be found in the *Proceedings of the Geological Society of America* for April, 1949, pp. 122-126.

W.R.B.
A.B.W.

NOTES ON AUSTRALASIAN SIMULIIDAE (DIPTERA). III.

By I. M. MACKERRAS and M. J. MACKERRAS,
Queensland Institute of Medical Research, Brisbane.

(Twenty-five Text-figures.)

[Read 28th May, 1952.]

Synopsis.

The paper includes a description of *Austrosimulium montanum* n. sp., a discussion of the races of *Austrosimulium victoriae* (Roub.), records of new distribution, and a table summarizing present knowledge of the family in Australia.

The Genus *CNEPHIA* End.

CNEPHIA AURANTIACUM (Tonn.).

A male, bred from a pupa collected near Ebor, N.S.W., is aberrant, in that the scutum is black and somewhat irregularly covered with deep golden hairs. At first sight it appears strikingly distinct from the typical form, but it differs in no other respects, and the pupal shell is typical.

New distribution.—New South Wales: Dorrigo Plateau, near Ebor, approx. 4,000 ft., September; Barrington Tops, 4,000 ft., March (McMillan); Williams R., 1,500 ft., March (McMillan).

CNEPHIA TONNOIRI ORIENTALIS M. & M.

New distribution.—New South Wales: Lahey's Creek, Moonbi Range, 2,000 ft., September; Macdonald R., Bendemeer, September; tributary of Coutt's Water, near Ebor, January; Barrington Tops, 4,000 ft., March (McMillan); several creeks between Mt. Canoblas and Bumberry, Orange district, October; Lett R., Hartley, October.

CNEPHIA UMBRATORUM (Tonn.).

Several females were collected hovering around the head at Narbethong, Victoria, in October. No males were found on sweeping vegetation, and an intensive search of the adjacent creek failed to reveal the life history. However, three strange larvae were taken in this creek, on reeds in rather gently flowing water, in company with the early stages of *Austrosimulium montanum*, n. sp., *A. victoriae* (Roub.) and *A. furiosum* (Sk.), and a fourth in a small, sluggish channel running into the Acheron R. at Buxton in the same district. These are described below, although it is to be emphasized that there is no proof that they belong to this species.

The possible larva of C. umbratorum.

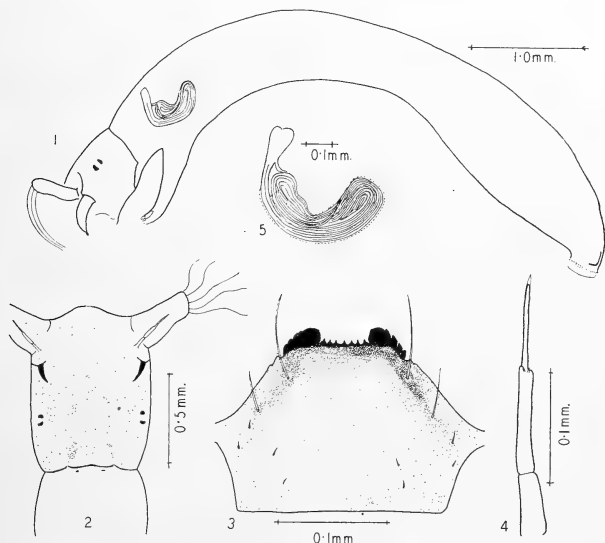
Length 6 mm.

The body is fusiform in shape, like a typical *Simulium* and unlike a typical *Cnephia*. The tip of the tail is much narrowed and bent ventrally (Text-fig. 1).

The head is relatively long, and the various chitinous struts are strongly developed and dark in colour in contrast to the rather pale background. The integument of the head is covered with minute, stiff hairs, which are fairly regularly arranged, and which are visible as dots under the dissecting microscope ($\times 32$). There is a wide, deep ventral incisure (Text-fig. 1). The pattern on the dorsum consists of a faint central stripe and an interrupted one on each side of it (Text-fig. 2). The pale antennae are remarkably short and inconspicuous, being little more than half the length of the basal piece of the fan. The proportion of the segments is shown in Text-figure 4. The submentum is different from all known species. There are seventeen teeth; the fifth tooth from each side is greatly enlarged, broadened and turned somewhat medially; in between these two prominent lateral teeth is a level row of seven small subequal trifold teeth (Text-fig. 3).

The gill-spot (Text-fig. 5) consists of a slender stem, directed downwards and forwards and giving rise to two large, unequal branches, which lie side by side and curve backwards, giving off branches and bifurcating at more or less equal distances from the main stem. The branches then sweep upwards and forwards towards the posterior surface of the main stem. The filaments, which are now very fine and delicate, turn back through a full circle and curve round the posterior angle of the gill-spot, continuing below the larger branches in a forward and finally upward direction, so that the tips lie anterior to the main stem as in other *Cnephias*.

The gill-spot of one specimen was dissected out, and it was found that the anterior of the two main stems gave off at intervals two branches, each of which bifurcated once; it then gave off two single filaments, and finally bifurcated, thus giving rise to



Text-figs. 1-5.—Possible larva of *Cnephia umbratorum* (Tonn.).

1, lateral view; 2, dorsum of head; 3, submentum; 4, antenna; 5, gill-spot.

eight filaments. The other main branch gave rise to two branches of unequal width; each of these bifurcated once; the main stem then gave off four single filaments at intervals, and finally bifurcated, thus giving rise to ten filaments in all. Near the base of the main stem, there arose a single, short, narrow branch with a rounded tip. This branch lay among the fine filaments from the main branches.

The proleg carries a well-developed circlet of spines. The posterior circlet is quite narrow, and the rows are widely spaced. There are about 60 rows, with up to seven spines per row. The spines, which are strong and very dark, diminish in size from before backward.

The anal sclerite is in the form of an inverted T, without lateral expansions or struts; it appears to be a relatively weak structure. Ventral papillae were not detected, and the rectal gills were not visible in any of the specimens.

CNEPHIA TEREBRANS (TONN.).

Females were taken biting on the banks of Molong Creek at the foot of Mt. Canobias, near Orange, New South Wales, in October. No larvae or pupae were discovered. We have searched quite strenuously for *Cnephia* life histories at Mt.

Canoblas, Bumberry, and the Blue Mountains in New South Wales, and at Sassafras and the Narbethong-Marysville-Buxton triangle in Victoria, including localities from which *C. umbratorum*, *C. terebrans* and *C. fergusonii* have been recorded; but the larva described above and that described by Wharton (These PROCEEDINGS, 73: 411, 1949) are the only ones so far found which could possibly belong to any of these species.

The Genus *SIMULIUM* Latr.

SIMULIUM ORNATIPES Skuse.

New distribution.—Victoria: Small tributary of Murray River, west of Merbein, December; Beechworth, November–December (Myers); Glen Rowan, December (Myers); Bacchus Marsh, January (Myers). (Not recorded previously from this State.)

SIMULIUM CLATHRINUM M. & M.

New distribution.—New South Wales: Bellingen River, North Coast, October; George's River, Leumeah district, October (McMillan). (Previously known only from Queensland.)

SIMULIUM NICHOLSONI M. & M.

New distribution.—New South Wales: Namoi River, Gunnedah, October; Gwydir River, Moree, November (Dyce); Coolah River, Coolah, October; Deniliquin, in ear of rabbit suffering from myxomatosis, November (Fennessy); Corowa, January–February, on cattle (Myers); Bullatate Creek, on horse, November (Fennessy). Victoria: Murray River, Yarrowonga State Forest, February (Lee, Ratcliffe and Myers); small tributary of Murray River, west of Merbein, December. (Previously known only from Queensland.)

SIMULIUM INORNATUM M. & M.

New distribution.—New South Wales: Dorrigo Plateau, approx. 4,000 ft., October; Mt. Solitary, Jamieson Valley, September (McMillan); Mt. Kuring-gai, near Sydney, December (McMillan); Badgery's Lookout, Tallong, December (McMillan). (Previously known only from South Queensland.)

SIMULIUM MELATUM Wh.

New distribution.—New South Wales: Pinch Creek and Barwick River, Dorrigo Plateau, about 4,000 ft., January; Kangaroo Creek, near Werris Creek, October; Coolah Creek, Coolah, October; Cudgegong River, near Mudgee, October; Molong Creek, near Orange, October; Coates Creek, Manildra, October; Bumberry, October; Lett River, Hartley, October; Fish River, Jenolan Caves, October (females hovering in spray of a small cataract); Badgery's Lookout, Tallong district, December (McMillan). Victoria: Yarrowonga, collected 7 p.m. on ears of rabbits suffering from myxomatosis, February (Myers, Mykytowicz); Beechworth, November (Myers).

This species is apparently distributed over a wide belt of country from South Queensland to the Victorian border. On the Murray it (possibly together with *S. nicholsoni*) is known as "the buffalo fly", and it has been incriminated in transmitting myxomatosis of rabbits (F. N. Ratcliffe, personal communication).

The Genus *AUSTROSIMULIUM* Tonn.

With the addition of *A. montanum*, n. sp., the *mirabile* group now contains six species, which are distinguished by the claws of the females being strongly toothed, and the five known larvae by having a dark, ventral, incomplete, chitinous ring at the posterior end, just anterior to the circlet. The second antennal segment of the adults is larger, sometimes much larger, than the third, which is a useful point in recognizing the males. It is preferable to use these characters to determine the group and the following keys to separate the species than to use our earlier incomplete keys. Gill-spot larvae and pupae may be recognized from the illustrations, which are uniform in the series of papers.

The young larvae of this group are extremely similar in general appearance and in the conformation of the antenna, which has a short basal segment (indistinctly divided

about one-quarter or one-fifth of its length from the apex) and a much longer slender apical segment. The general form of the submentum is similar in all; there are 13 teeth; the third from the outside and the central one are the largest, and there is one pair of very tiny teeth third from the centre on each side. The anal sclerites show only minor variations. All have large ventral papillae. The ventral chitinous ring is a very distinctive character, which is shared only with the New Zealand species of *Austrosimulium* and the Chilean *Gigantodax*.

Key to species of mirabile group—adults.

1. Wing with three conspicuous black spots on R_1 ; antennae with segments 4-6 orange *A. mirabile* M. & M.
Wings without black spots 2
2. Antennae with segments 4-10 orange *A. fulvicorne* M. & M.
Flagellar segments of antennae grey, not contrasting strongly with basal segments 3
3. Hind tibiae of both sexes markedly incrassate; abdomen uniformly dark .. *A. crassipes* Tonn.
Hind tibiae normal 4
4. Abdomen of ♀ dark grey, with ashy tomentose markings on tergites 5-8
..... *A. montanum*, n. sp.
Abdomen of ♀ grey, with velvety-black tergites, like *A. furiosum* *A. sp. C* (W.A.)
Abdomen of ♀ uniformly dark grey, with inconspicuous tergites *A. cornutum* Tonn.
Note: The males of *A. cornutum* and *A. montanum* cannot be distinguished satisfactorily.

Key to species of mirabile group—larvae.

1. Basal portion of antenna very short, less than one-half the length of apical portion. Central tooth of submentum projecting beyond the rim of the sclerite, which is not indented 2
Basal portion of antenna more than one-half the length of apical portion. Central tooth of submentum barely, if at all, projecting beyond the rim, which is distinctly indented (as in Text-fig. 14) 3
2. Basal portion of antenna less than one-third the length of apical portion. Ends of chitinous ring usually not expanded *A. crassipes* Tonn.
Basal portion of antenna more than one-third the length of apical portion. Ends of chitinous ring forming a triangular expansion *A. mirabile* M. & M.
3. Ends of chitinous ring not expanded, ring rather weak *A. cornutum* Tonn.
Ends of chitinous ring more or less expanded, ring strong 4
4. Head pattern of narrow linear type; base of antenna usually dark brown
..... *A. montanum*, n. sp.
Head pattern with dark circular patch posteriorly; base of antenna light yellowish-brown
..... *A. fulvicorne* M. & M.

AUSTROSIMULIUM MONTANUM, n. sp.

Types.—Holotype ♀, allotype ♂, morphotype larva and pupa from small streams near Ebor, N.S.W. (4,000 ft.), October, in the Division of Entomology, C.S.I.R.O., Canberra, A.C.T.

Distinctive Features.

♀: A dark species, separable from *A. cornutum* Tonn. by the velvety-black abdominal tergites, which are marked by ashy, tomentose patches on the fifth and subsequent segments. ♂: Indistinguishable from *A. cornutum*, except that the notch at the base of the calcpala may be more clearly defined. *Cocoon*: Resembles *A. cornutum* and *A. victoriae* Roub. *Pupa*: Distinguished by the very short, rounded, spinose horn, with short filaments plastered against the thorax. *Larva*: As in the key; gill-spot larva by the developing pupal horn, which could only be confused with that of *A. torrentium* Tonn., a species belonging to another group.

Female.

Head. Frons tapering strongly towards antennae, about one-fourth head width at narrow part, with silvery-grey tomentum and silvery hairs. Face similar. Proboscis short, dark grey, with some silvery hairs. Antenna with basal two segments black; third distinctly smaller (Text-fig. 6), black basally, grey with silvery hairs distally; remainder grey with short silvery hairs.

Scutum black, with a patch of grey tomentum in front of scutellum, the whole covered with dull golden hairs. Scutellum brownish-black, with black hairs. Pleurae

blackish-grey, with some silvery reflections. *Legs* (Text-fig. 7) blackish, with creamy-yellow hairs on femora and parts of tibiae; *calcipala* prominent, about two-thirds width of metatarsus; claws with large tooth. *Wings* clear, veins dark brown, halteres with grey stem and creamy knob.

Abdomen with first segment dark grey, dull yellowish apically, with creamy-yellow hairs. Remaining segments generally dark grey, paler at the apices of segments, with rather scattered, short, creamy-yellow hairs, especially posteriorly, and with velvety-black tergal plates, those on 2nd, 3rd and 4th segments entirely black, 5th with small patch of ashy tomentum in its centre, 6th and 7th with progressively larger ashy central areas, reducing the black to lunulate patches on each side, 8th and 9th entirely ashy.

Male.

Head. Antennae with basal two segments black; second larger than third; remainder dark grey, with fine silvery hairs. Palpi and mouth parts black.

Scutum velvety-black, with rather dense golden hairs. Pleurae dark grey, with silvery reflections anteriorly. *Wings* clear, veins black. Halteres with stem and basal half of knob black, distal half of knob dull yellowish-brown. *Legs* entirely greyish-black. Hind metatarsus appears to be as long and as wide as the tibia. *Calcipala* broad.

Abdomen dark grey. Fringe of first segment black. Tergites velvety-black (somewhat like the female of *furiosum* and more restricted than in *victoriae*), except the ninth, which is grey, and a variable hint of an ashy band at the edges of tergites 2 to 5 or 7. Venter grey. Hypopygium very like that of *A. cornutum*. Style with two terminal spines; anterior part of phallosome broadly oblong, with the usual setulose, ventral convexity; posterior part with a row of fine denticles, which are smaller and more delicate than those of *A. crassipes*; median piece not detectable.

Cocoon.

Length 3 mm. There is considerable variation in the form of the cocoon. The majority from the type locality and Barrington Tops were in the form of a long oval with a very low collar, a slight, rounded, central-dorsal projection, and a neat rolled edge (Text-figs. 10, 11). However, cocoons from Victoria were remarkably like those of *A. victoriae* (Roub.) from the same locality, having a long central dorsal horn, which curved forward and downwards (Text-fig. 8). Others from Victoria were intermediate in structure (Text-fig. 9), and one from Ebor had a well-developed "horn" like the Victorian specimens.

Although the finished products of the two species look alike, the methods of production evidently are different, and "horned" cocoons of *A. victoriae* are easily distinguished from those of *A. montanum*. In the former the "horn" is evidently made by prolonging the central thickened ridge, whereas in *A. montanum* there is no central thickened ridge and the "horn" appears to be continuous with the anterior rolled edge. The "hornless" varieties are not readily separated.

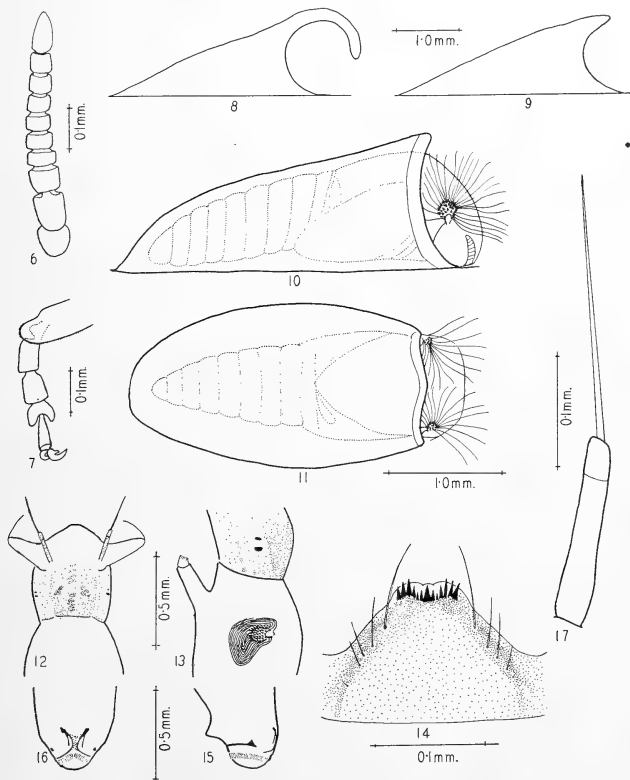
Pupa.

Length 3 mm. The cephalic and thoracic integument is marked by numerous minute, irregular ridges. The thoracic hairs are well developed, the three posterior dorso-central pairs being stiff and sharply pointed. The respiratory organ consists of a very short, rounded, flattened horn, which is covered with strong, black spines. The filaments are fine and numerous, arise chiefly from the margins, and spread out in all directions (Text-fig. 10).

The abdomen resembles that of some other members of the group in having spines on the ventral surface. There are the usual fine hairs on the first and second tergites, and four pairs of strong subapical hooks on the third and fourth tergites. Ventrally, there are two pairs of sharp, forwardly-directed spines placed close together on the fifth sternite, and two pairs of similar spines widely spaced on the sixth and seventh sternites. There are also stiff curly hairs laterally on these segments. The ninth segment bears small terminal hooks and a bunch of curly anchoring hairs laterally.

Larva.

Length 5.5 mm. Light creamy colour, with brownish or greyish markings. The head pattern consists of a dark central stripe, which is interrupted in the middle, and a dark patch on either side at the level of the eyes (Text-fig. 12). The basal segment of the antenna is usually brown, the shade varying from light to dark brown. The indistinct division of the basal part occurs near the distal end, as in other members of the group. The basal is more than half the length of the slender apical segment (Text-fig. 17). The submentum is armed with 13 teeth, of which the central and the

Text-figs. 6-17.—*Austrosimulium montanum*, n. sp.

Adult female: 6, antenna; 7, hind leg.

Cocoon: 8, "horned"; 9, intermediate; 10 and 11, "hornless".

Larva: 12, dorsum of head; 13, gill-spot; 14, submentum; 15 and 16, posterior ends; 17, antenna.

third from each side are the largest. The central tooth does not project beyond the rim of the sclerite. There is a very minute tooth third from the mid line. The rim of the sclerite is distinctly indented at each side of the central tooth (Text-fig. 14).

The gill-spot shows the short, rounded horn covered with black spines; the filaments sweep downwards and slightly backwards, and then curve forwards and upwards (Text-fig. 13).

The rectal gills are simple. The anal sclerite is similar to that of other members of the group. The ends of the chitinous ring are slightly expanded (Text-figs. 15 and 16).

Biology.

Larvae and pupae were found attached to vegetation in swift, cold streams on the Dorrigo Plateau in company with *A. victoriae* (Roub.) and *A. furiosum* (Sk.). In Victoria they were taken in moderately fast water in company with the same species as in New South Wales. Habits of the adults are unknown.

Distribution.—New South Wales: Coult's Water and smaller streams near Ebor, Dorrigo Plateau, 4,000 ft., September–October; Barrington Tops, 4,500 ft., March (McMillan). Victoria: Sassafras, February; Narbethong, October–November; Acheron River, Buxton, October–November.

AUSTROSIMULIUM CRASSIPES Tonn.

New distribution.—New South Wales: Waterfall on Dorrigo Mt., October; Barrington Tops, 4,500 to 5,000 ft., March (McMillan); Cooranbong, February (McMillan); Warrah Field Station, Hawkesbury River, July–August (McMichael).

AUSTROSIMULIUM BANCROFTI (Tayl.).

New distribution.—Victoria: Small tributary of Murray River, west of Merbein, December. (Not previously recorded from this State.) Also taken on dogs, man and rabbits in southern New South Wales (Myers).

AUSTROSIMULIUM FURIOSUM (Sk.).

Distribution.—As noted in earlier papers, the distribution of this species is extremely wide. It was included in the collections from almost every locality in New South Wales and Victoria mentioned in this paper. In one instance, an adult was collected in a rabbit warren near Deniliquin (Fennessy), and it has been taken biting man, horse, cattle, dog and rabbit in other localities in southern New South Wales (Myers) and northern Victoria (Fennessy).

AUSTROSIMULIUM VICTORIAE (Roub.).

We have been able to collect satisfactory material of this species recently in Victoria. The type locality is "Mountains of Victoria", and the type series (which included one *C. umbratorum* Tonn.) was collected by the late C. French in 1899. Mr. R. T. M. Pescott, Director of the National Museum, Melbourne, has informed us that Narbethong in the Blackspur Range was a favourite collecting ground of French at that time, and that it was as far afield as the old Field Naturalists' Club, of which French was an enthusiastic member, could conveniently go. Recently, we found *A. victoriae* abundant and obtrusive at Narbethong, in company with a few *C. umbratorum*, and French may well have had a similar experience. Narbethong would therefore seem to be as near the type locality as can be guessed.

The Narbethong material consists of adult females, larvae and pupae, and is supported by considerable series of all stages from various localities in high country through New South Wales to South Queensland. Our earlier confusion was due to the fact that the cocoons of Tonnoir's Canberra material were all fragmented, and we failed to understand his notes. A redescription of the early stages is therefore desirable.

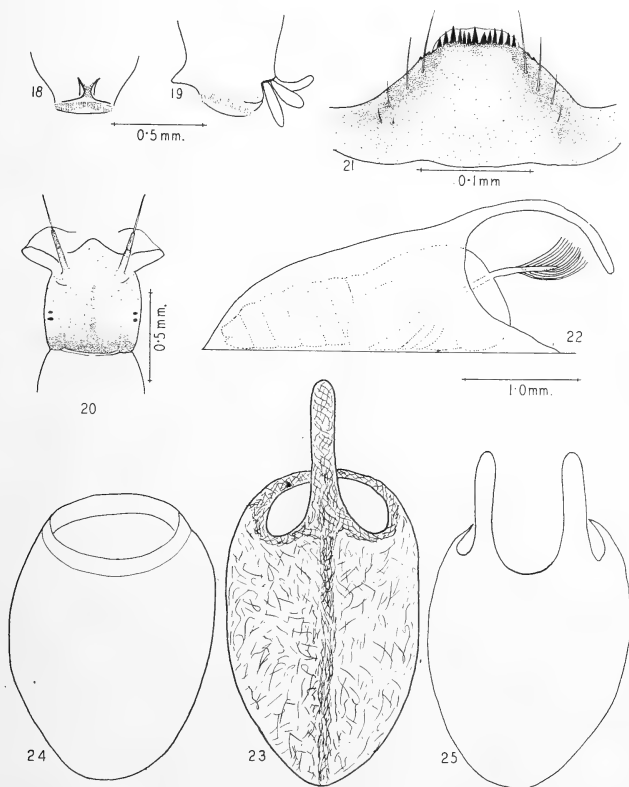
Larva.

Length 5 to 6.5 mm. Pale creamy-yellow, with greyish-brown mottling. Some individuals from shaded water were extremely pale, except for the dark basal part of the antenna. Well-developed ventral papillae present (Text-fig. 19).

The pattern on the dorsum of the head varies considerably, but basically it consists of a fairly broad basal band of dark brown and a narrow inconspicuous central streak (Text-fig. 20). Some very pale individuals had scarcely any pattern, while others were so heavily pigmented that the pattern was obscured. The stout proximal segment of the antenna is dark brown and indistinctly divided about its middle; it is the slender

apical portion which projects beyond the basal piece of the fan (Text-fig. 20). Submentum as in Text-figure 21.

The gill-spot consists of a strong, narrow horn, yellowish at the base, and covered with flat, dark tubercles on the more distal part, from which the filaments spring. The filaments arise from the sides and outer surface, and curve round anteriorly. The posterior cirlet is well developed, having about 90 to 100 closely set rows, each containing about 15 spines.



Text-figs. 18-25.—*Austrosimulium victoriae* (Roub.).

Larva: 18 and 19, posterior end; 20, dorsum of head; 21 submentum.

Pupa and cocoon: 22, lateral view of pupal respiratory organ and "horned" cocoon.

Cocoons: 23, with central dorsal "horn" (New South Wales and Victoria); 24, "hornless" (Queensland); 25, with double "horn" (Tasmania).

Pupa.

The head is covered with small, flat tubercles, rather uniformly arranged, and leaving a symmetrical L-shaped pattern of bare spots. The cephalic hairs are long and fine.

The thorax is covered with small, flat tubercles, arranged in tiny rosettes over that part of the thorax which is exposed. The more posterior covered part is decorated with smaller, flat tubercles uniformly arranged. The last pair of dorso-central thoracic hairs

is modified to form a pair of minute, forwardly-directed hooks; these occur just at the junction of the exposed and unexposed portions of the thorax. The other thoracic hairs are long and fine. The respiratory organ consists of a moderately short, narrow, flattened horn, covered with flat, dark tubercles. The filaments are fine, and arise chiefly from the sides and external surface of the horn (Text-fig. 22).

The first and second tergites of the abdomen each bear five pairs of fine, pale hairs; the third and fourth bear four pairs of strong, forwardly-directed subapical hooks; the fifth to the seventh have fine, stiff, curved hairs, with the points directed forward, the eighth has curly lateral hairs; and the ninth bears the usual strong hooks and bunch of curly anchoring hairs on each side. The ventral surface appears to be bare.

Cocoon.

All those from Victoria and southern New South Wales have a long, median dorsal projection, the Queensland ones have no projection, and the two forms occur together on the Dorrigo Plateau. The Tasmanian race, originally described by Tonnoir as *A. tasmaniense*, is remarkable in making cocoons with two long projections (Text-figs. 23 to 25).

The races of *A. victoriae*.

The adults bred from the three types of cocoons are indistinguishable. The larvae associated with them are also indistinguishable, except that the southern forms tend to be larger. The pupae are also very similar, except that those from Tasmania have a longer respiratory horn and the gill-filaments are bunched together and directed medially. We have hesitated to resurrect Tonnoir's name, although it is available if subspecific separation ultimately proves to be desirable. The confusion has arisen because the Tasmanian cocoon is so distinctive, and because no less than three mainland species (*A. victoriae*, *A. cornutum* and *A. montanum*) frequently make cocoons with a single, long, median, dorsal projection.

Distribution.—Tasmania: Localities given in earlier paper (Tonnoir). Victoria: Narbethong (? *type locality*), Buxton, Marysville, October–November; Sassafra, October; Mt. Buffalo, October (Tillyard and Currie); Tarra Falls, January (Sandars). New South Wales and A.C.T.: Deniliquin, in rabbit warren, November (Fennessy); Mt. Kosciusko, December; Black Mountain, Cotter River, Blundell's, etc., September–November (Tonnoir and others); Wentworth Falls, March (Wharton); Mt. Solitary, Jamieson Valley, September (McMillan); Lett River, Hartley, October; Williams River, 1,500 ft., March (McMillan); Barrington Tops, 4,000 to 4,500 ft., March (McMillan); Dorrigo Plateau, near Ebor, approx. 4,000 ft., September. Queensland: Little Nerang Creek, September; Springbrook area, December.

Biology.

In the southern part of Australia, the females feed rapidly on human blood, attacking particularly the ears, and sometimes being very annoying. In the north, they are less obtrusive, although the early stages are sometimes abundant. Larvae and pupae are found in clear, moderately swift to quite gently flowing water, usually attached to reeds, though sometimes on stones. They are common in water which is unpleasantly cold to work in.

AUSTROSIMULIUM TORRENTIUM Tonn. var.

New distribution.—New South Wales: Shoalhaven River, April (McMillan); Kedumba Creek, Jamieson Valley, September (McMillan); Bellingen River, North Coast, September; Macdonald River, near Bendemeer, September; Pinch Creek, Dorrigo Plateau, January. (Previously known only from A.C.T. and Mt. Kosciusko.)

This form is so constant, and we have now seen it from so many localities, that we wonder what its status should be, although we can still distinguish it only as a full-grown gill-spot larva.

CONCLUSION.

Experience over the past two years suggests that it may be a long time before we can fill the gaps in our knowledge of the Cnephias, or review effectively the Simuliid faunas of Western Australia and the Northern Territory. We would therefore conclude this part with a revised table summarizing the present state of our knowledge. We have omitted the species from New Guinea and New Zealand, about which we have no new information, and we have also omitted those from the Northern Territory. At least four species of *Simulium* occur there, *S.* ? *faheyi* Tayl. and sp. *B.*, known only from adults, and an undescribed representative of each of the *peregrinum* and *clathrinum* groups, known only from larvae.

References to earlier papers are given in the two previous parts of the series (These PROCEEDINGS, 73: 372-405, 1949, and 75: 167-187, 1950).

The Australian Simuliidae.

Stages Known.				Species.	Distribution.					
Larva.	Pupa.	♂	♀		Qld.	N.S.W.	Vic.	Tas.	S.A.	W.A.
CNEPHIA										
<i>aurantiacum</i> group										
x	x	x	x	<i>strenua</i> M. & M.	x					
x	x	x	x	<i>aurantiacum</i> (Tonn.)	x	x	x	x		
x	x	x	x	<i>tonnoiri tonnoiri</i> (Drum.) . . .						x
x	x	x	x	<i>tonnoiri orientalis</i> M. & M. . .	x	x	x	x		
(? x)	x	x	x	<i>tonnoiri fuscoflava</i> M. & M. . .	x					
(? x)			x	<i>umbratorum</i> (Tonn.)			x			
<i>terebrans</i> group										
(? x)			x	<i>terebrans</i> (Tonn.)		x	x			
			x	sp. <i>A.</i> (M. & M.)						x
			x	<i>fergusoni</i> (Tonn.)		x			x	
			x	<i>fergusoni</i> (Tonn.) var.						x
SIMULIUM										
<i>peregrinum</i> group										
x	x	x	x	<i>peregrinum</i> M. & M.	x					
<i>ornatipes</i> group										
x	x	x	x	<i>ornatipes</i> Sk.	x	x	x		x	x
<i>clathrinum</i> group										
x	x	x	x	<i>clathrinum</i> M. & M.	x	x				
x	x	x	x	<i>nicholsoni</i> M. & M.	x	x	x			
x	x	x	x	<i>faheyi</i> Tayl.	x					
x	x	x	x	<i>melatum</i> Wh.	x	x	x			
x	x	x	x	<i>inornatum</i> M. & M.	x	x				
x	x	x	x	<i>awreonigrum</i> M. & M.	x					
AUSTROSIMULIUM										
<i>mirabile</i> group										
x	x	x	x	<i>mirabile</i> M. & M.	x					
x	x	x	x	<i>fulvicorne</i> M. & M.	x					
x	x	x	x	<i>crassipes</i> Tonn.	x	x	x			
x	x	x	x	<i>montanum</i> n.sp.	x	x	x			
x	x	x	x	<i>cornutum</i> Tonn.	x	x		x		
			x	sp. <i>C.</i> (M. & M.)						x
<i>bancrofti</i> group										
x	x	x	x	<i>bancrofti</i> (Tayl.)	x	x	x	x		x
x	x	x	x	<i>pestilens</i> M. & M.	x	x				
<i>furiosum</i> group										
x	x	x	x	<i>furiosum</i> (Sk.)	x	x	x	x	x	x
x	x	x	x	<i>victoriae</i> (Roub.)	x	x	x	x	x	
x	x	x	x	<i>torrentium torrentium</i> Tonn. . .				x		
x	x	x	x	<i>torrentium hilli</i> M. & M. . . .		x				
x	x	x	x	<i>torrentium</i> Tonn. var.		x				

The only eggs known are those of *Simulium ornatipes* Sk.

ORDOVICIAN STRATIGRAPHY AT CLIEFDEN CAVES, NEAR
MANDURAMA, N.S.W.

By N. C. STEVENS.

(With Plates iii-iv and 4 Text-figures.)

[Read 28th May, 1952.]

Synopsis.

The Cliefden Caves Limestone, which contains abundant shelly fossils of Middle Ordovician age, conformably overlies basic volcanic rocks, and is overlain by siliceous limestones and tuffs with Upper Ordovician graptolites, trilobites and brachiopods. The structure of the area is discussed, and notes on facies and facies change are appended.

Introduction.

Cliefden Caves are situated 11 miles north of Woodstock and 12 miles west-north-west of Mandurama. Previous literature on the geology of the area is mainly concerned with the limestone, which was the first limestone discovered in Australia (Oxley, 1820). Caves in the limestone were reported upon by Wilkinson (1892) and Trickett (1908). Carne and Jones (1919) mapped most of the main limestone bed, and called it the Belubula Limestone Belt.

Until recently the limestone was assumed to be Silurian, largely due to a list of fossils collected by Trickett (1908). North of the Belubula River, Booker (1950) recorded Silurian fossils from a limestone which he assumed to be continuous with the limestone at Cliefden Caves.

However, detailed mapping and further fossil collections have shown that the main limestone bed and associated strata are of Ordovician age. A preliminary note (Stevens, 1950*b*) on this occurrence was the first record of fossiliferous Ordovician limestone in New South Wales.

The nearest locality from which Ordovician fossils have been recorded is Junction Reefs, five miles to the east (Hall, 1900; Pittman, 1900), but the exact locality is in doubt.

STRATIGRAPHY.

A generalized sequence is given in Table 1 and Text-fig. 2, the data being drawn from excellent sections along the Belubula River and tributary creeks.

TABLE 1.

Formation.	Lithology.	Age.
4. Angullong Tuff.	Andesitic tuffs, tuffaceous shales, calcareous tuffs, small limestone beds.	} Upper Ordovician.
3. Malongulli Formation.	Laminated impure limestones, limestone breccias, tuffs and shales.	
2. Cliefden Caves Limestone.	Massive and shaly limestones.	
1. Walli Andesite.	Andesites, basalts, spilites, tuffs and breccias.	} Middle Ordovician.

1. The Walli Andesite is the name given to the volcanic rocks which are the basal formation of the sequence. They are well developed between Walli and Limestone Creek, extending north to the edge of The Large Flat, and south beyond Woodstock. The width of outcrop is about four miles, but as the base is not visible and the structure is uncertain, the thickness cannot be estimated. The formation was regarded as Silurian, equivalent to the Cargo Andesite (Stevens, 1948, 1950*a*), before the Cliefden Caves area was examined.

The lavas, which make up about 70 per cent. of the formation, are mainly andesites, with some basalts and spilites. Most of the lavas are porphyritic in plagioclase (in laths up to 20 mm. in length) and some have augite phenocrysts as well. Amygdaloidal types are present, and at one locality south-west of "Cliefden" (860380)* there is a very good example of pillow-structure, with concentric rows of amygdules, radial fractures and deuteric minerals in the interstices between the pillows.

Tuffs and breccias of variable grain-size are interbedded with the lavas, especially near the top of the formation. A tuff near "Cliefden" is notable for the large rounded pebbles of porphyritic andesite it contains.

The relations between the Walli Andesite and the overlying formation, the Cliefden Caves Limestone, are best shown at the south-west corner of The Large Flat (Text-fig. 1), where breccias which overlie porphyritic andesite pass upwards into tuffs, calcareous tuffs, and limestone containing large brachiopods. The same conformable relations hold between the main mass of volcanic rocks and the overlying limestone south and south-west of "Boonderoo" homestead, though the outcrops are not so good.

2. The Cliefden Caves Limestone is the main limestone belt, taking its name from Cliefden Caves, situated in the more massive parts of the formation on the south side of the Belubula River (863482). The limestone occurs in two arcuate (equivalent) beds which, through faulting and folding, join near Copper Mine Creek. The formation occurs mainly between the Belubula River and the Mandurama-Canowindra Road, and reaches its maximum development on the Belubula River in the north-east.

The Cliefden Caves Limestone could be divided into two or possibly three members, as shown by the section on the east side of The Large Flat (Text-fig. 1). However, in other places the lower shaly beds thin out, and it is not easy to distinguish them, so that it is more convenient to map the limestone as one formation.

The lowest bed of the Cliefden Caves Limestone contains abundant and closely-packed large brachiopods, which may be a new genus of the Trimerellacea. The shaly limestones which make up the lower part of the formation are interbedded with more massive limestones in beds 8 to 30 feet thick. All these shaly limestones are richly fossiliferous. Some of the limestone in the first 50 feet of the formation is built almost entirely of corallia of primitive Tabulata (*Tetradium*, and forms like *Proheliolites*, *Foerstephyllum*, and *Lycophora*). These corals are most abundant on Fossil Hill (on the south side of The Large Flat), but are also found in a corresponding stratigraphical position (above the *Trimerella* bed) in the southern limestone belt beside the road from "Boonderoo" to "Kalimna". Near the top of the shaly limestones, well-preserved brachiopods are particularly abundant, associated with trilobites, gastropods and bryozoa. From these beds Dr. Opik has identified the following forms:

Brachiopoda—*Rhynchotrema*, Orthidae (two genera), Syntrophiidae (one genus), *Camerella*, *Spanodontia*, *Rafinesquina*, *Protozygia*;

Trilobitae—Asaphidae (two forms), Pliomeridae, *Encrinurella*, *Lichas*, *Trinucleus*, *Remopleurides*;

Gastropoda—*Lophospira*, *Hormotoma*, *Raphistomina*, *Raphistoma*, *Maclurites*, *Phragmolites*;

Bryozoa—*Pachydictya*, *Rhinidictya*, two of three genera of Trepostomata;

Coelenterata—Heliolitids, *Streptelasma*;

Nautiloidea—several coiled and straight forms;

Ostracoda—four genera.

These shaly beds, the lower part of the formation, are well-developed in only two restricted areas: between Fossil Hill and the Cliefden Caves near the crest of the more northerly plunging anticline, and in a similar position to the south near the road crossing of Davy's Creek. The sequence and fossils are the same in both places, so there is no doubt that the limestones are equivalent, and as both limestones overlie volcanic rocks conformably, then the volcanic rocks in both areas are of the same age.

* Military map grid co-ordinates, Canowindra 1 inch sheet.

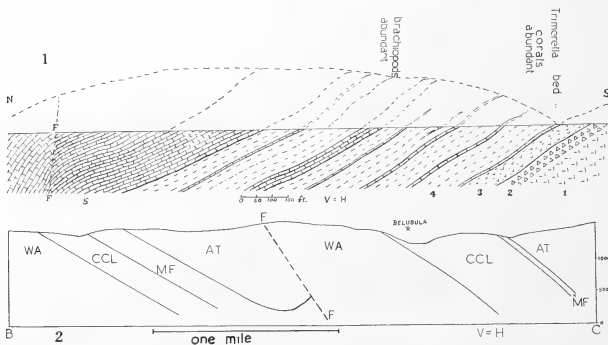
In addition to these two localities, the *Trimerella* bed has been found at the base of the limestones on Licking Hole Creek, and the coral beds occur near the base of the limestone north-west of "Boonderoo" (874467) and west of "Cliefden".

The maximum thickness of these shaly limestones is 480 feet on the eastern side of The Large Flat.

Thick massive limestones overlie the shaly members, reaching their maximum thickness (about 2000 feet) east of Cliefden Caves. In the section illustrated in Text-fig. 1, a fault interrupts the sequence, so that only 360 feet of massive limestone is shown.

The upper part of this member contains cherty siliceous nodules arranged in regular bands parallel to the bedding. Many, if not all, of these nodules are partly or wholly silicified fossils (corals). Fossils are not so abundant as in the shaly limestones, but include many of the same forms. A coral, *Favistella*, is most prominent, especially in the limestone on Licking Hole Creek.

A thin limestone bed on the west side of Limestone Creek, east of "Boonderoo", has been grouped with the Cliefden Caves Limestone, although it appears to overlie strata which are elsewhere above it. This may be due to faulting.



Text-fig. 1.

Section through the Cliefden Caves Limestone, east side of The Large Flat. 1, Porphyritic andesite; 2, breccia; 3, calcareous tuffs; 4, shaly limestone; 5, massive limestone.

Text-fig. 2.

Diagrammatic section BC (see Plate iii). WA = Walli Andesite; CCL = Cliefden Caves Limestone; MF = Malongulli Formation; AT = Angullong Tuff; F-F = Fault.

3. The Cliefden Caves Limestone is conformably overlain by the Malongulli Formation, which takes its name from the Parish and the hill around which the formation is well developed.

The formation consists mainly of impure siliceous limestones with some tuffs, shales and limestone breccia.

When fresh the impure limestones are fine-grained, black, hard, laminated, "cherty" rocks, composed of calcium carbonate (about 55 per cent.) and silica, with a little iron and alumina. The silica is in the form of sponge spicules. The fresh rocks occur along the river and major creeks, but rocks of the same formation occurring on the tops of hills present a very different appearance. They are grey in colour, less dense, and split more readily along the bedding. The lighter-coloured rocks have had calcium carbonate leached out of them and consist largely of sponge spicules.

Other fossils present are graptolites, brachiopods, trilobites and gastropods. The graptolites (determined by Mrs. K. M. Sherrard) include *Glyptograptus teretiusculus*, *Dicranograptus zic-zac* var. *minimus*, (?) *Thamnograptus* and *Climacograptus* cf.

antiquus. Opik notes also *Dicellograptus* and perhaps *Climacograptus bicornis*. These graptolites belong to the zone of *Nemagraptus gracilis*, zone 9 of the British succession, i.e., the lowest part of the Upper Ordovician. Trilobites are relatively abundant in some places (844468, 828453), and include *Trinucleus*, *Dionide*, *Remopleurides*, *Encrinurella*, and *Ceraurus*. Small Sowerbyellids, *Pseudolingula* and (?) *Chonetoides* are the brachiopods present.

Beds of limestone breccia occur near the top of the Malongulli Formation, overlying the laminated impure limestones. The sequence along the river at the western edge of The Large Flat is as follows (Text-fig. 3, A):

7. Tuffs.
6. Impure limestones.
5. Laminated siliceous limestones.
4. Limestone breccia.
3. Laminated siliceous limestones.
2. Brown clayshales and tuffs.
1. Cliefden Caves Limestone.

A number of limestone beds of varying size occur in the Malongulli Formation between Copper Mine and Sugarloaf Creeks. They are normal, massive limestones without many fossils, except near Copper Mine Creek, where gastropods are abundant.

Massive and impure laminated limestones are associated with fine tuffs south of The Sugarloaf (Malongulli Trig. Station). The relation of these rocks to the strata further north is obscured by an intrusion, but the graptolites *Nemagraptus explanatus* var. *pertenuis* and *Climacograptus* cf. *antiquus* show that they belong to the same zone as the beds nearer the river. Graptolites (including *Amplexograptus*) have also been obtained from a similar banded limestone, which occurs as fragments in a limestone breccia at the north-east end of The Large Flat (856482).

4. The Angullong Tuff is the next youngest formation; it is named after "Angullong" property (north of the Belubula River), where it is well developed, but it also occurs between the Belubula River and Licking Hole Creek, and north and east of "Boonderoo".

The relation with the underlying formation is best seen along the northern bank of the river at the north end of The Large Flat. A conformable passage from impure black limestone to tuff occurs.

The rock types of this formation are chiefly andesitic tuffs, with calcareous beds, small limestone lenses, and possibly some minor andesite flows (it is not yet certain whether the latter are flows or sills).

Well-bedded tuffaceous shales and banded tuffs occur along the river between "Kalimna" and the Upper Devonian quartzite gorge of The Needles. Diplograptid graptolites are present in calcareous beds associated with these tuffs west of "Kalimna" (830485 and 833494).

The similarity in lithology between the tuffs near "Boonderoo" and those north of the river, together with the fact that they both overlie the Malongulli Formation, leaves little doubt that the tuffs are of the same formation. East of "Boonderoo" the junction of the Malongulli Formation with the Angullong Tuff is irregular, as the upper beds of the Malongulli Formation grade laterally into tuffs over a short distance.

The Angullong Tuff appears to dip beneath limestone one mile north-north-east of "Kalimna". The limestone is possibly of Silurian age, as *Halysites* and *Heliolites* have been found in it further north, as well as poorly preserved compound corals at its southern end. It is probable that this is the limestone in which *Conchidium* was also found (Booker, 1950). It adjoins the Cliefden Caves Limestone at one place, and probably overlies it unconformably.

On the eastern side of Limestone Creek also, the Angullong Tuff seems to dip beneath limestone (three-quarters of a mile south of the Belubula River). This limestone is massive and unfossiliferous, and may be of Silurian age.

STRUCTURE.

It has been explained above that on palaeontological evidence, the limestone beds outcropping along the road between "Boonderoo" and Davy's Creek are equivalent to those to the north at Fossil Hill and near Cliefden Caves. The former beds dip north-east at angles mostly between 10° and 40° , the angle increasing somewhat to the south-east. The limestone beds in the more northerly area are folded into an anticline with a north-south axis, plunging to the north. Both limestones overlie volcanic rocks and are overlain by equivalent formations.

Repetition of beds may be due to faulting or overfolding, but in this case overfolding to give the existing sequence is impossible (Text-fig. 2), and the fossil beds show no overturning.

Faulting must have taken place between "Boonderoo" and Fossil Hill, the break occurring at the boundary of the Walli Andesite with the Angullong Tuff. Evidence of faulting is not very good, but near Davy's Creek there are extensive travertine deposits and south of Fossil Hill ferruginous breccias. Tracing this arcuate, east-west fault to the west, faulting in the limestone where the two limestone beds join is more evident. At least three faults join here, and fault-breccias made up of fragments of the Malongulli Formation are frequent. The fault has been drawn in south along Copper Mine Creek mainly because of opposing trends in the volcanic rocks and the limestone. West-north-west trends in the volcanic rocks are clearly seen on aerial photographs.

North-east of "Boonderoo" the main east-west fault seems to be intersected by another fault which terminates the southern extension of the Cliefden Caves Limestone and the adjoining Malongulli Formation. These beds are offset to the east and appear further south. The main fault appears to pass on the west side of this outcrop and continue south across Limestone Creek, where it is associated with shear zones in the limestone.

Some minor faulting is seen on Fossil Hill, but more important faults occur to the north. Evidence of faulting is present on the east side of The Large Flat (Text-fig. 1), and the same fault may account for the sudden change in trend (associated with strong folding) just south of the caves. The western extension of this fault is marked by fault breccia ten chains south of the confluence of Davy's Creek with the Belubula River. Faults occur along the river from Copper Mine Creek to Cliefden Caves, but most of them cannot be traced far from the river. One of them is shown in Text-figure 3, B.

North of The Large Flat, a fault which is seen on the south side of the river runs north, separating the Angullong Tuff from the Malongulli Formation (here interbedded with limestone). These formations dip in opposite directions.

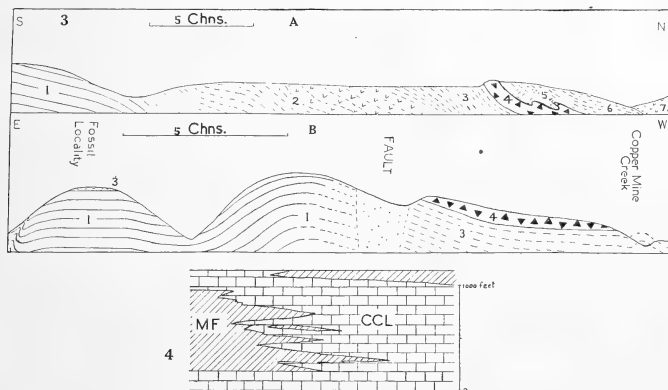
A fault is suggested along the west side of the limestone on Copper Mine Creek. Limestone in the Malongulli Formation is horizontal where it adjoins the steeply-dipping Cliefden Caves Limestone, and further south, near the head of Copper Mine Creek, the Malongulli Formation is strongly folded where it adjoins the limestone. Other examples of strong folding along this north-south line are seen near the junction of Copper Mine Creek and the Belubula River, and at "Kalimna" homestead. There is a notable change in strike (90°) in the Angullong Tuff north of "Kalimna", but from outcrops around the big bend in the river it is seen that the change is gradual, and is not due to faulting. It is likely that many of these faults die out in a relatively short distance.

Near the north-west corner of The Large Flat an almost horizontal overfold occurs in brecciated limestone and Malongulli Formation (Text-figure 3, A). This is due to sliding of the beds before consolidation. Small-scale slump-structures have also been observed in the Angullong Tuff.

In most cases it is not known which of the faults noted above are normal and which are overthrust, for frequently the presence of a fault is inferred from fault-breccias, shatter-zones, or even from relations of adjoining formations, and the actual fault plane is not visible. In section BC (Text-figure 2) the main east-west fault is assumed to be a thrust.

NOTES ON FACIES AND FACIES CHANGE.

Ordovician rocks are known from many parts of New South Wales, and most of the sediments belong to a graptolitic facies composed of shales, slates and fine sandstones. Shelly facies occur in Tasmania, Central Australia, western Queensland (David, 1950) and the Kimberley Division, Western Australia (Guppy and Opik, 1950), but prior to the discovery that the Cliefden Caves Limestone was Ordovician, a shelly facies had not been described from New South Wales (except for Pittman's record of (?) *Obolella* and an (?) agnostid trilobite from Junction Reefs).



Text-fig. 3.

Diagrammatic sketch-sections along the Belubula River. A—West side of The Large Flat, west bank of the river.—1, Cliefden Caves Limestone; 2, shales and tuffs; 3, laminated siliceous limestones; 4, limestone breccia; 5, laminated siliceous limestones; 6, impure limestones; 7, (Angullong) tuff. B—Around river bend upstream from Copper Mine Creek. Legend as in A.

Text-fig. 4.

Showing the relations between the Cliefden Caves Limestone (CCL) and the Malongulli Formation (MF) north of Cliefden Caves (dipping strata restored to a horizontal position).

The Cliefden Caves Limestone and the Malongulli Formation were built up in shallow water between periods of volcanic activity in the the midst of the Tasman geosyncline. Somewhat similar conditions seem to have prevailed through most of Silurian time in this meridional belt, for Silurian limestones and volcanic rocks are of frequent occurrence to the north, and in a number of places Ordovician graptolite-bearing rocks appear as inliers. Although shelly facies have not been recorded to the north, limestones of probable Ordovician age are associated with graptolite-bearing strata east of Cargo, and graptolite-bearing rocks similar lithologically to the Malongulli Formation have been noted west of Cadia.

North of the Belubula River, localized lithofacies change is exhibited where the Malongulli Formation and the Cliefden Caves Limestone pass into one another. The impure, laminated limestone with interbedded limestone breccia and more massive beds which constitute the Malongulli Formation pass laterally into massive limestones, the shaly, impure limestones tapering out over a short distance.

This accounts for the great thickness of massive limestone north and south of the river, east of Cliefden Caves, and the anomalous position of the Cliefden Caves Limestone north-west of the caves, where it appears to overlie the Malongulli Formation.

At least the upper part of the massive limestone east of Cliefden Caves seems to be a true reef. It shows the characteristic sudden tapering-out of the limestone, and the association with limestone breccia, representing débris from the reef (Twenhofel, 1950).

The upper part of the Malongulli Formation shows lateral gradation into the Angullong Tuff north-east of "Boonderoo", but this is not strictly a facies change.

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Some of the field work was done during the tenure of a Linnean Macleay Fellowship.

Access to aerial photographs of the area was made possible through the courtesy of Messrs. J. Taylor and R. Brewer, of the C.S.I.R.O. Division of Soils.

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EXPLANATION TO PLATES III-IV.

PLATE III.

Geological Sketch Map of the Cliefden Caves District.

PLATE IV.

1. The Cliefden Caves Limestone on the east side of The Large Flat.
2. Fossil Hill; shaly limestones of the lower part of the Cliefden Caves Limestone dip towards the observer.
3. Fold in the Cliefden Caves Limestone. The Malongulli Formation overlies these rocks on the left-hand side of the photograph.
4. Fold in siliceous limestones of the Malongulli Formation at the confluence of Copper Mine Creek and the Belubula River.
5. Overturned fold in siliceous limestone and limestone breccia of the Malongulli Formation at the north-west corner of The Large Flat.
6. Fold and thrust fault in limestones near junction of Davy's Creek and the Belubula River.
7. Strong folding in the Cliefden Caves Limestone south of Cliefden Caves at its junction with the Walli Andesite.

Photographs by H. J. Pemble and N. C. Stevens.

TAXONOMIC NOTES ON THE GENUS *ABLEPHARUS* (SAURIA: SCINCIDAE).

III. A NEW SPECIES FROM NORTH-WEST AUSTRALIA.*

By STEPHEN J. COPLAND, M.Sc.

(Plate v; three Text-figures.)

[Read 28th May, 1952.]

Synopsis.

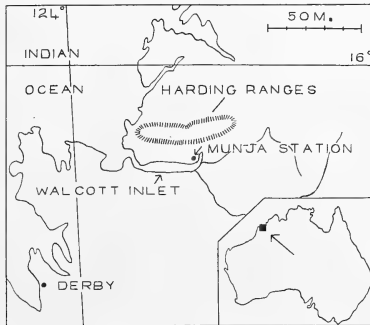
This paper on Australian members of the Scincid genus *Ablepharus* Fitzinger deals with an apparently new species from the Kimberley Division, north-west Australia. This third pentadactyl member of the group with frontoparietal single and interparietal distinct is described, figured and compared with its nearest relatives.

ABLEPHARUS DAVISI, n. sp.

Diagnosis: An *Ablepharus* with the frontoparietal single and interparietal distinct; differing from the more closely allied of the two other Australian pentadactyl members of the group, *Ablepharus ornatus* Broom, in having 24 midbody scale rows (*A. ornatus* 26-28), four supralabials anterior to subocular (3), colour, shorter limbs, separated prefrontals, and other characters as given in Table 2. The colour pattern alone sharply differentiates *Ablepharus davisii* from the only other pentadactyl member of the group, *Ablepharus kinghorni* Copland.

Holotype: No. 1916 in the author's collection; Harding Ranges, 8 m. W. to 8 m. N-W. from Munja Station, Walcott Inlet, N-W. Australia, collector Consett Davis, 17. viii. 1943. Munja Station is 110 miles N-E. of Derby, which is 17° 19' S, 123° 39' E.

Description of holotype: Rostral not projecting; smoothly rounded when seen from above, the area visible being equal to about half that of the frontonasal; four times broader than long; longest suture with frontonasal, almost straight, equal to about

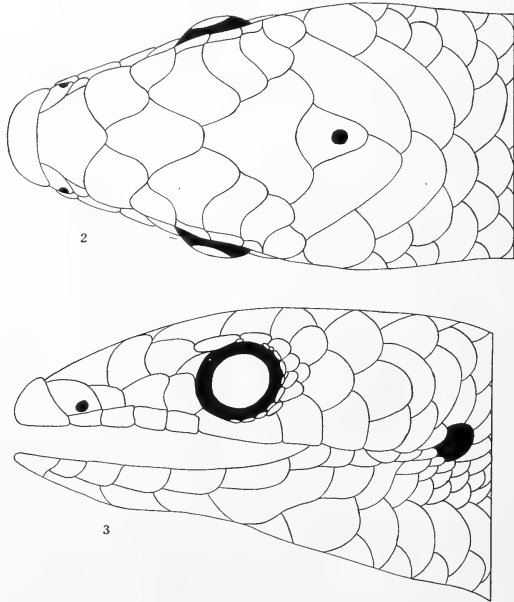


Text-fig. 1.—Map of part of the Kimberley Division of Western Australia showing type locality of *Ablepharus davisii*, n. sp.; with small index map of Australia indicating area dealt with on larger scale.

two-thirds the width of the frontal; suture with nasal nearly as long as that with frontonasal, nearly straight; very short, vertical suture with 1st supralabial. Nasals moderate, widely separated; irregularly quadrilateral, almost straight sides in decreasing order of length against frontonasal, rostral, whole upper edge of 1st supralabial, and postnasal;

* For Part ii, see These *Proceedings*, lxxiii: 362.

nostril directed somewhat backwards, diameter about one-third length of scale, near ventral border, a shallow groove runs horizontally from postero-dorsal edge of nostril to suture with postnasal. No supranasals. Postnasal half size of nasal, squarish; long rounded suture with frontonasal, prefrontal and anterior loreal; straight ones, subequal in length, with nasal and 2nd supralabial. Frontonasal slightly larger than frontal, with which it forms a short, convex suture one-sixth the width of the latter scale; long sutures, about equal in length, with rostral, nasals and prefrontals, first two straightish, third sinuous; short junctions with postnasals. Prefrontals large, each equal to about two-thirds the area of frontal; roughly quadrilateral; long straight side against frontal, long mainly convex one with frontonasal, and long concave one with 1st supraciliary; sutures with anterior loreal, postnasal and 1st supraocular are



Text-figs. 2, 3.—Head scales of *Ablepharus davisii*, n. sp. 2, Dorsal view. 3, Lateral view. Length of head of specimen figured, A.C. 1916, the holotype, 6 mm.

considerably shorter. Frontal moderate, kite-shaped; width nearly equal to supraocular region at its widest; length equal to its distance from the tip of the snout; longest sides against 1st supraoculars, next against prefrontals; short, indented anterior suture with frontonasal, and a shorter, convex one with frontoparietal; narrowly separated from 1st supraciliaries and widely from 2nd supraoculars. Frontoparietal single, equal in length to the frontal, but much wider and larger; concave sutures with the parietals are little longer than each of the straightish ones with 1st, 2nd and 3rd supraoculars, but much shorter than the indented, sinuous one with interparietal. Interparietal small, kite-shaped, rounded behind, enclosed between parietals and frontoparietal; half length of frontoparietal; a dark, rounded pineal area lies a little posterior to the centre. Parietals each slightly smaller than the frontoparietal; irregularly oblong; long axes, which diverge about 90° , twice the length of the short; meeting behind the interparietal in an oblique suture sloping backwards towards the left; other sutures, slightly convex

with the nuchals, shorter and straighter with upper secondary temporal, and slightly shorter in turn with interparietal, frontoparietal, 3rd supraocular and 5th supraciliary. There is a single pair of nuchals, each twice the size of a following body scale. Seven supralabials; 1st small, wedge-shaped, in contact with nasal dorsally; 2nd to 4th larger and higher; 2nd in contact with postnasal and anterior loreal; 3rd with both loreals; 4th with posterior loreal; 5th large, equal in size to two of the preceding supralabials, boat-shaped, the long concave upper margin forming the whole border of the eye; 6th and 7th taller than 5th, haystack-shaped. Two large postlabials are separated by a single scale from the ear opening. Primary temporal roughly hexagonal, anterior three borders against 5th supraciliary, 2nd postocular, postsubocular and 6th supralabial, posterior three against secondary temporals and 7th supralabial. The upper secondary temporal is twice the size of the primary temporal, which is subequal to the lower secondary temporal. The two tertiary temporals are little larger than the following body scales. Body scales begin behind the nuchals, upper secondary temporal, posterior tertiary temporal and posterior postlabial. The two loreals are large, subequal in size, irregularly quadrilateral; the anterior lies between postnasal, prefrontal, 1st supraciliary, posterior loreal, and 2nd and 3rd supralabials; the posterior between anterior loreal, 1st supraciliary, preocular, and 4th and 5th supralabials. The eye is incompletely surrounded by small rounded oblong granules, there being about nine or ten granules posteriorly and ventrally. The eye elsewhere is bounded directly by the 5th supralabial, posterior loreal, preocular and 2nd, 3rd and 4th supraciliaries. The preocular is triangular and lies between posterior loreal and 1st and 2nd supraciliaries. There are three rounded postoculars and a larger triangular postsubocular. Of the five supraciliaries, the 1st and 5th are by far the largest; the triangular 1st is more than twice the size of the 2nd and more than half the size of the prefrontal; it lies between prefrontal, 1st supraocular, 2nd supraciliary, preocular and loreals; the 2nd and 3rd are flattened plates lying directly above the eye; the 4th is rounded and lies between 3rd and 5th supraciliaries, 3rd supraocular, 1st postocular and two granules; the 5th is nearly as large as the 1st, rounded, and is surrounded by 4th supraciliary, 3rd supraocular, parietal, upper secondary temporal, primary temporal, and 1st and 2nd postoculars. There are three well-developed supraoculars, the 1st much the largest, then the 2nd and 3rd in turn; the frontal is in contact with only the 1st, the frontoparietal with all three, and the parietal with the 3rd. The postmental is at least twice the size of the mental and is followed by three pairs of chin-shields; the 1st pair are in contact, the 2nd separated by a single scale and the 3rd by three. There are six infralabials, the 4th and 5th being the largest.

The ear opening is irregularly rounded, three scales form a feeble denticulation anteriorly and below; less than half the size of the pupil of the eye; and three scales behind the 7th supralabial.

Scales are 24 at midbody, subequal. Subcaudal scales larger. Four anal scales, especially inner two, enlarged. Scales from above vent to parietals, 50.

Body rather short, the distance between the end of the snout and the forelimb is contained one and two-thirds in the distance between axilla and groin. Limbs moderately developed, distinctly separated when adpressed, pentadactyle, fingers and toes rather slender. Lamellar formula for fingers 3, 5, 8, 12, 6. Lamellar formula for toes 5, 7, 12, 19, 9. Lamellae are mainly flattened and become less distinct distally. Palms and soles granular.

The dorsal ground colour is greenish with much brown on the head, tail and limbs. Most dorsal scales have two or more blackish lines on low keels. These tend to form indistinct longitudinal lines. The head dorsally is pale brown with many small deep-brown spots. The preocular part is light straw coloured. The brown of the head extends down and includes the dorsal half of the supralabials, the remainder of these scales and the ventral surface of the head being an almost colourless, uniform pale brown. Blackish specks, occupying the centre of the scales, form four or five interrupted lateral lines between the limbs. The whole tail is much darker brown than the body and the aggregations of dots more prominent.

Measurements of the holotype are given with those of the paratype in Table 1.

The species is named for its collector, the late Dr. H. F. Consett Davis.

Paratype: In author's collection: No. 1917, same data as holotype. The single paratype is almost identical with the holotype, except that the blackish spots are much

TABLE 1.

Measurements in mm. and other details of the Holotype and Paratype of *Ablepharus davis*, n.sp.

	Number.	A.C. 1916.	A.C. 1917.
Snout-vent	26	25
Tail	37	32+
Snout-ear	6	5.5
Snout-forelimb	9	9.5
Axilla-groin	15	15
Head, width	4	4
Body, width	5	5.5
Forelimb, length	5	6
Hindlimb, length	9	9
Tail/Snout-vent	1.42	—
Axilla-groin/Snout-forelimb	1.67	1.58
Midbody scale rows	24	24
Dorsal scales between parietal and vent	50	53
Lamellae below 4th toe	19	20

more distinct (see Plate v, fig. 3). They form longitudinal lines laterally between the limbs and dorsally from the head to well along the tail. The boundary of the ear opening is quite smooth. Midbody scale rows, 24; scales from above vent to parietals, 53; and lamellae under 4th toe, 20.

Although Dr. Consett Davis almost always gave short ecological notes with specimens collected by him, he omitted to supply them for this species.

TABLE 2.

Differences between *A. davis* and *A. ornatus*.

	<i>A. davis</i> .	<i>A. ornatus</i> .
Snout	Short and rounded.	Short and pointed.
Granules round eye	Eye incompletely surrounded, there being about 10 posteriorly and ventrally.	Eye entirely surrounded by 19 uniform granules.
Suture between rostral and frontonasal.	Long.	Very short.
Prefrontals	Separated.	In contact.
Interparietal	Considerably smaller than frontonasal.	About equal in size to frontonasal.
Supralabials anterior to subocular.	4.	3.
Midbody scale-rows	24.	26-28.
Adpressed limbs	Separated.	Overlap.
Colour	Longitudinal lines at most narrow and black.	"Along the upper third of each lateral region passes a dark brown interrupted strip broken into small irregular squares by alternating fawn-coloured squares . . . along the middle lateral region passes a narrow light-coloured strip free from any spots . . . along the lower third of the lateral region is a regular-series of irregular darkish spots or mottlings . . ."

Ablepharus davis is well differentiated from its closest relative, *A. ornatus* Broom, from North Queensland (1896:343) as pointed out in the diagnosis and Table 2.

When comparing *A. davis* against descriptions of other *Ablepharids* collected in north-west Australia, I was struck by its rather close agreement in coloration and

several points in scalation with *A. broomensis* Lönnberg and Andersson (1913:11) from Broome. Broome is about 220 miles from Munja Station. Lönnberg and Andersson had two specimens—both with “frontoparietals and interparietal distinct, the latter somewhat smaller than either of the former” and “frontal rather small, not much larger than either frontoparietal”. This condition of the frontoparietals sharply separates *A. broomensis* from *A. davisi*—both specimens of which have a single, undivided frontoparietal. Since Boulenger's Catalogue of 1887, all workers, including Lönnberg and Andersson, have used Boulenger's division of *Ablepharus* into three groups of species—i.e., I. Frontoparietals and interparietal united into a single shield; II. Frontoparietal single, interparietal distinct (includes *A. davisi*); and III. A pair of frontoparietals and an interparietal (includes *A. broomensis*). The emphasis on this character for purposes of classification must remove all doubt. Other points of difference between *A. davisi* and *A. broomensis* are given in Table 3.

TABLE 3.

Differences between A. davisi and A. broomensis.

	<i>A. davisi.</i>	<i>A. broomensis.</i>
Granules round eye	None in front.	Some in front.
Frontal	Separated from 1st supra-ciliary.	Narrowly in contact with 1st supraciliary.
Frontoparietals	Form single shield.	Distinct, two shields.
Supraciliaries	Five.	Three.
Scales round body	24.	22.
Adpressed limbs	Distinctly separated.	Overlap.
Tail/Body ratio	1.42.	1.15.

Acknowledgements.

I wish to acknowledge help and advice from Professor P. D. F. Murray and Professor E. A. Briggs, of the University of Sydney, and Mr. J. R. Kinghorn, of the Australian Museum. I cannot express my gratitude to the late Dr. H. F. Consett Davis for unselfish help and encouragement.

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EXPLANATION OF PLATE V.

Ablepharus davisi, n. sp.

Fig. 1.—Dorsal view of holotype, A.C. 1916; length of head and body, 26 mm.

Fig. 2.—Lateral view of holotype.

Fig. 3.—Dorsal view of paratype, A.C. 1917; length of head and body, 25 mm.

Photos.—Miss A. G. Burns.

A MAINLAND RACE OF THE SCINCID LIZARD *LYGOSOMA TRUNCATUM*
(PETERS).

By STEPHEN J. COPLAND, M.Sc.
(Plate vi; three Text-figures.)

[Read 25th June, 1952.]

Synopsis.

This paper deals with an apparently new race of one of Australia's rarest lizards, *Lygosoma truncatum* (Peters), of which only two specimens seem to have been previously collected. The new subspecies is described and figured from three specimens, and compared with the nominate race.

The first known and type specimen of *Lygosoma truncatum* was found on Peale Island in Moreton Bay, Queensland, during the voyage of the "Gazelle" and was described by Peters (1877:528). The second specimen was collected 39 years later on Moreton Island, also in Moreton Bay, and noted by Longman (1916:49).

I collected three specimens in December, 1940, under logs in clearings in rain forest on Wilson's Peak on the Queensland-New South Wales border at an elevation of about 3000 feet. This environment near the crest of the Macpherson Range is strikingly different from the low coastal islands where the two earlier specimens were found.

Peters' description (1877:528) reads:

"*Cotoscincus* nov. gen.

Pedes omnes monodactyli; reliqua *Anomalopus*.

Diese Gattung schliesst sich eng an die anderen australischen Gattungen *Rhodona*, *Anomalopus*, *Ophioscincus* u.a. an und zeichnet sich nur durch die vier sehr kurzen ungetheilten krallenlosen Extremitäten aus. Man könnte sie alle auch als eine einzige Gattung betrachten, besonders da zu erwarten steht, dass noch mehr Zwischenstufen in der Entwicklung der Extremitäten gefunden werden.

C. truncatus n. sp. (Taf. Fig. 1.)

C. squamis corporis per series 20 longitudinales dispositis; supra cinereo-fuscus, nigro punctatolineatus, lateribus nigricans, subtus albidus, mento caudaeque apice nigro adpersis.

Long. tota, 0,078; ad caud. bas. 0,042; cap. 0,0045; caudae 0,036; lat. corp. 0,003; dist. ped 0,030.

Habitatio: Australia orientalis, Insula Pealei (Moreton Bai).

Vom Ansehen ganz wie *Ophioscincus australis* (Monatsb. 1878, p. 746). Oben graubraun, mit vier Längslinien dunkler Punkte, die Körperseiten, das Unterkinn und das Schwanzende dicht mit schwarz besprengt, welches an jeder Schwanzseite eine schärfer begrenzte Längsbinde bildet.

Rostrale viel breiter als lang, mit drei Fortstätzen, welche die vordere Hälfte der grossen Nasalia zwischen sich nehmen, nahe deren vorderem Rande das Nasloch ausmündet. Internasale viel breiter als lang; Frontale kaum länger als breit, die Präfrontalia weit auseinander drängend; Frontoparietalia länger als breit; Interparietale gross, rhomboidal, hinten mit längerem spitzen Winkel; vier Supraorbitalia, von denen das erste klein; ein längliches Frenale; 4 Supralabialia, 5 Infralabialia; Ohröffnung versteckt.

Körperschuppen glänzend glatt, in 20 Längsreihen (bei *Ophioscincus australis* in 23); mittlere Präanalschuppen etwas grösser. Hintere Extremität 1 millim., vordere nur halb so lang. Schwanzconisch, auf der unteren Seite mit einer Reihe sehr breiter Schuppen.

Ein einziges Exemplar von Peale Island in Moreton Bai."

Boulenger had no specimens and in his catalogue (1877:343) draws from Peters' type account.

Lucas and Le Souef (1909:257) confine their brief mention of the species to the character of the limbs.

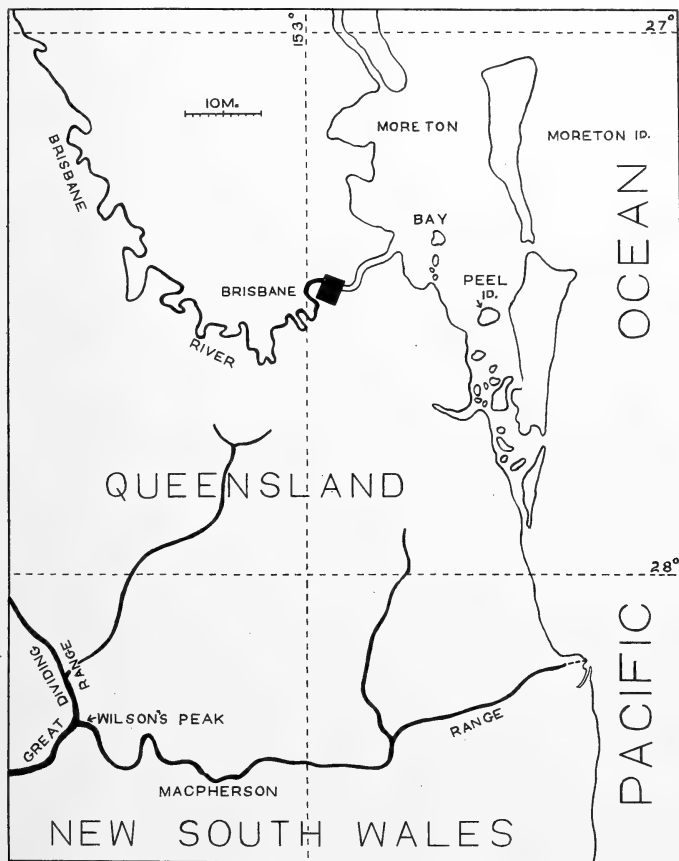


Fig. 1.—Map of south-east Queensland, showing type locality of *Lygosoma truncatum monswilsonensis*, n. subsp., and islands where *L. t. truncatum* has been found.

Longman's short note (1916:49) on the second individual of the species found reads:

"A specimen which agrees well with Peters' description was found at Moreton Island last April by Mr. R. W. McMillan and donated to the Queensland Museum. This rare lizard is 90 mm. in length and nearly 4 cm. in diameter."

The only other reference to the lizard that I have been able to find is Zietz's mention in his catalogue (1920:219).

I believe that the specimens collected by me at Wilson's Peak are racially distinct from those from Moreton Bay and now describe them as members of a new subspecies.

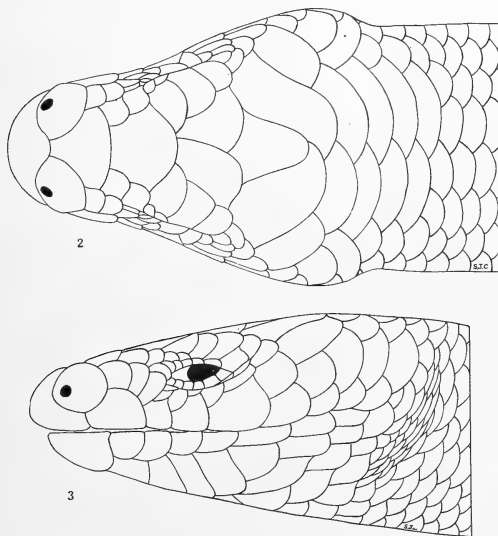
LYGOSOMA TRUNCATUM MONSWILSONENSIS, n. subsp.

Diagnosis: *Lygosoma truncatum monswilsonensis* is separated from the typical race *L. t. truncatum* by the greater development of the limbs.

Holotype: No. 876 in the author's collection; Wilson's Peak, at the junction of the Macpherson Range with the Great Dividing Range; in Queensland about 400 yards from the New South Wales border. Altitude about 3000 feet. Under log on moist, grassy slope. 10. xii. 1940.

Description of A.C. 876: Rostral large and prominent with sweeping postero-ventral wings on each side; scale much thickened (as also are the nasals, 1st supralabials, mental and 1st infralabials, which together form a kind of digging shield); projecting well over the mental; smoothly rounded and practically semicircular when seen from above, the area visible being nearly equal to that of the frontonasal; long, concave, nearly semicircular sutures with the nasals; straight, sloping sutures, about one-quarter the length of those with the nasals, with 1st supralabials; the short, convex junction with the frontonasal is equal to about one-sixth the width of the frontal. Nasals large, roughly circular, not widely separated; all sutures convex, longest with rostral, then in order with frontonasal, 1st supralabial and postnasal; scale ungrooved, a single pit on left side; rounded nostril with diameter equal to one-fifth length of scale, close to anterior border. No supranasals. Postnasal rhombic, about one-third the area of nasal; anterior border against nasal; posterior against anterior loreal; ventral against 1st supralabial; and dorsal against frontonasal and prefrontal; well separated from 2nd supralabial by loreals. Frontonasal large, about equal in area to frontal, with which it forms a suture two-fifths the width of the latter scale; wedge-shaped, with anterior indented point against rostral; long concave sutures at sides with nasals and postnasals, the former being at least twice the length of the latter; long, sweeping convex border against frontal and prefrontals, the three sutures being about equal in length. Prefrontals moderate; each slightly more than a quarter the size of the frontal; roughly square; anterior suture with frontonasal, dorsal with frontal, posterior with 1st supraciliary, and ventral with postnasal and anterior loreal. Frontal large, its length two-thirds its width; wider than the supraocular region; a long anterior contact with the frontonasal; a moderate posterior one with the left frontoparietal and a very short one with the right; each side against prefrontal, 1st supraciliary and 1st supraocular; well separated from 2nd supraocular. Frontoparietals paired; left, which is slightly smaller than the frontal, a little larger than the right; longest sutures with each other, then next in length with interparietal; the remaining four contacts on each side, with frontal, 1st, 2nd and 3rd supraoculars, are shorter and mildly concave. Interparietal kite-shaped; large, at least equal in size to the frontal and somewhat larger than a frontoparietal; rounded behind; enclosed between parietals and frontoparietals; lateral points well separated from 3rd supraoculars. No trace externally of pineal area. Parietals are by far the largest head shields, each half again the size of the interparietal; irregularly oblong; long axes, which diverge at about 70° , more than twice the length of the short; meeting behind the interparietal in a short suture sloping backwards towards the left; other sutures, long with upper secondary temporal, slightly shorter, but still long, with interparietal, considerably shorter with anterior nuchal on each side, and much shorter again with frontoparietal, and still shorter with 3rd supraocular, and 5th and 6th supraciliaries; the right scale is also narrowly in contact with the anterior nuchal on the left side. There are four well-developed pairs of nuchals, each twice the width of a body scale behind the 4th pair. Five supralabials; 1st large and thickened, roughly pentagonal, dorsally in contact with nasal, postnasal, and the two loreals; 2nd the smallest supralabial, squarish, dorsally in contact with posterior loreal, presubocular and 2nd subocular; 3rd slightly larger than 2nd, the 2nd, 3rd and 4th suboculars lie above it; 4th large, approaching the 1st in size, roughly pentagonal, antero-dorsal side against 4th subocular and 3rd postocular, postero-dorsal against primary temporal; 5th slightly smaller than 4th, haystack-shaped, dorsal peak between primary and lower secondary temporals; a small postlabial and then two rather large scales and a small one separate the 5th supralabial from the oblique groove of the ear.

Primary temporal squarish, tilted, anterior two sides against 4th supralabial, 3rd postocular and 6th supraciliary; posterior two against secondary temporals and 5th supralabial. The upper secondary temporal is a large scale, more than twice the size of the lower, which is slightly smaller than the primary. A large, upright, lens-shaped tertiary temporal is the most anterior of the three similarly shaped scales. Body scales begin behind the nuchals, upper secondary temporals, tertiary temporals and postlabials. The two oblong loreals are equal in size, and are each slightly smaller than the postnasal; the anterior lies between the postnasal, prefrontal, 1st supraciliary, preocular, posterior loreal and 1st supralabial; the posterior between anterior loreal, preocular, 1st lower palpebral, 1st subocular, presubocular, and 1st and 2nd supralabials. The eye is recessed and cannot be seen from above. Five scales form the upper palpebral chain. The first, which lies against the preocular, and the fifth, which abuts against



Figs. 2, 3.—Head scales of A.C. 876, type of *Lygosoma truncatum monswilsonensis*. 2, Dorsal view. 3, Lateral view. Length of head, 8 mm.

the 4th supraciliary, are largest. Six prominent scales form the lower palpebral series; the scales become larger posteriorly and the last two are strongly keeled. The preocular is a moderately large scale lying between the loreals, the anteriormost of the upper and lower palpebrals and the 1st supraciliary. The presubocular is a small triangular scale wedged between the 1st and 2nd suboculars, posterior loreal and 2nd supralabial. The first of the three postoculars is very small and underlies the 6th lower palpebral, being only about a third its size; the 2nd postocular underlies the 4th supraciliary and is narrowly in contact with the 5th and 6th supraciliaries; the large 3rd postocular underlies the 1st and 2nd postoculars, overlies the 4th supralabial, and is bounded in front by the 4th subocular and behind by the 6th supraciliary and primary temporal. There are four suboculars; the 1st and 3rd small and overlying the presubocular and 3rd supralabial respectively, the large 2nd is wedged between the 2nd and 3rd supralabials, and the slightly larger 3rd between the 3rd and 4th supralabials. The supraciliary chain is broken above the eye by the palpebrals. The 1st supraciliary is large and contained between the prefrontal, frontal, 1st supraocular, 2nd supraciliary, 1st upper palpebral, preocular, and anterior loreal; the 2nd and 3rd are much smaller

scales between the supraoculars and upper palpebrals; the 4th, 5th and 6th supraciliaries are large and about the size of the 1st; the upper and lower palpebral chains both abut against the 4th, which is also in contact with the 3rd supraocular, 5th supraciliary and 2nd postocular; the 5th and 6th both touch the parietal and the 6th also the upper secondary temporal and primary temporal. There are three well-developed supraoculars, subequal in size; the frontal is in contact with the 1st only, the frontoparietal with all three, and the parietal with the 3rd. The mental is large, semicircular and thickened. The single, band-like postmental is in contact with two infralabials on each side. There follow three pairs of chin-shields; the 1st in contact; the 2nd, but for an abnormality on the right side, would be separated by a single scale; and the third pair by three scales. Three pairs of elongated postgenials follow the chin-shields. Six infralabials, in order of decreasing size, 2, 1, 3, 5, 6, 4.

The ear is marked by a pronounced bulge on each side, forming the greatest width of the head, and then, about four scales behind the mouth, a shallow, scale-covered, rather narrow depression running obliquely downwards and forwards.

Scales are 20 at midbody, subequal. Caudal scales larger, especially the mid-ventral set. Two moderately enlarged preanal scales. Scales from above vent to parietals, 82.

Body elongated, the distance between the end of the snout and the forelimb is contained nearly three and a half times in the distance between axilla and groin. Fore- and hindlimbs are rudimentary, slightly flattened, roughly club to paddle shaped, circled by small scales at the base, and then about five series of larger scales to the tip. The limbs fit back into grooves. The tail ends in a small rounded tubercle.

Measurements are given in Table 1.

TABLE 1.
Measurements of Specimens of Lygosoma truncatum in mm.

Number.	*	J. 6898.	A.C. 875.	A.C. 876.	A.C. 902.
Snout-vent	42	56	76	78	52
Tail	36	56	71	52†	44†
Snout-ear	—	7	7	8	6
Snout-forelimb	—	14	17	17	13
Axilla-groin	—	42	58	58	39
Head, length	4.5	7	7	8	6
Head, width	—	4	5	6	4
Forelimb, length	0.5	0.7	1	1.3	1
Hindlimb, length	1	1.2	2	2.3	1.7
Tail/Snout-vent	0.86	1.00	0.93	0.67†	0.85†
Axilla-groin/Snout-forelimb	—	3.00	3.41	3.41	3.00

* Peters' type. † Tail regenerated.

Ground colour of the body light rather honey brown, but the dorsum appears much darker because each scale is flecked and stippled with dark brown. Dorsally, and less marked laterally, each scale has a large, single, black dot at its anterior margin, forming six interrupted dorsal rows. These rows are most distinct on the neck. Lateral rows are prominent on the neck, but less marked on the body. The underside of the body is pale yellow. There are no black dots on the head, but much dark brown. The underside of the head from the plain mental is prettily marked until well back on the throat by longitudinal lines of dark brown along each scale row. The tail is dorsally and laterally much darker than the body. The yellow ventral area becomes narrower caudad until it dies out about two-thirds of the way down the tail leaving the posterior third blackish.

Variation in paratypes and J. 6898.: Peters' type is the only one of the five known specimens I have not examined, and for this I have relied on his original description (1877:528). J. 6898 is the specimen from Moreton Bay noted by Longman (1916:49)

now in the Queensland Museum. Of my three lizards A.C. 875 and A.C. 902 are paratypes. They both come from Wilson's Peak, where A.C. 875 was collected with the holotype. A.C. 902 was found nearby on 11. xii. 1940 under a log in a damp clearing. There seems to be little doubt that *L. t. monswilsonensis* occurs in New South Wales as well as in Queensland, because the three specimens described were found within a quarter of a mile of the border which follows the crest of the Macpherson Range and similar conditions of heavy rainfall with dense jungle and clearings are common to both north and south slopes.

In J. 6898 there are three pairs of nuchals plus an irregular scale on the right side between the 1st nuchal and parietal. The anterior shields are much less thickened than in A.C. 876. Colour and pattern are almost identical with A.C. 876. In A.C. 875 the postnasal and posterior loreal meet just above the 1st supralabial on the left side and by so doing exclude the anterior loreal from contact with that scale. This tendency is also noticeable in A.C. 876 and A.C. 902, whereas in J. 6898 the anterior loreal is about twice the size of the posterior, and the contact of the posterior loreal with the 1st supralabial is greatly narrowed. A.C. 875 is in process of sloughing. Absolute measurements of the limbs are given in Table 1. Some relative measurements are given in Table 2.

TABLE 2.

Ratio of Snout-vent to Limb Measurements in Lygosoma truncatum.

Number.	*	J. 6898.	A.C. 875.	A.C. 876.	A.C. 902.
Forelimb	84	80	76	60	52
Hindlimb	42	47	38	34	31

* Peters' type.

Acknowledgements.

I wish to thank Professor P. D. F. Murray and Professor E. A. Briggs, of the University of Sydney, and Dr. A. B. Walkom and Mr. J. R. Kinghorn, of the Australian Museum, for help and advice. Mr. George Mack, director of the Queensland Museum, kindly made available the specimen in his collections. Miss A. G. Burns, of Gordon, is to be thanked for the photographs.

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EXPLANATION OF PLATE VI.

Figs. 1-2.—*Lygosoma truncatum monswilsonensis*, n. subsp.

Fig. 1.—Dorsal view of holotype, No. A.C. 876.

Fig. 2.—Lateral view of forepart of A.C. 876.

Length of head and body, 78 mm.

Photos.—Miss A. G. Burns.

THE PETROLOGY OF THE COWRA INTRUSION AND ASSOCIATED
XENOLITHS.

By N. C. STEVENS,

formerly Linnean Macleay Fellow in Geology.

(Plate vii and 4 Text-figures.)

[Read 25th June, 1952.]

Synopsis.

The Cowra Intrusion consists of granodiorite, with a porphyry margin. The numerous xenoliths are described and their origin is discussed, in particular the pelitic xenoliths, the mineral assemblages of which include cordierite, sillimanite, spinel and almandine.

INTRODUCTION.

Some of the results of an extensive field and laboratory study of the Canowindra District have been recorded in two earlier papers (Stevens, 1950, 1951). In one of these (1951, p. 51) a preliminary account is given of an elongate mass of granodiorite which extends from the neighbourhood of Cowra northerly for about 16 miles. This is the subject of the present paper, and is named the Cowra Intrusion. It is characterized by an abundance of foreign xenoliths.

FIELD RELATIONS.

The small map (Text-fig. 1) shows the extent, general character and relationships of the Cowra Intrusion. The map published in 1951 gives the geological setting of this pluton in the larger province. As indicated in the earlier paper, the mass is sill-like and almost conformable with the Silurian strata which it invades. These country-rocks, exposed on the eastern side of the intrusion, comprise slates, tuffs and occasional sandstones. Observations along this eastern margin suggest that the intrusion dips to the west at a moderate angle.

The slates are buff or greenish-coloured and of low metamorphic grade. Along certain zones they have been somewhat sheared, so that they have passed into phyllites. Analyses (Table 4) show that there is some variation in silica, magnesia and alkalis.

The country on the west of the Cowra Intrusion is made up mostly of the Canowindra Porphyry (a quartz-felspar-porphyry with sparsely-distributed red garnets). In many places this porphyry is a concordant intrusion, but in others it appears to be a flow. This type of rock also occurs on the east, separated from the Cowra pluton by the narrow strip of Silurian rocks already mentioned.

There is a general lack of contact metamorphism associated with the Cowra Intrusion; slates at the contact do not seem to have suffered appreciably, but biotite has been developed in some of the more arenaceous tuffs.

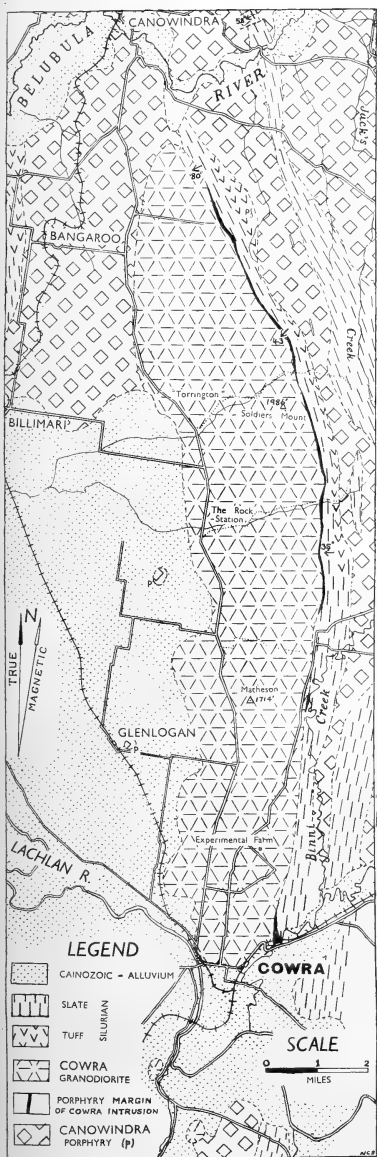
No pegmatites or apfites have been observed in or near the Cowra pluton and quartz veins are relatively scarce.

The Cowra Intrusion can be divided into (a) the Cowra Granodiorite and (b) the porphyry margin.

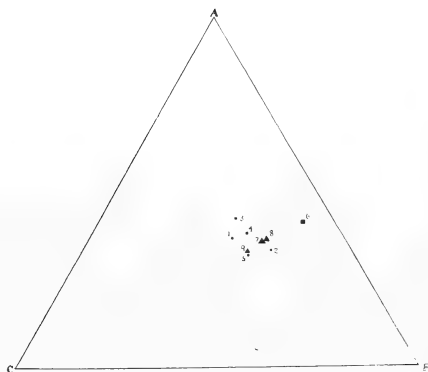
(a). The Cowra Granodiorite constitutes the major part of the intrusion, being fairly uniform in constitution and texture except for numerous and varied xenoliths. These are dealt with below. The assimilation of xenolithic material has resulted in a rock which is not a normal granodiorite, for hornblende is absent.

(b). The granodiorite-porphyry margin occupies a narrow portion of the pluton, along its eastern side. The width of outcrop varies (up to a maximum of 200 yards) and a complete gradation is seen from the granodiorite into porphyritic types.

Another notable feature of the Cowra Intrusion is the occurrence of abundant red garnet which seems to be associated with the numerous xenoliths. The garnet has been remarked upon by Dr. W. R. Browne (1929, p. xxii), who suggested that it may have been derived from strata through which the granodiorite magma passed.



Text-fig. 1.—Map of the Cowra Intrusion and Associated Xenoliths.



Text-fig. 2.—Analyses of Table 1 plotted on an A-F-C diagram. ● (1-5), granodiorites; ■ (6), gneiss; ▲ (7-9) porphyries and dacite. The diagram emphasizes the similarity in chemical composition between the granodiorites, porphyries and dacite. The Albury Gneiss is quite different, although the silica percentage is comparable.

PETROLOGY.

(a). The Cowra Granodiorite.

The normal rock is mottled, phanocrystalline, coarse to medium-grained, with clear quartz, dull white felspar and lustrous well-formed biotite. Red garnet is often seen, especially near the south end of the intrusion.

Under the microscope one notes the absence of hornblende and the presence of muscovite which is not primary. The plagioclase (andesine $Ab_{60}-Ab_{65}$) is idiomorphic with zoning and twinning invariably present. The alteration is generally strongly developed, deuteric sericitization and katamorphic kaolinization being the rule. Some epidote and clinzoisite are occasionally developed. Biotite is idiomorphic, red-brown in colour and showing change in varying degrees to chlorite, epidote (sometimes radiating), sphene and ilmenite, the last two products indicating a not inconsiderable amount of titanium in the mica.

TABLE I.

	1	2	3	4	5	6	7	8	9
SiO ₂	67.64	67.67	67.75	66.13	67.07	66.94	66.30	67.17	66.63
Al ₂ O ₃	14.54	14.50	16.11	16.83	15.55	16.65	15.26	14.86	14.86
Fe ₂ O ₃	2.24	0.87	0.50	1.11	0.50	0.40	1.28	0.43	2.01
FeO	4.05	3.78	4.00	4.17	3.38	4.77	4.18	3.87	3.75
MgO	1.13	2.21	0.79	1.83	1.69	2.19	2.32	1.61	1.73
CaO	2.70	2.18	2.68	3.26	2.97	0.94	2.87	2.84	2.55
Na ₂ O	3.04	2.38	2.60	2.25	3.21	2.11	2.22	2.48	2.99
K ₂ O	3.12	3.42	3.42	3.14	3.80	3.56	3.08	3.77	3.78
H ₂ O+	0.93	1.81	0.96	1.68	1.02	2.13	0.92	0.90	0.73
H ₂ O-	0.23	0.11	0.20	0.23	0.15	0.12	0.28	0.12	0.47
TiO ₂	0.94	0.61	0.85	tr.	0.61	0.60	0.80	0.87	0.77
P ₂ O ₅	0.12	tr.	0.09	tr.	0.23	0.01	0.08	0.53	0.06
MnO	0.04	tr.	tr.	0.07	0.04	0.06	0.06	0.07	0.05
S	abs.	—	—	—	0.04	—	—	0.02	—
CO ₂	—	—	—	—	—	—	—	0.20	—
	100.72	99.54	99.95	100.70	100.37	100.48	99.65	99.74	100.38
S.G.	2.76	—	2.68	2.68	—	—	2.74	—	2.72

Loss of O for S taken into account for analysis No. 5.

1. Cowra Granodiorite. 4½ miles N. of Cowra; grid reference 680254, Cowra 1-Inch Military Map. Anal. N. C. Stevens.
2. Grey Biotite-Granite. East of Lot 8, Section VII, Par. of Cudgewa. Anal. F. F. Field, A. B. Edwards and J. G. Easton. *Proc. Roy. Soc. Vict.*, 50, 1937: 82.
3. Granodiorite. Quarry, Gellibrand Hill, Broadmeadows. Anal. H. C. Richards. F. L. Stillwell. *Ibid.*, 24, 1911: 156.
4. Granodiorite. S.W. of Bulla. Anal. F. Watson. A. V. G. James. *Ibid.*, 42, 1929: 323.
5. Granodiorite. Talbot Drive, Marysville. Anal. E. S. Hills. *Geol. Mag.*, 69, 1932: 145.
6. Cordierite-bearing Gneiss. Weir Quarry, par. 65, Par. of Thurgona (Albury, N.S.W.). Anal. G. A. Joplin. *Proc. Linn. Soc. N.S.W.*, 72, 1947: 87.
7. Granodiorite-porphry. 3¼ miles E. of Bangaroo Railway Station. Grid reference 664416 on Canowindra 1-Inch Military Map. Anal. N. C. Stevens.
8. Rhyodacite. Wood's Point Road, Marysville. Anal. E. S. Hills. *Geol. Mag.*, 69, 1932: 145.
9. Canowindra Porphyry (garnetiferous). 6 miles E. of Canowindra. Grid reference 731476 on 1-Inch Military Map (Canowindra).

Orthoclase, much subordinate to the plagioclase, is allotriomorphic, and the abundant allotriomorphic quartz shows a variable grain size up to a maximum of 5 mm. diameter. Sub-parallel cracks and undulose extinction are notable, and the interference figure is frequently rendered biaxial by strain effects. Some intergrowth with orthoclase has occurred around the quartz margins, and this is more widespread when the proportion of orthoclase in the rock is higher. Zircon and magnetite are minor accessories.

Muscovite, sometimes in quite large flakes, replaces plagioclase and is intergrown with quartz in interstices. The mode of occurrence of the mica suggests that it has effected greisenization during a late-magmatic phase before the magma had completely consolidated. It is possible that some of the muscovite is due to reaction between magma and xenoliths.

An analysis of the granodiorite, as far as possible free from xenoliths, is given below (Table 1), where it is compared with its porphyritic marginal phase, the Canowindra Porphyry, and some Victorian granodiorites in which garnet has been noted in association with xenoliths rich in ferromagnesian minerals.

The Cowra Granodiorite differs from the other rocks in possessing higher contents of soda and total iron, along with lower alumina. Nevertheless the chemical data tabulated emphasize the close correspondence in composition of the Cowra rock with many Victorian granodiorites and comagmatic rhyodacites.

Potash in the Cowra rock is normal, although there is a limited amount of orthoclase; prominence of biotite and muscovite accounts for this. The dominance of intermediate plagioclase expresses itself in the relatively high percentage of soda.

(b). The Porphyry Margin.

The typical porphyry from Soldier's Mount shows phenocrysts of quartz, biotite, plagioclase and occasional orthoclase in a fine-grained groundmass of the same minerals. Quartz is subidiomorphic, corroded and cracked, and has notable sub-parallel trains of minute inclusions. Sometimes it shows marginal intergrowth with the feldspar of the groundmass. The plagioclase, somewhat sericitized, is andesine (Ab_{60}). Biotite is deep reddish-brown in colour and contains inclusions of zircon and rutile, the latter sometimes exhibiting sagenitic webs.

The porphyries are more melanocratic than the granodiorite and become progressively darker as the slate contact is approached. Under the microscope these darker phases become enriched in plagioclase and biotite and deuteric alteration is more pronounced.

Near the margin of the intrusion cordierite appears as small xenocrysts; under the microscope these are seen to be subidioblastic and veined with yellow pinitic, and concentration of the cordierite occurs in certain parts of the rock associated with clots of green mica. As in the granodiorite, these minerals are the result of contamination.

In some specimens the quartz-feldspar groundmass appears to have been recrystallized, but it is unlikely that the granodiorite was a later and separate injection, as there is a complete gradation between granodiorite and porphyry, and the width of the porphyry selvage is fairly uniform along the eastern side of the granodiorite.

Analysis No. 7 in Table 1 is of a granodiorite-porphyry from the north-east end of the Cowra Intrusion. Compared with the granodiorite it possesses slightly less silica, iron and soda, and a little more alumina and magnesia (see also Text-fig. 2).

(c). The Xenoliths.

Xenoliths are much more numerous and varied in the main mass of the granodiorite, so our attention will be mainly confined to these. They may be divided into five groups on the basis of composition, and to some extent of implied origin. Thus we have (1) pelites, (2) psammites (including psammopelites), (3) calcareous xenoliths, (4) igneous xenoliths and (5) granitized xenoliths.

The assemblages found are listed in Table 2, with the names of the less common minerals enclosed in brackets.

(1) Pelites.

Xenoliths derived from pelites constitute probably the most abundant type in the Cowra Intrusion. They are dark and fine-grained, up to several inches in length, and mostly show signs of the original bedding. They are sheathed in micaceous reaction-rims, and in the smaller xenoliths the reaction-rim may make up the greater part, giving them the appearance of biotite-schists.

Both silica-rich and silica-poor types occur, as at Albury (Joplin, 1947), the latter being characterized by spinel. Cordierite, sillimanite, spinel and almandine garnet are characteristic minerals of the pelitic xenoliths.

Cordierite forms large plates intergrown in places with sericitized plagioclase. Usually the cordierite itself is highly pinitized, alteration having taken place along cracks and cleavages. Zircon inclusions with distinctive yellow pleochroic haloes are seen both in fresh and altered cordierite. When occurring with quartz, cordierite is xenoblastic towards it, and sericite-filled cracks in the cordierite radiate outwards from the boundaries with the quartz grains. Most of the cordierite is biaxial negative, but a single case of positive cordierite has been observed.

TABLE 2.

	Chief Minerals.	Associated Minerals.
(1) <i>Pelites.</i>		
	(a) <i>Silica-poor.</i>	
	cordierite, sillimanite, spinel.	plagioclase, (clinozoisite).
	cordierite, spinel.	plagioclase, (orthoclase, quartz).
	sillimanite, spinel.	
	(b) <i>Silica-rich.</i>	
	cordierite, sillimanite.	plagioclase, (biotite, orthoclase, quartz).
	cordierite, orthoclase.	biotite, quartz.
	cordierite, plagioclase.	biotite, quartz.
	cordierite, garnet.	biotite, (plagioclase).
	cordierite, garnet, sillimanite.	quartz, biotite.
	garnet, hypersthene.	biotite.
	garnet, hypersthene, cordierite.	biotite, (quartz).
	hypersthene, plagioclase, orthoclase.	biotite, quartz.
(2) <i>Psammites and Psammopelites.</i>		
	quartz, andesine.	
	quartz, andesine, biotite.	(hypersthene or diopside).
	quartz, sodic plagioclase, orthoclase.	(epidote).
(3) <i>Notably Calcareous Xenoliths.</i>		
	clinozoisite, plagioclase, quartz.	(orthoclase).
	clinozoisite, quartz.	(tremolite).
	quartz, epidote, actinolite.	
(4) <i>Xenoliths of Igneous Origin.</i>		
	hypersthene, plagioclase, magnetite.	quartz, biotite (in reaction-rim).
	hypersthene, plagioclase, biotite.	
	plagioclase, quartz, biotite.	orthoclase, ilmenite, epidote, etc.
(5) <i>Granitized Xenoliths.</i>		
	plagioclase, quartz, biotite.	orthoclase.

Sillimanite usually occurs as groups of needles in cordierite or garnet, but sometimes it forms a large proportion of the xenolith, in swirling masses which follow the plications of the original pelite. It suffers sericitization with advancing reaction with the magma.

Spinel, sometimes associated with magnetite, occurs in groups of dark green to black crystals and grains which vary in degree of perfection of form. It is probably rich in the hercynite molecule, and is most abundant in those areas of the xenoliths which are biotite-poor and rich in cordierite and sillimanite.

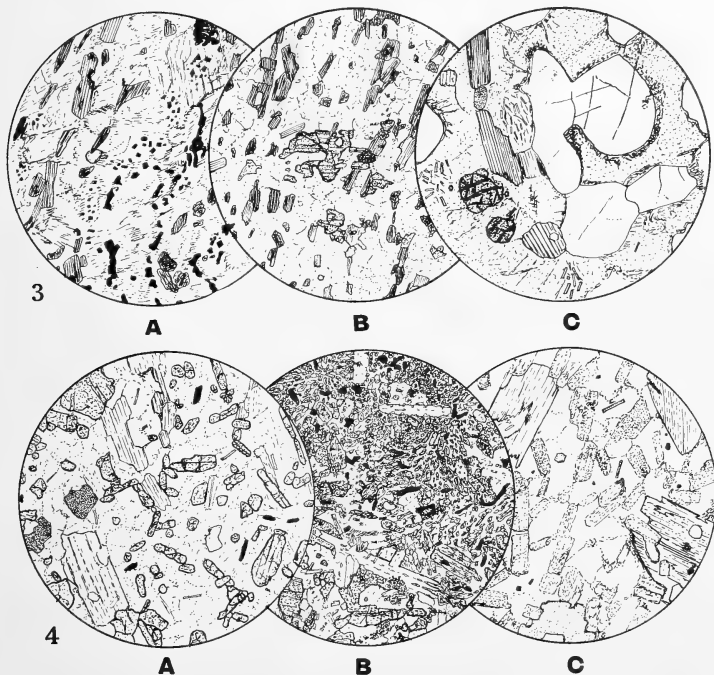
Pale pink subidioblastic rounded garnets up to 1.5 cm. in diameter are often present in the silica-rich pelites, generally associated with the biotite. In places garnet is present as angular fragments in a mass of sericitic material, which may have resulted from original cordierite. Cracks in the garnet are sometimes filled with bright green chlorite, sericite or a little quartz, but on the whole it is not greatly altered and seems moderately stable.

Garnet from Matheson Trig. Station has a R.I. of $1.805 \pm .005$, the S.G. is 4.12 and the percentage of MnO is 2.06. These figures are close to those obtained for garnet from silica-rich pelitic xenoliths at Albury (Joplin, 1947), and indicate an almandine with minor percentages of pyrope (20%) and spessartine (5%).

Another interesting association is that of garnet with hypersthene, the latter as subidioblastic inclusions in garnet as well as an outer reaction-rim, beyond the zones

of magnetite and biotite. The hypersthene is pale green, with intense pleochroism from grey-green to beige, and is probably rich in iron.

Hypersthene occurs in quite a different manner in the quartz-biotite-plagioclase-hypersthene hornfelses. Here, garnet is absent and the pyroxene is in occasional xenoblasts of smaller grainsize.



Text-fig. 3.

A. Pelitic xenolith containing cordierite, plagioclase, spinel (black) and biotite, showing biotite-rich and spinel-rich bands.

B. A biotite-plagioclase xenolith with occasional hypersthene.

C. A cordierite-rich xenolith, with quartz (clear), biotite, garnet and sillimanite (small needles).

(Magnification \times sixteen.)

Text-fig. 4.

Xenoliths of probable igneous origin.

A. A hypersthene-plagioclase-biotite assemblage.

B. Hypersthene-biotite-magnetite xenolith.

C. Plagioclase-quartz-biotite xenolith with some chlorite and apatite.

(Magnification \times sixteen.)

Biotite is the most abundant mineral in many of the pelitic xenoliths, whose original bedding may be delineated by biotite-rich bands. Zircon inclusions and sagenite webs are notable, also alteration to epidote. In some mottled pelites, cordierite forms a diablastic intergrowth with biotite (Plate vii, fig. 8), giving a rude micrographic fabric.

Plagioclase varies in grainsize and degree of alteration, but its composition is mainly andesine, Ab_{52} to Ab_{65} , roughly equivalent to the plagioclase in the granodiorite.

Although plagioclase of such a composition would crystallize from the granodiorite (as a result of the Reaction Principle), it seems likely that some plagioclase was an original constituent of the xenoliths.

Clinzoisite is present in the calcareous pelites, and occurs in subidioblastic crystals associated with quartz and plagioclase. This association rapidly grades into one in which hypersthene takes the place of clinzoisite. Clinzoisite or epidote, in strings of granules, occurs in some of the silica-poor pelites. Its occurrence here is rather unexpected, and its presence may be due to extremely thin calcareous bands in the original sediment (cf. Tilley, 1924, p. 40). Sediments exhibiting such a degree of metamorphism could well be expected to have all the clinzoisite converted to calcic plagioclase (Harker, 1932).

Other minerals in the pelitic xenoliths which make an occasional appearance are sphene and blue-grey tourmaline. The latter may be derived from recrystallization of tourmaline in the original sediment, as no tourmaline has been found elsewhere in the Cowra Intrusion.

(2) Psammites and Psammopelites.

Psammitic xenoliths are of much rarer occurrence than pelitic. They are fine to medium-grained banded granulites with quartz, feldspar and biotite. Some hypersthene-bearing types are found, and these grade into the quartz-feldspar-hypersthene assemblages of the pelitic xenoliths, marking the gradation in the original sediment from pelite through psammopelite to psammite.

Diopside has been detected in one of these xenoliths, showing alteration to a fibrous green amphibole. Epidote, muscovite, apatite and zircon may also be present. Plagioclase shows more variation in composition than in the pelites, ranging from albite-oligoclase to andesine.

(3) Calcareous Xenoliths.

These are characterized by the minerals clinzoisite and epidote, and they are accordingly yellowish-green in hand specimen. The grain size is fine and most of the minerals are xenoblastic. Some xenoliths are made up mostly of quartz and clinzoisite, with accessory tremolite, and others (richer in iron) consist of quartz and yellow-green epidote, with a little actinolite. Reaction-zones of such xenoliths consist of biotite, quartz, plagioclase and hypersthene. It is possible that some of the quartz-feldspar-hypersthene assemblages previously noted may have been calcareous types which have suffered much reaction with the magma.

(4) Xenoliths of Igneous Origin.

Very few of the xenoliths are of definite igneous origin. A former basalt or dolerite is represented by a hypersthene-plagioclase-magnetite rock with blastophitic fabric. A reaction-rim, one-fifth of the diameter of the xenolith, consists of biotite, quartz and plagioclase.

A plagioclase-hypersthene-quartz-biotite xenolith, similar in mineralogical composition to some derived from pelites, differs from them in its texture and complete lack of evidence of former bedding. Occasional large plagioclases are intergrown with quartz, and the hypersthene in these xenoliths is notable for its strong pleochroism. The chemical analysis (Table 3) corresponds to that of an igneous rock, e.g., an andesite.

(5) Granitized Xenoliths (quartz-feldspar-biotite assemblages).

There are numerous xenoliths containing the same minerals as the granodiorite, but showing no signs of bedding. They are of slightly finer grain size than the granodiorite and more melanocratic. At Cowra, a few transition types between sedimentary xenoliths and "igneous-looking" xenoliths have been found.

ORIGIN OF THE XENOLITHS.

(a) Sedimentary Xenoliths other than those of the Silica-Poor Group (1a, 2 and 3 above).

As the Silurian wall-rocks are not greatly affected by the intrusion, and all xenoliths (even near the margin of the intrusion) have suffered fairly high-grade metamorphism, it is likely that the sedimentary ones have been derived from Ordovician or older sediments occurring at depth, and have been carried upward by the magma, i.e., they are hypoxenoliths (Goodspeed, 1948).

The mineral assemblages of the pelitic xenoliths indicate an abundance of iron oxides, magnesia and alumina. It is not certain, however, that the original sediment was abnormally high in these oxides, for we do not know to what extent chemical change has affected the composition. Garnet in the pelitic xenoliths probably occurred in the country rock before it was enclosed in the magma, and may have been a constituent of pre-existing regionally metamorphosed schists. When isolated from the xenoliths by mechanical disintegration, it is found in the granodiorite encased in a reaction rim of biotite and, less commonly, hypersthene and magnetite (Plate vii, fig. 4). The pelitic xenoliths of Cowra differ from those of Albury mainly in the amount of plagioclase in the former, indicating that the original pelites at Cowra were richer in soda and lime.

TABLE 3.

	1	2	
SiO ₂ ..	59.44	59.20	
Al ₂ O ₃ ..	14.27	15.98	
Fe ₂ O ₃ ..	0.45	3.30	
FeO ..	8.48	3.69	
MgO ..	4.84	3.10	
CaO ..	5.61	7.02	1. Hypersthene - plagioclase - biotite - quartz
Na ₂ O ..	3.47	3.31	xenolith. The Beacon, Cowra. Anal. N. C.
K ₂ O ..	0.95	1.26	Stevens.
TiO ₂ ..	1.35	0.55	2. Hypersthene andesite. Blair Duguid, N.S.W.
P ₂ O ₅ ..	pd.	0.17	Anal. H. P. White. W. E. Browne and
MnO ..	0.10	0.30	H. P. White, <i>J. Proc. Roy. Soc. N.S.W.</i> , 60
H ₂ O+ ..	0.75	1.13	(1926): 372.
H ₂ O- ..	0.22	0.73	
Etc. ..	—	0.48	
	99.93	100.22	
S.G. ..	2.86	2.74	

The psammites and psammopelites also show the same tendency, as shown by the presence of intermediate plagioclase and occasional diopside, epidote and clinozoisite. The calcareous xenoliths, with their high proportion of quartz, appear to have been calcareous sandstones or tuffs.

(b) Igneous Xenoliths.

The few igneous xenoliths that have been found seem to have been derived from basalts and andesites (Table 3), probably of Ordovician age, similar to types outcropping a few miles north-east of Cowra.

(c) Granitized Xenoliths (5, above).

It is considered from the general features of texture and constitution that these types could be either (a) cognate xenoliths or (b) sedimentary xenoliths showing a high degree of reaction with the magma, i.e., granitization. Grout (1937) cites much evidence to show that sedimentary xenoliths can be converted to "igneous-looking" rocks having the same minerals as the enclosing rock and thus being in complete equilibrium with the surrounding magma. The texture may be finer-grained, with the occurrence of "phenocrysts". In view of the transition between sedimentary and igneous-looking xenoliths (mentioned above) it is possible that the more siliceous pelites gave

rise to the quartz-felspar-biotite assemblage (after granitizing reaction), while the pelites with 50%-60% silica were the source of the silica-poor xenoliths (see next paragraph).

(d) Silica-poor Xenoliths (1a).

The silica-poor xenoliths, represented by those containing spinel in association with cordierite or sillimanite or both, are very similar to those described by Joplin (1947) from gneiss contaminated by Ordovician sediments at Albury, N.S.W. The occurrence of spinel-bearing xenoliths in a rock with nearly 67% SiO₂ is unusual, especially when

TABLE 4.

	1	2	3	4	5	6	7	8
SiO ₂	43.11	44.52	45.30	42.08	40.16	62.23	70.17	69.98
Al ₂ O ₃	32.61	28.63	30.51	32.40	29.50	12.20	13.00	12.74
Fe ₂ O ₃	0.68	1.78	0.24	13.44	19.66	6.49	5.22	6.25
FeO	7.51	10.75	8.80		5.80	0.84	1.26	
MgO	3.93	4.14	3.11	3.30	tr.	3.07	1.83	4.19
CaO	2.90	1.25	0.90	1.42	0.85	3.23	0.32	0.76
Na ₂ O	0.77	3.21	1.65	1.60	1.46	3.21	1.15	pnd.
K ₂ O	6.01	2.69	4.84	2.20	1.36	2.48	3.17	pnd.
TiO ₂	2.06	2.05	1.48	2.16	—	1.30	0.97	0.82
P ₂ O ₅	pnd.	0.03	0.12	—	—	pnd.	0.14	pnd.
MnO	0.10	tr.	0.20	—	—	0.14	0.06	0.23
H ₂ O+	0.62	0.45	1.05	1.60	—	3.34	2.47	—
H ₂ O-	0.25	0.20	0.26		—	—	2.07	0.96
S	—	0.27	1.32*	—	0.82	—	—	—
SO ₂	—	tr.	0.04	—	—	—	—	—
Etc.	—	—	0.30	—	—	—	—	—
	100.55	99.97	100.12	100.20	99.61	100.60	100.72	—
S.G.	2.89	—	2.835	—	—	2.54	2.62	2.69

* 0.36% FeS₂ and 0.96% Fe₂S₃.

1. Cordierite-sillimanite-spinel xenolith. $\frac{1}{2}$ mile N. of Cowra Post Office. Anal. N. C. Stevens.
 2. Cordierite-spinel hornfels, at contact with diorite. Craig More, Comrie, Scotland. Anal. C. E. Tilley. *Quart. J. Geol. Soc. Lond.*, 80, 1924: 22.
 3. Corundum-cordierite-spinel hornfels. Ascunty Mtn., Vermont. Anal. W. F. Hillebrand. R. A. Daly, *U.S. Geol. Surv. Bull.*, 209, 1903: 29.
 4. Cordierite-hornfels. N. end of Black Hill, Aberdeenshire. Anal. J. J. H. Teall, *Geol. Surv. Gr. Brit.* (Braemar), 1912: 16.
 5. Manhattan Schist, on contact of Cortlandt Series. Anal. F. L. Nason. G. H. Williams, *Amer. J. Sci.*, 36, 1888: 259.
 6. Slate (buff-coloured, somewhat weathered). Cowra Brickworks Quarry.
 7. Slate (buff-coloured). Mining Reserve, Burdett; N.N.W. of Canowindra.
 8. Phyllitic slate (greenish-coloured). Cowra Brickworks Quarry.
- Analyses 6, 7 and 8 by N. C. Stevens.

there is an apparent lack of silica-poor sediments among the country rocks. The acidity of the Cowra Granodiorite is comparable with that of the Albury Gneiss, and it is to be noted that no silica-poor sediments have been found near Cowra. Analyses of slates from the Cowra district (Table 4) show that they are even more siliceous than the normal pelites at Albury.

Dr. Joplin suggests that the silica-poor xenoliths were derived from chlorite-rich bands or knots, the latter being formed by segregation during contact metamorphism. Xenoliths derived from these knots would be limited in size, and would not show bedding. At Albury, iron oxides, alumina and magnesia are higher in an analysed silica-poor xenolith than in the average normal pelite (and silica is lower). According to Dr. Joplin, "storing up of these constituents within the xenolith . . . may be accounted for by assuming that certain minerals lower in the reaction series than those being

precipitated by the magma were dissolved out, thereby enriching the xenolith in phases higher in the reaction series".

These ideas are similar to those expressed by Tattam (1925), when dealing with silica-poor xenoliths in the granodiorite of Bulla, Victoria. Quartz is melted out of quartz-chlorite-sericite xenoliths and plagioclase crystallizes within them, so that they are desilicated, with the formation of sillimanite and spinel.

It is difficult to imagine these processes taking place without complete disintegration of the xenolith, and if such a disruption did not occur, why should the quartz have shown such a marked tendency to leave the xenolith and enter the magma?

An analysis of a typical silica-poor xenolith from Cowra is compared in Table 4 with rocks of similar composition and with some Silurian slates.

Such changes have been illustrated by Daly (1903), who described a progression in contact metamorphism in the same lithologic unit at Ascutey Mtn., Vermont. Variation from phyllite to corundum-cordierite-spinel hornfels occurred as the contact with an intermediate plutonic rock was approached.

Reynolds (1946) has shown that pelitic rocks undergo changes in two stages, first desilication then granitization; also that during desilication there is commonly an introduction of Fe, Mg, Ca and one or more of TiO_2 , P_2O_5 and MnO. Iron and magnesia are regarded as constituents driven from country rocks which have been granitized; however, the abnormal alumina percentages noted above remain unexplained. Read (1951) gets closer to this problem by suggesting that in certain cases "NaSi has been extracted with consequent piling up of $AlFeMg$ " and that some occurrences of highly aluminous rock might be due to subtractions connected with metamorphic differentiation.

Acknowledgements.

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EXPLANATION OF PLATE VII.

1. Cowra Granodiorite ($\times 30$).
2. Granodiorite porphyry (crossed nicols, $\times 30$).
3. Cordierite-sillimanite-spinel xenolith ($\times 50$).
4. Magnetite and hypersthene at the margin of a garnet xenocryst in the granodiorite ($\times 60$).
5. Clinzoisite-quartz xenolith ($\times 50$).
6. Sillimanite-spinel xenolith ($\times 50$).
7. Spinel bordering sillimanite in a xenolith ($\times 60$).
8. Intergrowth of biotite and cordierite in a mottled pelitic xenolith ($\times 30$).

Photomicrographs by G. E. McInnes and N. C. Stevens.

ROPY SMUT OF LIVERPOOL PLAINS GRASS.

By DOROTHY E. SHAW,

Faculty of Agriculture, University of Sydney.

(Plate viii; one Text-figure.)

[Read 30th July, 1952.]

Synopsis.

A smut attacking Liverpool Plains Grass (*Stipa aristiglumis* F. Muell.) is described from the north-western slopes of New South Wales. Another grass (*Stipa* sp. (?)) was also found attacked. The spore balls of the fungus develop in, and ultimately replace, the parenchyma of the stem, so that when the balls are released at maturity, the separated vascular bundles give the stem a ropy appearance.

Germination of the smut was obtained in water, sporidia were produced on dextrose agar medium, and the fungus was obtained in pure culture. The nuclear condition of the promycelium and sporidia was determined. The name *Tolyposporium restifaciens* is proposed for the fungus.

In 1950 diseased specimens of Liverpool Plains Grass (*Stipa aristiglumis* F. Muell.) were collected in the Piallaway area of the north-western slopes of New South Wales. The causal organism did not appear to conform to any previously described on species of *Stipa* or on any other grass. The disease was tentatively described as "Ropy Smut". Further collections of diseased material have since been made throughout the area, as follows:

TABLE 1.

S.U. Acc. No.	Date Collected.	Collector.	Locality.	Host.
241	28. 8.50	D. Shaw and A. L. Dyce.	Piallaway.	<i>S. aristiglumis</i> .
534	10. 7.51	D. Shaw.	Breeza Plains.	<i>S. aristiglumis</i> .
535	10. 7.51	D. Shaw.	Piallaway.	<i>Stipa</i> sp. (?).
681	23.10.51	P. G. Valder.	Gunnedah.	<i>S. aristiglumis</i> .
693	10.12.51	G. Dickson.	Breeza Plains.	<i>S. aristiglumis</i> .

Stipa aristiglumis is a native perennial grass, and on the north-western slopes forms large tussocks usually about six feet in height. The grass collected as S.U. Accession No. 535 consisted of diseased stems and some unaffected heads, with, however, only the glumes remaining. The clumps of this grass were about 1-1½ feet high, in an area where *S. aristiglumis* was about five feet high. The specimen was thought to be a small species of *Stipa*, but after examination Miss Vickery of the Botanic Gardens stated that even the generic identification was uncertain. It was not, however, *S. aristiglumis*.

SYMPTOMS.

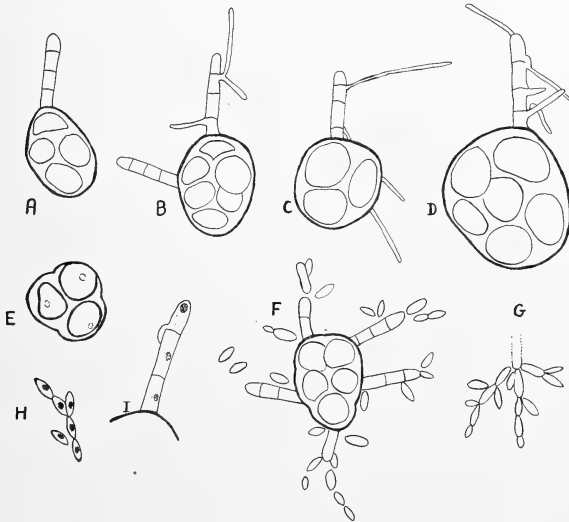
Macroscopically, the disease is not obvious as a smut. Diseased stems resemble lengths of teased-out, twisted rope. In the specimens of *S. aristiglumis* only the upper internode had the ropy appearance (Plate viii, A). Several internodes of the grass stems of S.U. Accession 535, however, were diseased, with the vascular bundles held together at the nodes.

The disease could not at first be easily detected in the green stems as no "teasing-out" appeared at this stage,

THE CAUSAL ORGANISM AND LOCATION IN THE HOST.

The spore balls of the fungus are dusty at maturity and brown (Sandford's Brown; Ridgway, 1912) to the naked eye. In most cases the balls are slightly longer than broad, and from *S. aristiglumis* measure $18-28 \times 20-38 \mu$, being composed of 5-15 spores permanently united. Balls from S.U. Acc. 535 measure $18-40 \times 26-40 \mu$, composed of 7-26 spores permanently united. The spores are yellowish (Raw Sienna; Ridgway, 1912) in reflected light, and $8-10 \mu$ in diameter. They are subglobose to slightly angular, with adjacent and free sides smooth.

Transverse sections were made through diseased stems of *S. aristiglumis* of the current season's growth, in order to trace the extent of the fungus and its location in the host tissues. At a position one inch from the tip most of the spore balls were pigmented, and some remained unstained with cotton-blue lacto-phenol. The average



Text-fig. 1.

A-D, Germination of *T. restifaciens* in water, showing strongly septate promycelia with thin lateral and terminal branches. E, Surface view of small spore ball with one germ pore per spore. F, Germination on P.D.A. after presoaking in water, showing production of abundant promycelia and sporidia (slightly displaced during staining). G, Budding sporidia on P.D.A. H, Budding sporidia from culture with one nucleus per cell. Stained with Giemsa. I, Promycelium with one nucleus per cell. Stained with Giemsa. Camera lucida drawings, $\times 700$.

width of the spore balls was 19μ . Nearly all the parenchymatous tissue between the bundles was replaced by the spore balls, but the epidermis was still intact. A section through this region is shown in Plate viii, B.

Sections taken at various intervals down the stem revealed that, as the distance from the tip increased the spore balls became less pigmented, smaller in size, contained fewer spores, and were not nearly so numerous as at the tip. In sections 12 inches from the tip and four inches above the uppermost node, the average width of the spore balls was 14μ , and many of the balls consisted of a few spores only. Many parenchyma cells were still identifiable as such, with distorted cells surrounding developing spore balls. The balls were more widely scattered throughout the parenchyma, with the concentration heaviest at the centre. No spore balls at all could be detected in the area 1-2 inches above the uppermost node or in the lower

internodes. In S.U. Acc. 535, however, development of the organism had proceeded beyond the first internode from the tip, and spore balls had replaced most of the parenchyma of the lower internode. Longitudinal sections through the diseased internodes revealed that spore balls were placed with the long axes parallel to the stem.

At maturity, when the spore balls have replaced all the parenchyma, they are released as a brown dust, and the vascular bundles, without any connecting tissue, remain to give the stem the ropy appearance.

GERMINATION.

One germ pore is located in the centre of the free side of each spore, and is most easily seen after the spore balls have been soaking for several days. Germination was obtained in water after three-six days. Up to five promycelia were noted from individual spore balls, each promycelium arising from a separate spore. Usually, however, one or two promycelia only were recorded from each spore ball. The promycelia were short (10-22 μ long and 2-4 μ wide), straight and three-septate. Young promycelia stained deeply with cotton-blue lacto-phenol. Thin branches were produced at the sides of the promycelia, either at or near the septa, and more rarely from the tip. Some branches arose at an acute angle, and as these hyphae elongated the promycelia became vacuolated. No development past this occurred in water, and no sporidia were detected. Spore balls dusted dry on to agar medium failed to germinate.

Sporidial production was induced, however, by presoaking spore balls in water until some spores had produced promycelia (about three days). The spore balls (both germinated and ungerminated) were then transferred to potato dextrose agar plates. Within twenty-four hours many promycelia were produced with abundant sporidia (Plate viii, D and E). No thin hyphal branches were produced at all. A colony developed around each spore ball by the production of chains of budding sporidia, in size 4-6 \times 1-2 μ . Germination on P.D.A. was fairly similar to that recorded by Kamat (1933) for *Tolyposporium filiferum* in sterile distilled water (his illustrations A, B, D in fig. 2).

Colonies were isolated and obtained in pure culture, being maintained on P.D.A. On this medium the colonies were dirty-white in colour, waxy and opaque. The edge was smooth and slightly lobed, with the centre of the colony becoming evenly convoluted by the masses of cells produced.

THE NUCLEAR CONDITION.

The promycelia and sporidia were stained with Giemsa after the method used by Knaysi et al. (1950) for bacteria, and which has been adapted for fungi (Shaw, unpublished).

One chromatinic body was observed in each cell of the promycelium (Text-fig 1, I) and in the sporidia. The nuclear condition of old and young cells produced on P.D.A. is shown in Plate viii, F, and Text-fig. 1, H.

NAME OF THE CAUSAL ORGANISM.

The production of a strongly septate promycelium with lateral and terminal sporidia, places the organism in the Ustilaginaceae, and as the spores are firmly united into balls, with the sori dusty and not agglutinated; *Thecaphora* and *Tolyposporium* appear to be the closest genera.

Germination in *Thecaphora*, however, is difficult to obtain (Barrus, 1944), and when it does occur is usually by a promycelium with a simple terminal sporidium (Clinton, 1902), although Woronin in 1882 (as cited by Ainsworth and Sampson, 1950) recorded the production of thin branches from a septate promycelium for *T. seminis-convoluti*. The sori of *Tolyposporium* are usually located in the inflorescence, and are usually darker than the sori of *Thecaphora*. The organism does not conform entirely to either genus, but the production of abundant lateral sporidia seems to indicate a closer affinity to *Tolyposporium* than to *Thecaphora*. Dr. Ellis, of the

Commonwealth Mycological Institute, Kew, who very kindly examined specimens, also agreed that this type of germination is in favour of the fungus being placed in *Tolyposporium* rather than in *Thecaphora*.

Because of the rope-like appearance of the diseased host, the name *Tolyposporium restifaciens* is proposed for the causal organism.

TOLYPOSPORIUM RESTIFACIENS, n. sp.

Sori between the lignified tissue of the internodes; spore balls dusty at maturity, brown (Sandford's Brown) to the naked eye, $18-40 \times 20-40 \mu$, composed of 5-26 spores permanently united; spores yellowish (Cadmium yellow) in reflected light, $8-10 \mu$ in diameter, subglobose to slightly angular, with adjacent and free sides smooth; promycelia with thin lateral and terminal branches in water, or with lateral and terminal sporidia on potato dextrose agar after presoaking in water.

Habitat.—In stems of *Stipa aristiglumis* F. Muell. and another unidentified grass.

Type.—S.U. Accession No. 693 collected at Breeza Plains, N.S.W., and held at University of Sydney. (Material also lodged at the C.M.I. as Herb. I.M.I. No. 47686.)

Distribution.—North-western slopes of New South Wales.

Tolyposporium restifaciens, sp. n.

Sporae in glomerulos arcte coacervate pulverulentos cum maturi, $18-40 \times 20-40 \mu$, conflatos e 5-26 sporis perpetuo conjunctis; sporae fulvae, $8-10 \mu$, nunc subgloboasae nunc subangulatae, adhaerenti et libero latere leves; promycelis in aqua ramis tenuibus a latere et a termino, in solido quodam lateralibus et terminalibus sporidiis praeditae.

Habitat.—In caulibus *Stipae aristiglumis* F. Muell.

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EXPLANATION OF PLATE VIII.

- A. Ropy Smut (*Tolyposporium restifaciens*) on Liverpool Plains Grass (*Stipa aristiglumis*). $\times \frac{1}{2}$.
 B. Transverse section through green stem one inch from the tip, showing spore balls replacing the parenchyma. Stained with cotton-blue lacto-phenol. $\times 100$.
 C. Spore balls of *T. restifaciens*. $\times 200$.
 D. Germination of spore ball on P.D.A., with septate promycelia and budding sporidia, which are slightly displaced owing to staining with cotton-blue lacto-phenol. $\times 500$.
 E. Colony of budding sporidia developing around germination spore ball on P.D.A. Stained with cotton-blue lacto-phenol. $\times 250$.
 F. Budding sporidia from culture stained with Giemsa showing one nucleus per cell. $\times 1000$.
 G. Pure culture of *T. restifaciens* on P.D.A. $\times 1$.

REVISION OF THE GENUS *CALOTIS* R.BR.

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(One hundred and forty-five Text-figures.)

[Read 30th July, 1952.]

Synopsis.

Twenty-two species of *Calotis* are redescribed and figured from a large range of material, and four species are reduced to synonymy. Two former varieties have been raised to specific status, but it has not proved necessary to describe any new species.

An introductory section includes a brief historical account of the genus and also a description of the procedure adopted and a discussion of all characters shown by the plants from the point of view of their taxonomic importance. Attention is drawn to the correlation between distribution and the burr-like qualities of the fruits, in support of which certain extra-Australian records are cited.

INTRODUCTION.

Historical.

The first reference to *Calotis* is in the Botanical Register, 6 (1820) 504, the text of which was written by J. Bellinder Ker (alias Ker Gawler) and is as follows: "the character of *Calotis* was formed, but not published, by Mr. Brown, about 15 years ago, from *C. dentex*, a species first observed by himself in New Holland, where it is not uncommon in the neighbourhood of Port Jackson. The present (i.e., *C. cuneifolia*) has since been found during an expedition into the interior of the above country, growing on the banks of the river Lachlan, in 1817, by Mr. Allan Cunningham, who is commended by Mr. Brown as 'an indefatigable collector and acute observer'. The generic name has been derived from the two membranous ear-shaped paleae of the seed-crown, which are constant in number and form in the only two certain species yet known, and constitute the most important character of the genus."

The nineteenth century was a period of great activity in the description of new genera and species, as the country was opened up and the collection of specimens became more extensive. Inevitably a number of these names have since been shown to be synonyms. In *Calotis*, as in other genera, with the description of each new species the generic characters were modified accordingly, and the original description of Brown was shown to apply only to the two species he handled. No reflection is implied on this or other pioneer work, since generic characters cannot be recognized as distinct from specific in an unfamiliar group with very limited material. In this instance, Brown considered that the pappus scales "constitute the most important character of the genus" and the significance of the awns was only determined when further material representing other species was collected. It was left to Bentham (1866), in collaboration with Mueller, to collate much independent work and define the genus in its current sense, incorporating in it three other genera, *Huenefeldia*, *Goniopogon* and *Cheiriloma*.

Below (p. 147) is a chronological list of all described species and synonymous genera, discussion of which will be found under the appropriate species headings. Extra-Australian species are included for the sake of completeness.

Distribution.

Apart from two species from Annam (*C. Gaudichaudii* Gagnep and *C. anamitica* Merrill) and one from China (*C. caespitosa* Chang), the genus is confined to the mainland of Australia where it is widespread in inland areas.

Certain species are notorious for their burr-like fruits which, at maturity, are loosely held in the infructescence and become readily attached to passing animals by their barbed awns. These are the species which possess the widest distribution and are found in coastal districts as isolated plants near railway lines, stock routes or stock

Date.	Name.	Type Locality.	Collector.	Current Name.
1820	<i>Calotis dentex</i> R.Br.	Neighbourhood of Port Jackson.	R. Brown.	<i>C. dentex</i> R.Br.
	<i>C. cuneifolia</i> R.Br.	Lachlan River.	A. Cunningham.	<i>C. cuneifolia</i> R.Br.
1836	<i>C. dilatata</i> DC.	Near Peel's Ra., Exley, etc.	A. Cunningham.	<i>C. cuneifolia</i> R.Br.
1837	<i>C. breviseta</i> Benth.	Swan R. and King George's Sound.	F. Bauer.	<i>C. breviseta</i> Benth.
	<i>C. lappulacea</i> Benth.	Swan R. and King George's Sound.	F. Bauer.	<i>C. lappulacea</i> Benth.
	<i>C. microphylla</i> Benth.	Swan R. and King George's Sound.	F. Bauer.	<i>C. ? lappulacea</i> Benth.
1840	<i>Huenefeldia coronopifolia</i> Walp.	New Holland.		<i>C. ? glandulosa</i> F. Muell.
	<i>H. angustifolia</i> Walp.	New Holland.		<i>C. ? erinacea</i> Steetz.
1845	<i>C. erinacea</i> Steetz.	Hay, W.A.	L. Preiss.	<i>C. erinacea</i> Steetz.
1848	<i>C. scapigera</i> Mitch.	Between Sydney and the Gulf of Carpentaria.	T. L. Mitchell.	<i>C. scapigera</i> Mitch.
1851	<i>Goniopogon multicaulis</i> Turcz.	W.A.	Drummond.	<i>C. multicaulis</i> (Turcz.) Druce.
1852	<i>Cheiroloma hispidulum</i> F. Muell.	Cudnaka and Crystal Brook.	F. Mueller.	<i>Calotis hispidula</i> F. Muell.
	<i>Calotis cymbacantha</i> F. Muell.	Crystal Brook.	F. Mueller.	<i>C. cymbacantha</i> F. Muell.
	<i>C. Muelleri</i> Sond.	Cudnaka.	F. Mueller.	<i>C. scabiosifolia</i> F. Muell.
	<i>C. polyseta</i> Sond.	Cudnaka.	F. Mueller.	<i>C. lappulacea</i> Benth.
	<i>C. scabiosifolia</i> Sond. et F. Muell.	Wilpena, S.A.	F. Mueller.	<i>C. scabiosifolia</i> Sond. et F. Muell.
1855	<i>C. hispidula</i> F. Muell.	Crystal Brook.	F. Mueller.	<i>C. hispidula</i> F. Muell.
	<i>C. anthemoides</i> F. Muell.	Station Peak.	F. Mueller.	<i>C. anthemoides</i> F. Muell.
	<i>C. glandulosa</i> F. Muell.	Snowy R. near Monaro.	F. Mueller.	<i>C. glandulosa</i> F. Muell.
1859	<i>C. plumulifera</i> F. Muell.	Murray Plains.	F. Mueller.	<i>C. multicaulis</i> (Turcz.) Druce.
	<i>C. tropica</i> F. Muell.	N.W. Australia.	F. Mueller.	<i>C. breviseta</i> Benth.
1861	<i>C. palmata</i> A. Gray.	Hunter R., N.S.W.	A. Gray.	<i>C. cuneifolia</i> R.Br.
1866	<i>C. microcephala</i> Benth.	Murray and Darling Rivers.	F. Mueller.	<i>C. porphyroglossa</i> F. Muell.
	<i>C. porphyroglossa</i> F. Muell.	Cooper's Creek.	Murray.	<i>C. porphyroglossa</i> F. Muell.
	<i>C. pterosperma</i> F. Muell.	Islands of the Gulf of Carpentaria.	R. Brown.	<i>C. breviseta</i> Benth.
1881	<i>C. Kenpei</i> F. Muell.	Finke R.	H. Kempe.	<i>C. Kenpei</i> F. Muell.
1890	<i>C. latiuscula</i> F. Muell. et Tate.	Finke R.	H. Kempe.	<i>C. latiuscula</i> F. Muell. et Tate.
1901	<i>C. inermis</i> Maiden et Betche.	Urising, N.S.W.	E. Betche.	<i>C. inermis</i> Maiden et Betche.
1917	<i>C. multicaulis</i> (Turcz.) Druce.	W.A.	Drummond.	<i>C. multicaulis</i> (Turcz.) Druce.
1921	<i>C. ancyrocarpa</i> J. M. Black.	Murteree, Strzelecki Creek.	S. A. White.	<i>C. ancyrocarpa</i> J. M. Black.
	* <i>C. Gaudichaudii</i> Gagnep.	Annam, Tourane.	Gaudichaud.	<i>C. Gaudichaudii</i> Gagnep.
1929	<i>C. suffruticosa</i> Domin.	Jericho, Q.	Domin.	<i>C. lappulacea</i> Benth.
	* <i>C. xanthosoidea</i> Domin.	Jericho, Q.	Domin.	<i>C. xanthosoidea</i> Domin.
1930	* <i>C. anamitica</i> Merrill.	Tourane, Annam.	O. Kuntze.	<i>C. anamitica</i> Merrill.
1937	* <i>C. caespitosa</i> Chang.	Ngai district, China.	H. Y. Liang.	<i>C. caespitosa</i> Chang.
1946	<i>C. glabrescens</i> C. T. White.	Bybera, Q.	C. T. White.	<i>C. glabrescens</i> C. T. White.
	<i>C. scabriuscula</i> C. T. White.	Chesterton, Q.	S. T. Blake.	<i>C. dentex</i> R.Br.
	<i>C. squamigera</i> C. T. White.	Goondiwindi, N.S.W.	C. T. White.	<i>C. squamigera</i> C. T. White.
1952	<i>C. cuneata</i> (F. Muell. ex Benth.) G. L. Davis.	Rockhampton.	Thozet.	<i>C. cuneata</i> (F. Muell. ex Benth.) G. L. Davis.
	<i>C. breviradiata</i> (E. H. Ising) G. L. Davis.	Hughes, Nullabor Plains.	E. H. Ising.	<i>C. breviradiata</i> (E. H. Ising) G. L. Davis.

* These species have not been examined by the present writer.

yards. Cheeseman (1925) recorded *C. lappulacca* from "various ports in the North and South Islands of New Zealand", where it doubtless gained entrance with Australian imports, probably wool. In this connection a specimen of *C. squamigera* from Galashiels, Scotland, is interesting since it is from a collection of alien plants growing in that locality from seed brought in with Australian wool.

It is probable that the wide distribution of some species is a recent development and that prior to the arrival of white settlers and their domestic animals, their ranges were considerably more confined and approximated the present ones of those species whose fruits are not so readily transported.

Economic Importance.

Although most species are highly drought resistant and of good fodder value, the most common are regarded with disfavour by graziers since their burr-like fruits are troublesome in wool. *C. hispidula* is variously described in collectors' notes as "wonderful fodder", "very excellent fodder", "a very bad burr", and "one of the worst pests in the district". Maiden (1920) stated that the burrs of *C. cuneifolia* "greatly injure wool, besides being a source of great irritation to man and domestic animals", while Johnston and Cleland (1943) reported of *C. porphyroglossa*, *C. ancyrocarpa* and *C. multicaulis* that "the awns of the fruits are troublesome to the natives".

Species are referred to in different districts as Daisy Burr, Martagai, Bogan Flea, Bindie, and Bindy Eye.

Nomenclature.

Syntype material of the majority of species and varieties has been examined and lectotypes selected. When this was not possible, the meaning of the name was established by comparison between the original description and the supposed population. "Flora Australiensis" was used extensively in this connection since, as well as the type specimens, Bentham listed a number of others, of which duplicates exist in the National Herbarium, Melbourne, and these have served as a useful basis of comparison in the absence of the type.

Categories.

In general, the principles formulated in an earlier paper (Davis, 1948) have been followed, but intraspecific variation in the size and form of the fruits is wider than in *Brachycome*. This is reflected in the comparatively large number of varieties which have been described at various times. One species in particular, *C. erinacea*, has presented considerable difficulty, but to subdivide it in any way would be to anticipate evolution, since variation is continuous in both fruits and vegetative characters, and the species is best regarded as polytypic.

In only two species has the category "variety" been employed since it implies fixed vegetative variation with a sharp discontinuity separating it from the parent species on vegetative characters.

Specific Descriptions.

All species have been redescribed from specimens loaned for that purpose by the various public herbaria of Australia and a number of private collectors, and in each case the original meaning has been expanded. Where varieties exist, a general description embraces them and is followed by a key in which the parent population is given varietal rank with the specific epithet repeated.

The various measurements in the descriptions serve merely as a guide and have little or no meaning in themselves.

In each case the type locality and collector, as supplied in the original description, is quoted under "type data", and in the case of synonyms referred to in the discussions, this information is provided in brackets immediately following the first mention of the name.

Each description is accompanied by a figure of the habit and camera lucida drawing of the fruit, but where variation is considerable additional figures are provided.

Specimens Examined.

More than 900 specimens are quoted in the text but the number examined was considerably in excess of that figure. The source of each specimen is indicated as in previous papers (Davis, 1948; 1950) with the altered designation of one herbarium and the addition of two others:

State Herbarium, Perth	(P)
New England University College, Armidale	(NE)
Mr. K. Ingram, Mudgee	(KI)

Evaluation of Taxonomic Characters.

In each genus it is necessary to determine which characters are generic, which specific, and which tend to be rather an environmental expression than an indication of affinity. In order to revise a genus satisfactorily a large number of specimens must be examined from a wide geographic range which embraces a variety of climatic and ecological conditions. Ideally, representatives of each species should be grown under varying experimental conditions and statistical analyses carried out in the field. Due to a variety of reasons, however, taxonomists must rely chiefly on herbarium specimens, but despite the handicaps inherent in such a method, a high degree of accuracy can be achieved provided a sufficiently large series of specimens is available.

In a monotypic genus recognition of specific, as distinct from generic, characters is impossible and any attempt to do this, even by analogy with related genera, is little more than wishful thinking. In genera other than monotypic, specific criteria must be clearly established at the outset and adhered to consistently. The practice of describing one species on, say, fruit characters, another on leaf shape and a third on floral details is unsound taxonomic practice.

Characters of a plant which have survival value tend to be influenced by selection in such a way that affinities are obscured, and convergent evolution may lead to morphologically similar structures being shown by species which are not, in fact, closely related. For this reason the description of new species differing in only one character should be avoided, and such existing species should be viewed with suspicion. The most reliable primary taxonomic characters are those of the least survival value since they are not acted on by selection and therefore similarity in these is a reasonable guide to relationship. However, in practice, field determination is based on the indefinable "look" of a plant in which primary taxonomic characters play little or no part, and is based on the unconscious use of secondary taxonomic characters. These are ones which, in themselves, are variable, and alone are of little significance, but of which a certain combination tends to occur in a particular species. It is unfortunate that such a knowledge can only be gained by experience and the written word is of little assistance. It is hoped, however, that the extensive figures in the present paper will, in some measure, meet this need.

Under their respective headings, the various parts of *Calotis* are discussed in relation to their value and reliability in taxonomy.

Habit: This is a secondary taxonomic character whose value depends on the species concerned. For example, the number of scapigerous species of *Calotis* is limited, and the much-branched type of growth quite common, but in a perennial species a young plant may closely resemble, in habit, a fully grown annual. Since the habit is greatly influenced by the environment, care should be taken in comparing plants from different habitats.

Indumentum: The presence of septate hairs is a generic character though the amount of indumentum is variable.

Leaves: In their nature, form and number, leaves are an important secondary taxonomic character, though the effect of the environment on their form must be borne in mind. This is one of the most difficult characters to assess from herbarium specimens as usually no indication is given of the height of the plant. As a result, what are actually the upper leaves of a large plant may be inadvertently compared with the lower leaves of a small one and so lead to an erroneous conclusion since the marked variation

shown by some species concerns only the lower leaves. This variation is more striking in herbarium specimens than in the field.

Inflorescences: These may be solitary, axillary or arranged in cymose or racemose panicles so are to be regarded as a secondary taxonomic character which, together with habit and leaf form, are the characters generally used in field determination.

Involucral bracts: No marked differences were found in the shape or size of the involucral bracts in the various species and details of them were of no assistance in identification.

Ray florets: The colour of the ray florets, while of occasional assistance, is a character to be used with caution since on drying a change may occur from white to pink or blue, and from blue, pink or pale yellow to white on expanding from the bud. The deep yellow of *C. latiuscula* and others, however, is quite constant. Both *C. hispidula* and *C. squamigera* possess extremely minute rays which are usually exceeded by the stylar arms, but apart from these, the size of the ray is not a reliable character.

Disc florets: The colour and form of the disc florets are constant throughout the genus and in all but two species (*C. hispidula* and *C. squamigera*) their ovaries are abortive.

Receptacle: The degree of pitting varies with different species, but is an unreliable character to use in herbarium specimens since, on drying, shrinkage of the receptacle may influence considerably the depths of the pits. In both *C. scabiosifolia* and *C. cuneata* the tissue between the pits is extended to form 5-6 long scale-like structures around the base of each floret.

Fruits: Form, size and structure of the fruits constitute the primary taxonomic characters of *Calotis*, and of these, awn details are the most important. Since the awns are highly specialized structures with a very considerable survival value, they are of little or no guide to interspecific relationships and it is to be regretted that the only primary taxonomic characters found in this genus are ones so modified by selection.

TAXONOMY.

COMPOSITAE, tribe ASTEROIDEA.

CALOTIS R.Br., *Bot. Reg.*, t. 504 (1820).

Synonymy: *Huenefeldia* Walp., *Linnaea*, 14 (1840), 307; *Goniopogon* Turcz., *Bull. Soc. Nat. Mosc.*, 24 (1851), 173; *Cheiroloma* F. Muell., *Linnaea*, 25 (1852), 401.

Annual or perennial herbs, or occasionally sub-shrubs, with a varying amount of septate-hairy indumentum. *Leaves* entire or variously dissected, petiolate or sessile, radical and/or cauline. *Inflorescence* a capitulum, solitary, axillary or forming cymose or racemose panicles, heterogamous, rarely almost sessile. *Involucral bracts* green, septate-hairy on the outer surface, entire, and arranged in a compressed spiral to form 3 or occasionally 4 pseudowhorls. *Ray florets* female, ligulate, in 1 to several rows around the periphery of the capitulum; the rays white, pink, mauve, blue or yellow. *Stylar arms (ray)* linear, entirely receptive. *Disc florets* usually male with abortive ovaries, but hermaphrodite in two species, tubular, 5-toothed, yellow. *Stamens* 5, inserted on the corolla tube alternately to the teeth. *Anthers* obtuse at the base, with the connective extended beyond the level of the pollen sacs to form a lanceolate appendage. *Stylar arms (disc)* lanceolate, papillate, stigmatic lines only present in fertile florets and not enclosed by the arms. *Receptacle* hemispherical, pitted, naked except in two species where 5-6 scale-like filiform upgrowths surround the base of each floret. *Fruit*, an inferior achene, flattened, cuneate, smooth or tuberculate, glabrous or hairy. *Pappus* represented by awns which are usually rigid and armed with recurved barbs, but occasionally plumose and very rarely absent. Scales, alternating with the awns, are present in some species.

Type species, *Calotis cuneifolia* R.Br.

Key to the Species.

1. Pappus represented by rigid awns alternating with an equal number of scales, or awns absent.
2. Awns 2-5.
 3. Awns barbed only distally, otherwise smooth. Fruits glabrous.
 4. Scales broader than long. Body of the fruit with a few minute tubercles.
 5. Scales fringed at their free edges; awns 1-2, occasionally 3, with barbs in the form of a terminal arrow head. Erect sparsely branched perennials with broad-linear to oblanceolate, distally serrate or pinnatifid cauline leaves 1. *C. dentata*.
 - 5.* Scales infolded distally so as to appear entire; awns usually 2, occasionally 3-4, barbed along distal half. Erect much-branched perennials with cuneate cauline leaves which are distally lobed and basally auriculate 2. *C. cuneifolia*.
 - 4.* Scales longer than broad. Body of the fruit minutely but densely tuberculate. Erect or ascending perennials with pinnatifid leaves tapering into a broad petiole 4. *C. glandulosa*.
 - 3.* Awns very finely but densely barbed along their whole length.
 6. Erect perennials with ovate-cuneate to cuneate cauline leaves, which are proximally narrowed and auriculate, and distally coarsely serrate. Inflorescences on slender peduncles. Ray florets about 9 mm. long, disc florets sterile. Fruit glabrous; awns and scales 5-8, spreading, the scales entire and minutely ciliate at their free edges. Body of fruit sparsely and minutely tuberculate *C. xanthosoidea*.
 - 6.* Procumbent annuals with cuneate-spathulate cauline leaves on slender petioles and distally toothed. Ray florets minute, shorter than or hardly exceeding the stylar arms; disc florets fertile. Awns and scales 4-5, erect or spreading.
 7. Scales entire or very shallowly lobed; awns erect. Fruit glabrous, the body minutely and sparsely tuberculate. Inflorescences on extremely short peduncles so as to appear sessile 6. *C. squamigera*.
 - 7.* Scales deeply dissected, often obscured by hairs; awns spreading, proximally hairy. Body of fruit hairy. Inflorescences on slender peduncles 7. *C. hispida*.
 - 2.* Awns absent or in the form of a minute barbed lateral bristle arising from the collar-like circular scale. Body of the fruit tuberculate, glabrous. Erect branching perennials with oblanceolate mucronate-serrate and sessile cauline leaves 3. *C. Kempei*.
- 1.* Pappus represented by awns only; scales absent.
8. Fruits wingless.
 9. Awns robust and rigid.
 10. Awns 2-5, equal in length. Fruit hairy at the apex between and on the bases of the awns.
 11. Erect much-branched perennials with numerous cauline leaves. Bases of the awns expanded and united.
 12. Awns 2-4, coarsely barbed, when only 2, these arise in the same plane as the flattened face of the fruit. Fruit glabrous and smooth. Leaves sessile, broad-linear to linear-cuneate, serrate 8. *C. erinacea*.
 - 12.* Awns 2, arising at right angles to the flattened face of the fruit, barbs are replaced proximally by a few hairs. Body of fruit glabrous, tuberculate. Leaves sessile, broad-linear to spatulate, coarsely serrate to pinnatipartite 9. *C. cymbacantha*.
 - 11.* Stoliferous perennials with a basal cluster of linear to linear-lanceolate entire leaves. Fruits with 5 awns, distally finely barbed and proximally hairy, not united at base 15. *C. scapigera*.
 - 10.* Awns more than 4, of unequal length.
 13. Major awns 2-3, finely barbed distally.
 14. Major awns 2, at right angles to the flattened face of the fruit. Secondary awns barbed, in two groups of 3 and 1 or 5 and 3, members of each group shortly united at base, giving the fruit a 2-lipped appearance when viewed from above. Body of the fruit glabrous. Much-branched perennials with linear and entire or toothed to pinnatifid cauline leaves 10. *C. lappulacea*.
 - 14.* Major awns 2-3 with no constant arrangement. Secondary awns not barbed, hairy, unequal. Branched perennials with narrow-oblanceolate to linear leaves, entire or with a single lateral tooth 11. *C. glabrescens*.
 - 13.* Major awns 4 or more, usually barbed distally.
 15. Awns with expanded and united bases, coarsely barbed. Fruits glabrous and smooth. Erect perennials with sessile, broad-linear to linear-cuneate, serrate, cauline leaves 8. *C. erinacea*.
 - 15.* Awns free.
 16. Stoliferous perennials with a basal cluster of linear and entire or variously shaped and dissected radical leaves.
 17. Awns in a single ring, the longest distally barbed. Body of fruit with a central area of simple hairs or glabrous 12. *C. scabiosifolia*.
 - 17.* A second ring of fine plumose awns present within the first. Longest awns distally barbed or smooth; smaller awns with a few barbs or entirely hairy. Body of fruit tuberculate or hairy on central area 13. *C. cuneata*.

- 16.* Erect (?) perennials with numerous oblanceolate to cuneate cauline leaves, dentate or entire, sessile. Radical leaves only present on young plants. Fruits with an expanded hairy central cone; awns twisted in various directions, minutely barbed distally, hairy proximally 14. *C. latiuscula*.
- 9.* Awns fine and flexible, without barbs but with numerous short straight hairs. Branching annuals with cuneate, toothed, cauline leaves 16. *C. bicruris*.
- 8.* Fruits winged.
18. Body of fruits more or less hairy.
19. Awns coarsely barbed, 6-11, 0.5-1 mm. long; hairs on body and wing margins simple or forked.
20. Wings narrow, thick, not sharply demarcated, hairs along margins sparse. Awns equal to or slightly exceeding the central cone. Branching perennials with linear to narrow-oblanceolate entire cauline leaves 17. *C. breviseta*.
- 20.* Wings expanded and sharply demarcated, with numerous long hairs along wing margins. No central cone present on fruit. Branching annuals with narrow-cuneate to cuneate cauline leaves, toothed or acutely lobed .. 18. *C. porphyroglossa*.
- 19.* Awns entirely barbed or barbs replaced by very short straight hairs, 12-24, 0.5-2.5 mm. long; hairs on body and wing margins simple or plumose.
21. Awns equal to or exceeding the length of the body of the fruit, fine and flexible, with short straight hairs or finely barbed; bases of the awns obscured by long white plumose hairs of the body and fruit apex. Plumose hairs form a dense border to the wings. Branching annuals with narrow-cuneate to cuneate distally toothed cauline leaves 19. *C. multicaulis*.
- 21.* Awns shorter than the body of the fruit, stiff but not rigid, with straight hairs along their whole length giving a plumose appearance, not barbed. Body and wing margins bear long stiff straight hairs; wings distally concave, their apices incurved. Sparsely branching (?) annuals with cuneate, distally toothed cauline leaves 21. *C. breviradiata*.
- 18.* Body of fruits glabrous.
22. Wings much expanded, anchor-shaped, with long simple hairs fringing their outer margins. Awns 15-25, 1-1.7 mm. long, stiff, with a few apical barbs and the remainder occupied by long simple hairs. Branching annuals with broad-linear to oblanceolate cauline leaves, with a few linear lobes 20. *C. ancyrocarpa*.
- 22.* Wings narrow, glabrous. Awns 7-14, 0.2-2 mm. long, rigid, minutely barbed distally, finely hairy proximally; apex of fruit forms a hairy and conspicuous central cone. Stoliferous perennials with a basal cluster of bipinnatisect radical leaves with long petioles 22. *C. anthemoides*.

1. CALOTIS DENTEX R.Br., *Bot. Reg.*, 6 (1820), 504. (Text-figs. 1-14.)

C. scabriuscula C. T. White, *Proc. Roy. Soc. Q.*, 57 (1946), 31.

Type data: "In the neighbourhood of Port Jackson", R. Brown.

Lectotype, Port Jackson, R. Brown (MEL).

Erect branching septate-hairy perennials up to 82 cm. high. *Lower cauline leaves* up to 8 cm. long, very broad-linear to oblanceolate, distally serrate or dentate, occasionally pinnatifid with acute lobes 1.5 cm. long, 3 mm. broad. *Upper leaves* usually entire. *Inflorescences* up to 50, 1.1-3 mm. diameter, on axillary peduncles. *Involucral bracts* 9-15, 5.5-10 mm. long, 2.5-4 mm. broad, lanceolate to ovate, with acute to acuminate apices and entire margins. *Ray florets* up to 73, the rays 10 mm. long, 1.2 mm. broad, white. *Receptacle* 1.5-1.9 mm. high, hemispherical and shallowly pitted. *Fruits* reddish-brown, the body cuneate, 1.7-2.2 mm. long, 1.2-1.6 mm. broad, flattened, smooth or minutely papillate on each face. Pappus scales 2, broader than long and fringed distally, alternating with 2 distally barbed awns, 4.2-6.6 mm. long. Occasionally 3 awns are present, in which case a small scale separates the supernumerary from the closest normal awn. When only a single awn is present the scales form a single structure extending around the apex of the fruit.

Habitat: Forest country on sandy or loamy soils.

Range: Coastal and South-eastern Queensland, through New England and coast of New South Wales to Fitzroy Falls.

Specimens examined:

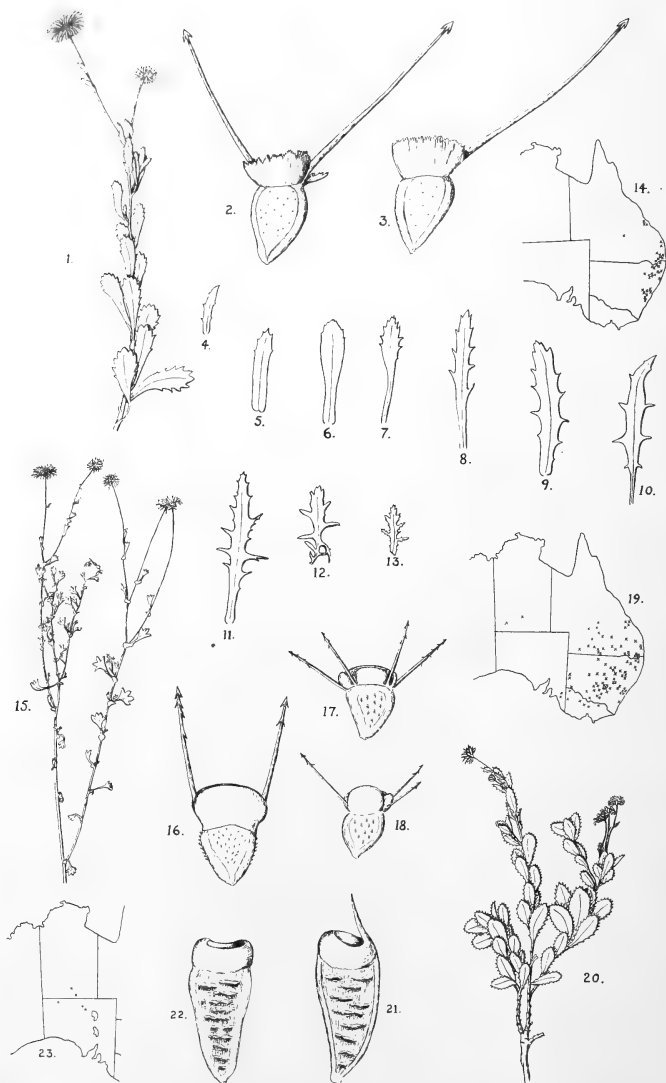
Queensland: Marlborough, 2.1918, H. W. Simon (BRI); Rockhampton, O'Shaney (MEL); Gracemere, dry places, 1.11.1870, P. O'Shaney (MEL); Bundaberg district, road to Gin Gin, N. Michael (BRI); Burnett River, F. Mueller (MEL); Gympie, F. H. Kenny (BRI); Benarkin, 5.1921, E. W. Bick and W. D. Francis (MEL); Spring Bluff,

on rocky hillsides in *Tristania conferta-Eucalyptus* forest on dark grey fine sand, ca. 1,500 ft.; 2-4 ft. high, ray white, 21.2.1935, S. T. Blake 7,717 (BRI); Flagstone Creek. 21.10.1934, N. Michael (BRI); Taylor's Range, 8.7.1844, L. Leichhardt (MEL); Brisbane. 8.6.1929, C. S. Sutton (MEL); Brisbane River, W. Hill (MEL); Camp Mt., top and upper slopes, 1,000-1,300 ft., common in *Eucalyptus* forest among grass on stony light grey soil, erect sparsely branched perennial herb of 1-1½ ft., ray white, 30.3.1945, S. T. Blake 15,493 (BRI); Moggill, in *Eucalyptus* forest on Brisbane schist, undershrub 2 ft. high. fls. white, 3.4.1931, C. T. White 7,264 (BRI); Jimboomba, 4.1907, J. L. Boorman (NSW 14,642); Gladfield, 6.1892, F. M. Bailey (NSW 14,647); Mt. Edwards, on lower slopes, diffuse herb about 2 ft., 1.4.1934, S. L. Everist 577 (BRI); Applethorpe, on granite sand, on flat, in stringybark forest, 22.11.1946, S. L. Everist and L. J. Webb 1,304 (BRI); Chesterton, in *Callitris* and *Eucalyptus* forest on very sandy soil, ca. 1,900 ft., 8.4.1936, S. T. Blake 11,140 (BRI).

New South Wales: Mt. Lindsay, 11.1912, H. M. R. Rupp (NSW); Boonoo Boonoo sandstone ridges by the side of the road, 11.1904, J. L. Boorman (NSW 14,666); near Timbarra, Marsh, C. Stuart (MEL); between Drake and Tenterfield, 15.12.1916, J. B. Cleland (AD); Torrington, J. L. Boorman (NSW 14,667); Emmaville, 10.1901, J. L. Boorman (NSW 14,642); Grafton to Dalmorton, 11.1903, J. H. Maiden and J. L. Boorman (NSW 14,661); Pheasant Creek, Glen Elgin, 12.1913, J. L. Boorman (NSW 14,664); Glen Innes, granite, 1.1914, H. M. R. Rupp (NSW 14,665); Tingha, 6.1917, J. L. Boorman (NSW 14,669); head of R. Gwydir, L. Leichhardt (NSW 14,662); Guyra, 6.1917, J. L. Boorman (NSW 14,643); Snowy Range, 4,500 ft., granite soil, Eucalypt forest, 11.3.1931, G. L. Davis (NE); Big Hill, Armidale-Kempsey road, ray blue, 3,000 ft., 27.1.1941, C. Davis (NE); Uralla, 3.1912, A. McNutt (NSW 14,656); Walcha Road, 12.1912, J. L. Boorman (NSW 14,668); Moona R., Walcha, 12.1884, A. Crawford (MEL); Macleay R., Beckler (MEL); Port Macquarie, 2.1898, J. L. Boorman (NSW 14,654); Rylstone road, red loam on roadside, 2,500 ft., 22.9.1948, E. F. Constable (NSW 14,707); Blue Mountains, Atkinson (MEL); The Peaks, Burragorang, 8.1905, R. H. Cabbage (NSW 14,657); Nepean R., 14.1.1888, J. J. Fletcher (NSW 14,653); Richmond, 10.4.1910, W. Greenwood (NSW 14,973); Norton's Basin, Nepean R., 17.11.1935, G. L. Rodway (FAR); Parramatta (MEL); Port Jackson, R. Brown (MEL); Centennial Park, Sydney, 12.1902, A. A. Hamilton (NSW 14,651); Carlton, 2.1893 (AD); Como railway station, 3.1893, J. H. Camfield (NSW 14,659); Glenfield, 27.12.1918 (NSW 14,652); Bargo, 26.1.1940, W. F. Blakely and W. J. Burkinghan (NSW 14,972); 7 miles S.W. of Fitzroy Falls, forest, F. A. Rodway (NE; FAR).

Robert Brown described *Calotis* from specimens of *C. dentex* collected by himself "in the neighbourhood of Port Jackson", some of which are in the National Herbarium, Melbourne, and from these a lectotype has been selected. The fruits of these specimens bear one awn, a condition noticed in a number of specimens, particularly in those from Queensland, and Brown himself stated (1820), ". . . from 1-3 barbed awns". This diagnosis of the species was followed by Bentham (1866), but White (1946) limited the name to cover only those plants with fruits "with 1-2 awns, and in the latter case one markedly smaller than the other". He then described those with two nearly equal awns as a new species, *C. scabriuscula*. In the specimens examined by the present writer, a continuous series was found in the fruits, from the one to the three-awned condition, passing through all degrees of inequality in length and not associated with any other differences. The attempt to divide a population into separate units on a single character with continuous variation can only be regarded as arbitrary, and in this revision the name *C. dentex* is applied in its original sense.

Members of this species are usually robust, rather coarse, leafy herbs with conspicuous inflorescences. They exhibit little vegetative variation except for the margins of the lower leaves (Text-figs. 4-13), which are sometimes rather deeply dissected, but this is more conspicuous in herbarium specimens than in the living state.



Text-figures 1-23.

1-14, *C. dentex*.—1, Habit $\times 0.3$; 2-3, Variation in fruits $\times 6.3$; 4-13, Variation in lower cauline leaves $\times 0.3$; 14, Distribution; 15-19, *C. cuneifolia*.—15, Habit $\times 0.3$; 16-18, Variation in fruits $\times 6.3$; 19, Distribution; 20-23, *C. Kempei*.—20, Habit $\times 0.3$; 21-22, Variation in fruits $\times 9$; 23, Distribution.

2. *CALOTIS CUNEIFOLIA* R.Br., *Bot. Reg.*, 6 (1820), 504. (Text-figs. 15-19.)

C. dilatata A. Cunn. in *DC. Prod.* 5 (1836), 302; *C. palmata* A. Gray, *Proc. Am. Acad.*, v (1861), 121; *C. cuneifolia* R.Br. var. *biaristata* Domin, *Biblioth. Bot.*, 89 (1929), 1208; *C. cuneifolia* R.Br. var. *glabrescens* C. T. White, *Proc. Roy. Soc. Q.*, 57 (1946), 30; *C. scabriuscula* C. T. White var. *lobata* C. T. White, *l.c.*, 31.

Type data: "Growing on the banks of the River Lachlan, 1817, Allan Cunningham."

Erect, ascending or sometimes prostrate much-branched perennials up to 60 cm. high, with an indumentum of stiff septate hairs. *Cauline leaves* numerous, the lower up to 4 cm. long, 2 cm. broad, cuneate with an abruptly expanded base and usually auriculate, with 3-6 acute distal lobes which are usually entire but occasionally are minutely toothed. *Radical leaves* with slender petioles, but only present on young plants. *Inflorescences* very numerous on established plants, on which 200 or more are not unusual. Individual inflorescences 1-2 cm. diameter, on terminal and axillary peduncles. *Involucral bracts* 16-29, up to 3.5 mm. long, 1.4 mm. broad, narrow-obovate to linear, entire, subacute to acute, glandular on the outer surface. *Ray florets* 27-45, the rays 3-9 mm. long, 0.5-1.5 mm. broad, white or lilac. *Receptacle* 1-1.9 mm. broad, 0.8-1 mm. high, conical, shallowly pitted. *Fruits* reddish-brown, the body 0.8-1.6 mm. long, 0.6-1.5 mm. broad, cuneate, flattened. Awns barbed distally, usually 2, but occasionally 3-4, 1-3.5 mm. long, alternating with an equal number of smooth infolded scales which are broader than long.

Habitat: On sandy soils or clay-loams among grasses in open Eucalypt forest.

Range: Widely spread in the eastern States, particularly in inland areas, with two records from south-eastern South Australia and Northern Territory.

Specimens examined:

Queensland: Torrens Creek, *Eucalyptus* forest, in sandy soil near Warrigal swamp, 20.3.1933, C. T. White 8,700 (BRI); west of Pentland, on slopes of Great Dividing Range on sand overlying sandstone, 1,500-1,650 ft., tufted, rather spreading and ascending to 1 ft., flowers scented, ray white, 19.10.1935, S. T. Blake 9,945 (BRI); Warrigal, in mixed *Eucalyptus* forest, on reddish-brown sandy soil, 2.2.1931, C. E. Hubbard and C. W. Winders 7,111 (BRI); 200 miles W. of Hughenden, 8.1889, C. Chisholm (MEL); Glenbar, common in *Eucalyptus* forest, heads purple-white, 8.2.1930, S. F. Kajewski (BRI); Canal Creek, 1882, Hartmann (MEL); Rockhampton, G. O'Shanesy (MEL); Dundee Sta., in red-brown fine sandy loam with Box, Mulga and Sandalwood, ray florets mauve, 20.3.1947, S. L. Everist 2,750 (BRI); Jericho, 3.1946, M. C. Clemens (BRI); Barcoo, 1870, E. Schneider (MEL); about 8 miles S.W. of Yalleroi, sub-shrub, 23.10.1940, L. S. Smith and S. L. Everist 917 (BRI); Tambo 1871, E. Schneider (MEL); between the Barcoo and Roma, 1871, Birch (MEL); Armadilla, 1867, M. Barton (MEL); Charleville, in mulga country, on reddish-brown very sandy loam, ca. 1,000 ft.; ray purplish, 19.4.1934, S. T. Blake 5,370 (BRI); Roma, fairly common weed in sandy soil, 25.10.1933, C. T. White, 9570 (BRI); Miles, B. Scortechini (MEL); each of Thargomindah, 1885, Spencer (MEL); Murweh, 9.1916, R. Cameron (BRI); Boatman Station, in red-brown silty clay-loam with Box, rays pale-purple, 18.7.1947, S. L. Everist 3,093 (BRI); 21 miles W. of Bollon, in gutter on clay loam at foot of hard red ridge, rays lilac, 7.8.1946, S. L. Everist 2,603 (BRI); Honeyamah, in heavy grey clay with deep melon-holes, ring-barked Belah, rays lilac, 16.7.1948, S. L. Everist 3,471 (BRI); Ballandool River, 1867, H. W. Looker (MEL); Currawillighi, I. C. Dalton (MEL); Lochnagar, 17.11.1930, A. M. Sutherland (BRI); 30 miles W. of St. George, in *Eucalyptus* forest, on reddish fine sand, ca. 600 ft., low bushy dull-green annual up to 6 in., ray purplish to white, 15.3.1936, S. T. Blake 10,791 (BRI); Glenoie, very common in red sandy loam with *Euc. melanophloia*, 7.4.1939, S. L. Everist 1,749 (BRI); N.N.W. of Bungunya, in mallee scrub, ca. 800 ft., stem tufted, ascending or oblique, rays light mauve, 26.7.1945, S. T. Blake 15,863 (BRI); Wyaga, 9.1919, C. T. White (BRI); Kindon Station, 54 miles N.N.E. of Goodwindi, 5.12.1938, L. S. Smith 520A (BRI); Bybera, very common in sandy soil, freely eaten by stock, 2.9.1934, C. T. White 9,722 (BRI); Thulimbah, Granite belt, 2.1934, C. Schindler (BRI); Ballandean,

14.10.1933, C. T. White 9,420 (BRI); Eukey, via Stanthorpe, 11.1944, Goebels (BRI); Stanthorpe, in *Eucalyptus* forest at foot of granite mountain in grit quartzite, 3,000 ft.. 11.3.1931, C. E. Hubbard 5,729 (BRI); between Tablinga and Nanango, 6.1912, C. T. White (BRI); hills about Chermiside, 1.1918, C. T. White (BRI); Moreton Bay, 1872, Eaves (MEL); Broadwater, near Brisbane, cleared *Eucalyptus* forest country, on stony slopes, amongst grasses, 5.10.1930, C. E. Hubbard 4,361 (BRI); Brisbane River at St. Lucia moderately common as undergrowth among grass in mixed *Eucalyptus* forest, on Brisbane schist, flowers white, drying off a pale lavender, 6.4.1945, C. T. White 12,645 (BRI).

New South Wales: Thirty miles S.W. of Woodenbong on Stanthorpe road, granite sand, 23.11.1946, S. L. Everist and L. J. Webb 1,388 (BRI); Wallangarra, 5.1914, J. L. Boorman (NSW 14,731); near Tenerfield, C. Stuart (MEL); Timbarra, C. Stuart (MEL); Mt. Russell, 20.1.1915, pastures, E. Breakwell (NSW 14,675); 7 miles from Guyra, Inverell road, 18.2.1941, G. L. Davis (NE); Castle Doyle road, 4 m. from Armidale, 3,000 ft., granite, open *Eucalypt* forest, 17.3.1951, G. L. Davis (NE); Wollomombi, cleared grassland, granite, 31.1.1941, C. Davis (NE); Warialda, 5.1905, H. M. R. Rupp (NSW 13,726); Baradine and Narrabri, 12.1916, G. Burrows (NSW 14,997); Cuttabri, Pilliga scrub, 8.1913, J. L. Boorman (NSW 14,724); Gunnedah, 9.1910, J. L. Boorman (NSW 14,681); Coonabarabran, 9.1916, J. L. Boorman (NSW 14,950); Liverpool Range, J. E. Tenison-Woods (MEL); Rocky hills, Peel Range, 1817, A. Cunningham 335 (MEL); Murrurundi, 5.1902, J. H. Maiden and J. L. Boorman (NSW 14,739); 11 miles on the Dubbo-Mendooran road, rocky hill, 10.8.1944, G. W. Althofer (NSW 14,741); plains near Dubbo, 10.1883, E. Betche (NSW 14,712); Gulgong, 4.1901, J. H. Maiden and J. L. Boorman (NSW 14,700); Mudgee, 1870, Taylor (MEL); Rylstone road, red loam on roadside, 2,500 ft., 22.9.1948, E. F. Constable (NSW 14,707); Paroo River district, 9.1900, E. Betche (NSW 14,720); Wanaaring, 18.9.1939 (NSW 14,717); Bourke, 9.1912, J. L. Boorman (NSW 14,718); between the Bogan and Darling, 1877, L. Morton (MEL); Coolabah, 12.1908, J. H. Maiden and J. L. Boorman (NSW 14,689); Cobar, 22.9.1924, A. Morris (NSW 14,683); Nyngan, 5.1913, J. H. Maiden (NSW 14,695); Duck River, 9.1914, A. A. Hamilton (NSW 14,723); 90 miles E. of Broken Hill, 20.8.1939, I. Pidgeon and J. Vickery (NSW 14,949); Lake Cawndilla, 2.9.1921, MacGillivray (NSW 14,737); Wentworth, Ford (MEL); Euabalong, 5.1906, J. L. Boorman (NSW 14,729); Cargellico, 9.1918, J. L. Boorman (NSW 14,703); Harvey Ranges, Peak Hill, 11.1905, J. L. Boorman (NSW 14,682); Condobolin Station yard, 8.1897, J. H. Maiden (NSW 14,719); Parkes, red loam, 1,035 ft., E. F. Constable (NSW 4629); Bumberry, 2.10.1916, J. B. Cleland (AD); Bogan Gate, 4.1924, E. H. Ising (NSW 14,685); Cowra, 4.1915, J. Beattie (NSW 14,677); Young, 10.1923, C. M. Western (NSW 14,742); Temora, 9.1915, J. W. Dwyer (NSW 14,732); Barmedman, 29.8.1926, C. S. Sutton (MEL); Beckom, 11.1917, J. L. Boorman (NSW 14,738); Ardlathan, 30.9.1916, R. H. Cabbage (NSW 14,678); Wyalong, 10.1905, J. E. Carne (NSW 14,734); Hay, J. J. Fletcher (NSW 14,721); Deniliquin, 9.1904, J. J. Tadgell (MEL); Brookong, Wagga, 1873, A. Crouch (MEL); Pleasant Hills, 1889, Fischer (MEL); Henty, Cemetery Reserve, 18.2.1949, E. J. McBarron (NSW 14,691); Blackheath, 4.1899, J. H. Maiden (NSW 14,715); Valley Heights, Blue Mountains, 7.1899, W. Bauerlen (NSW 14,722); Liverpool, amongst grasses on hill, in forest, 15.4.1931, C. E. Hubbard 8,484 (BRI); Chester Hill, on outskirts of *Leptospermum* scrub, 16.9.1945, M. Tindale (NSW 3,102); Homebush, 5.1887, J. H. Maiden (NSW 14,697); Rookwood, 7.5.1887, J. J. Fletcher (NSW 14,716); Hornsby, 3.1915, W. F. Blakely (NSW 14,679); reclaimed ground, Govt. Domain, Sydney, 10.1902, J. H. Camfield (NSW 14,736); Kogarah, railway embankment, 10.1894, J. H. Camfield (NSW 14,740); Nowra, 1932, P. Monaghan (FAR).

Victoria: Mildura, 9.1912, H. B. Williamson (MEL); near Lake Hindmarsh, 10.1892, St. Eloy D'Alton (MEL); Kamarooka, Northern Whipstick, 10.1941, A. J. Tadgell (MEL); Lower Loddon River, R. Thom (MEL); Campaspe River, 10.1875 (MEL); Goulburn River, near Seymour, 27.10.1902; F. M. Reader (MEL); Chiltern, H. B. Williamson (MEL).

Northern Territory: Connor's Well, 10.1939, B. A. Dale (NSW 14,708); Glen Edith, mulga scrub, 1894, R. Tate (AD).

South Australia: Murray pine scrubs, Lower Murray River, 10.1886, C. French (MEL); Murray River, R. Brown (MEL).

Although it was not possible to examine the type specimen in the preparation of the redescription of this species, the detailed nature of the original description and the excellent plate showing the habit, fruits and florets, leave no doubt as to the identity of the species.

A specimen, accompanied by the collector's label bearing the type data of *C. dilatata* ("Rocky hills, Peel's Range, interior of N.S.W., 1817, Cunningham"), is in the Melbourne Herbarium. It is unfortunate that this specimen bears no fruits, but since it is vegetatively identical with *C. cuneifolia*, Bentham's synonymy (1866) of these two species is accepted.

According to Gray (1861) the fruits of *C. palmata* ("Hunter River, N.S.W.") are "smooth on both sides; pappus of 2-4 scales and 1-2 awns, with sparse recurved bars towards the apex" and the leaves "cuneate or fan-like, palmate, 3-5 lobed, the lower with winged petioles, tapering basally and slightly auriculate". This description is an exact one of *C. cuneifolia* of which *C. palmata* is now listed as a synonym.

Domin's type specimens of var. *biaristata* ("near Jericho, Q") are also not available in Australia, but as this variety was established on a normal character of the species (i.e., 2 awns on the fruits), it is not upheld by the present writer.

White (1946) described var. *glabrescens* from some Queensland specimens ("Torrens Creek, in Eucalyptus forest, sandy soil near Warrigal swamp, 20.3.1933, C. T. White 8,700") in which the indumentum was more sparse than usual. The degree of development of a character, alone, as the basis for separate status is unsound taxonomic procedure, and consequently this variety is relegated to synonymy.

C. scabriuscula var. *lobata* ("Eukey, via Stanthorpe, 11.1944, E. Goebels (BRI)"), although vegetatively identical with *C. cuneifolia*, was excluded from that species by White (1946) on account of the distribution of bars on the awns. Certainly, those of *C. dentex* are usually localized at the ends of the awns with an almost arrow-head arrangement, and this is seen in the holotype of this variety, but the same condition does occur in *C. cuneifolia*. The second distinguishing character used by White, that of infructescence size, does not hold when a large series of specimens is examined. The variety was based on a single record of two specimens from Eukey, Darling Downs, and is relegated to synonymy within this species.

Variation in the fruits involves primarily the number of awns, which is not always constant even within the same head. The usual condition is for two opposite awns to diverge in the same plane as the flattened face of the fruit and for two broad scales to occupy the intervening region between their bases. Supernumerary awns do not affect the position of the basic pair, and are usually not symmetrically placed. The dimensions of the scales in such fruits depends on the available area, and when two awns are close, the intervening scale may be longer than broad (Text-figs. 17-18).

Vegetative variation is confined to leaf size and, to a lesser extent, leaf shape. Specimens from Pilliga Scrub, Cononabarabran and Warialda, in particular, bear leaves which are 1 cm. or less in length but of typical shape. Since no discontinuity could be found on this character, these small-leaved plants are best regarded as extreme variants.

3. *CALOTIS KEMPEI* F. Muell., *Trans. Proc. Roy. Soc. S. Aust.*, 4 (1881), 112. (Text-figs. 20-23.)

Type data: "In the vicinity of the River Finke, MacDonnell Ranges, Rev. N. Kempe."

Lectotype, Mission Station, Finke River, 1879, H. Kempe (MEL).

Erect branching glabrous or microscopically glandular perennials up to 39 cm. high, with a long tap root. *Leaves* cauline, up to 3.2 cm. long, 1 cm. broad, oblanceolate, sessile, regularly mucronate-serrate. *Inflorescences* up to 19, about 1.5 cm.

diameter, forming a cymose panicle. *Involucral bracts* 16-21, 4-5-5 mm. long, 1.5-2.1 mm. broad, lanceolate, acuminate, entire, shortly glandular and septate hairy. *Ray florets* about 30, the rays 5 mm. long, 1 mm. broad, yellow. *Receptacle* 1.5 mm. high, 1.2 mm. broad, shallowly pitted. *Fruits* brown, the body 1.5-2 mm. long, 0.7-1 mm. broad, flattened, narrow cuneate, microscopically tuberculate; pappus represented by an apically in-rolled collar one-fourth the length of the body, which may bear a solitary short awn.

Habitat: No data available.

Range: Central Australia.

Specimens examined:

Northern Territory: Mission Station, Finke River, 1879, H. Kempe (MEL); Burt's Well, 9.8.1931, J. B. Cleland (JBC); The Goyder, Horn Expedition (AD).

South Australia: Mt. Everard, 1882, E. Giles (MEL); Tietkins Creek, Musgrave Ra., 20.7.1914, S. A. White (JMB); 20 miles west of Lambana, Musgrave Ra., 23.7.1914, S. A. White (JMB); Todmorden, 9.4.1950, J. B. Cleland (JBC); Oodnadatta, 11.1914, Staer (NSW 14,873; JMB).

The type series is represented by a number of specimens in the Melbourne Herbarium, from which a lectotype was selected.

Apart from a vegetative resemblance to certain specimens of *C. erinacea*, this species is so distinct from any other that Mueller (1882) suggested it might merit generic status, and provisionally placed it in the section *Anacantharia*. The occasional presence of a single small awn (Text-fig. 21), first observed by Black (1929), justifies its retention within this genus. There is a possibility that the awn is always present but is either deciduous or withers on drying, so that it frequently cannot be found in herbarium specimens.

4. *CALOTIS GLANDULOSA* F. Muell., *Trans. Vict. Inst.* (1855), 129. (Text-figs. 24-27.)

Type data: "On dry grassy ridges near the Snowy River and its tributaries, towards Maneroo."

Lectotype, "On dry grassy ridges near the Snowy River, towards Maneroo, Dec., 1854, F. Mueller" (MEL).

Glandular, ascending or erect branched perennials up to 32 cm. high, with a woody tap root. *Leaves* cauline, the lower up to 3 cm. long, 8 mm. broad, cuneate in gross outline but distally pinnatifid with 5-7 acute lobes. Upper leaves broadly sessile. *Inflorescences* about 20, 2 cm. diameter, of terminal and axillary peduncles. *Involucral bracts* 12-16, 4.5-6.5 mm. long, 1.8-2.8 mm. broad, ovate-lanceolate, entire and acute. *Ray florets* about 50, 7 mm. long, 1-1.5 mm. broad, blue. *Receptacle* 1.6 mm. broad, 1.3 mm. high, conical, shallowly pitted. *Fruits* reddish-brown, the body cuneate, flattened, papillate, 1.6-2.5 mm. long, 1.2-2.5 mm. broad; awns 4-5 of unequal length, 1.5-5 mm. long, barbed only at the tip and alternating with an equal number of marginally ciliolate scales which are longer than broad and almost as long as the body of the fruit.

Habitat: Grassland and open forest country at high altitudes.

Range: Southern highlands of New South Wales and a single record from near the Blue Mountains.

Specimens examined:

New South Wales: Duckmaloi, pasture, 2.1935, V. May (NSW 14,672); Cooma, 12.1890, E. Betche (NSW 14,671); Wollandibby, Jindabyne, 4.1890, J. H. Maiden (NSW 14,673); Berridale, on the Monaro Plains, extends up into the lower forest country of the Kosciusko Plateau, 5.1947, A. B. Costin (MEL); on dry grassy ridges near the Snowy River, towards Maneroo, 12.1854, F. Mueller (MEL); Snowy Mts., 4,000 ft., 1.1890, W. Bauerlen (MEL).

Bentham (1866) listed *Huenefeldia coronopifolia* Walp. as a synonym of this species, but it is not treated as such in this paper since not only are Walpers' specimens

("New Holland") not available in Australia, but the original description* is so brief and superficial as to be useless from the point of view of recognition. The matter is of some importance since, should Bentham be correct, Walpers' epithet must be given priority and the new combination published. Pending location and examination of Walpers' type specimens the current name is retained.

The type locality is thought to be an incorrect spelling of Monaro, from which district this species has been collected within recent years.

5. *CALOTIS XANTHOSIDEA* Domin, *Biblioth. Bot.*, 89 (1929), 655. (Text-figs. 28-30.)

Type data: "Sandstone hills of Darling Range near Jericho,* Queensland, Domin III, 1910."

Erect branching perennials up to 23 cm. high, with an indumentum of long white septate hairs. *Leaves* cauline, ovate-cuneate to cuneate, serrate, up to 6 cm. long, 3-3 cm. broad, sessile, rather abruptly narrowed proximally and auriculate. *Inflorescences* about 80, 2 cm. diameter, on axillary terminal peduncles. *Involucral bracts* 14-18, 3-3.5 mm. long, 0.6 mm. broad, linear, entire, acuminate, glandular and septate-hairy on the outer surface. *Ray florets* 25-28, the rays 9 mm. long, 1.6 mm. broad, white or mauve. *Receptacle* 0.7 mm. broad, 0.5 mm. high, conical, hardly pitted. *Fruits* reddish-brown, the body cuneate, flattened, 1-1.6 mm. long, 0.7-1.1 mm. broad, minutely tuberculate; awns 5-8, 1.5-2 mm. long, rigid, horizontally placed, distal barbs passing proximally into long straight hairs, scales short, alternating with the awns, entire and marginally ciliolate.

Habitat: Sandy soil in open forest.

Range: Mitchell and Gregory South districts of Queensland.

Specimens examined:

Queensland: Twenty miles east of Corinda Sta., erect herb on red sandy soil, ray florets white, 7.4.1946, S. L. Everist 2,569 (BRI); near Lochnagar, in *Eucalyptus* forest on fine sand, ca. 1,100 ft., bushy dull green annual of about 6 in., 29.11.1935, S. T. Blake 10,278 (BRI); about 5 miles east of Jericho, tufted prostrate herb with yellow flower heads, 24.10.1940, L. S. Smith and S. L. Everist 982 (BRI; MEL); east of Jericho, in mixed open forest on sand, ca. 1,250 ft., tufted, ascending, ray lilac, 16.7.1934, S. T. Blake 6,827 (BRI); Tenham Sta., 25 miles S.S.E. of Windorah, on stony ridge with *Acacia*, bushy subglaucous annual of ca. 6 in., ray light mauve, 9.6.1936, S. T. Blake 12,033 (BRI).

The redescription of this species was based on a number of specimens from the type locality which agree with the original description and are not referable to any other species.

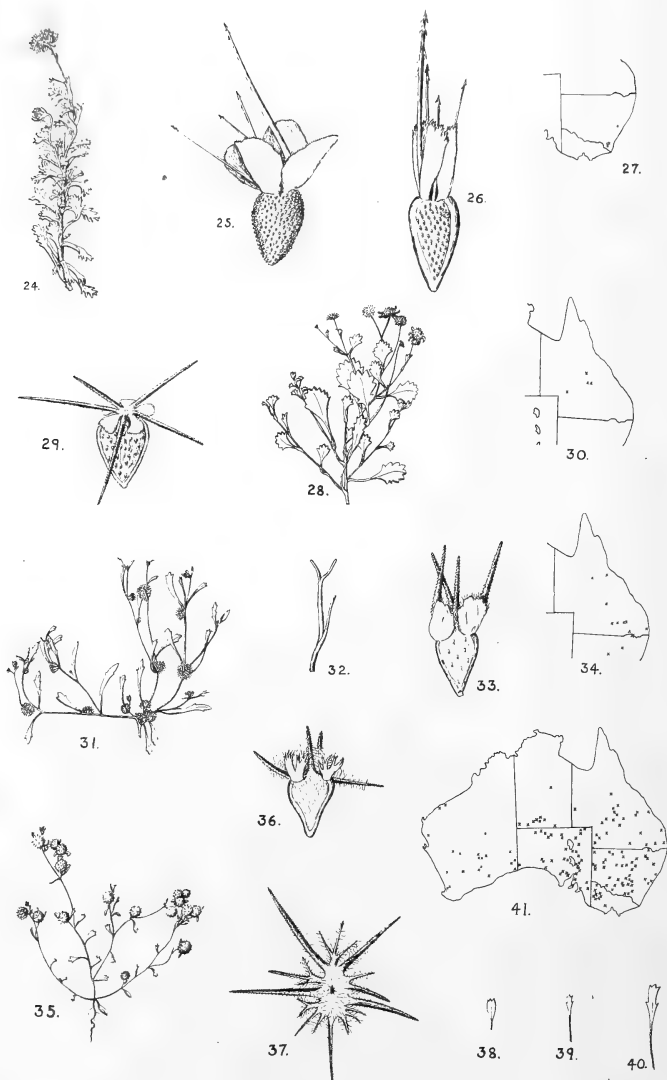
Both Domin (1929) and White (1946) have commented on the resemblance of this species to *C. cuneifolia* in the shape of the leaves, but the fruits are distinct and are not unlike those of *C. squamigera* in the entirely barbed awns and the nature of the scales.

6. *CALOTIS SQUAMIGERA* C. T. White, *Proc. Roy. Soc. Q.*, 57 (1946), 32. (Text-figs. 31-34.)

Holotype, Macintyre River, near Queensland border at Goondiwindi, 9.1944, C. T. White 12,621 (BRI).

Branching, more or less septate-hairy, procumbent annuals, up to 21 cm. high. *Cauline leaves* cuneate-spathulate, the lower up to 4 cm. long, 4 mm. broad, distally toothed and tapering into a short petiole. *Radical leaves* present only on young plants, up to 7 cm. long, 6 mm. broad, similar in shape to the cauline leaves of the same plant but with a long slender petiole. *Inflorescences* about 50, 4 mm. diameter, axillary, on very short peduncles so as to appear almost sessile, and each exceeded by a subtending leaf. *Involucral bracts* about 15, 3-3.5 mm. long, 1-1.5 mm. broad, narrow-elliptical, entire, acute, septate-hairy on outer surface. *Ray-florets* about 12, the rays very minute, up to 0.8 mm. long, 0.1 mm. broad, exceeded by the stylar arms. *Disc florets* fertile.

* "Short bushy erect stem with ascending branches; leaves sessile, linear, pinnatifid, glandular-pilose on both sides; capitula solitary at the apex of almost leafless peduncles.—In New Holland."



Text-figures 24-41.

24-27, *C. glandulosa*.—24, Habit $\times 0.3$; 25-26, Variation in fruits $\times 6.3$; 27, Distribution; 28-30, *C. xanthosidea*.—28, Habit $\times 0.3$; 29, Fruit $\times 9$; 30, Distribution; 31-34, *C. squamigera*.—31, Habit $\times 0.3$; 32, Ray floret $\times 15.3$; 33, Fruit $\times 6.3$; 34, Distribution; 35-41, *C. hispidula*.—35, Habit $\times 0.3$; 36-37, Fruit, lateral and apical views $\times 6.3$; 38-40, Variation in lower cauline leaves $\times 0.3$; 41, Distribution.

Receptacle 1.5 mm. broad, slightly convex, *septa* present between the bases of the florets. *Fruits* reddish-brown, the body 1.7-2.2 mm. long, 1.1-1.3 mm. long, cuneate, flattened, minutely tuberculate; awns 4-5, 1.7-2.5 mm. long, vertical or slightly divaricate, minutely barbed along the whole length, alternating with short entire scales with ciliolate margins.

Habitat: Grassland and open forest.

Range: Well distributed, but not common, throughout inland districts of Queensland, with only two records from Western New South Wales.

Specimens examined:

Queensland: Charters Towers, weed on racecourse, 6.8.1942, H. Flecker (BRI); Maxwellton, in grassland, ca. 550 ft., shortly creeping, ascending or erect, fls. yellowish, 22.8.1936, S. T. Blake 12,650 (BRI); Blackall, small tufted plant on sandy loam near Barcoo River, leaves and flower heads pale green, 24.8.1935, S. L. Everist 1,210 (BRI); Murweh, Warrego River, 9.1916, R. Cameron (BRI); Mungallala, 8.1913, W. Dunn (NSW 14,860); Bungeworgorai, 25.10.1933, C. T. White 9,532 (BRI); Eight-Mile Plains, near Brisbane, weed of cultivation introduced with sheep manure, 26.10.1930, C. T. White (BRI); NNW. of Gungunya, in brigalow-belah "scrub", compact brown soil, ca. 700 ft., more common in open places, spreading annual, 26.7.1945, S. T. Blake 15,874 (BRI).

New South Wales: Macintyre River, near Goondiwindi, 28.9.1944, C. T. White 12,621 (BRI); near Wangan, Pilliga scrub, in pasture, 13.10.1918, J. B. Cleland (AD); Cobar, J. B. Cleland (AD).

This species appears to be centred in western Queensland, and the isolated plants collected elsewhere are probably the result of fruits being distributed attached to the wool of sheep or, according to White, in sheep manure. In this connection, there is an interesting record in the National Herbarium, Sydney, of a well-grown specimen of this species from Galashiels, Scotland, April, 1915, collected by Miss Hayward, who was interested in alien plants appearing in this locality from seeds brought in with imported wool.

As already noted by White (1946), this species is most closely allied to *C. hispidula*, from which he distinguished it by the colour of the fruits and the shape of the alternating scales. To these differences may be added the absence of hairs on the fruits of *C. squamigera*, and the entire or only shallowly lobed scales. In the field, this species can be readily identified by its axillary and solitary inflorescences which are very shortly pedunculate and at the fruiting stage appear sessile. In all the specimens examined there was a single inflorescence at ground level, from immediately below which the branches passed off from the very short main stem.

The ray florets cannot be distinguished in some specimens, due to the microscopic size of the ray which, in dried specimens, has usually shrivelled and disappeared, so that the stylar arms are apparently naked. (Text-fig. 32.)

7. *CALOTIS HISPIDULA* (F. Muell) F. Muell, *Trans. Vict. Inst.* (1853), 129. (Text-figs. 35-41.)

Cheiroloma hispidulum F. Muell., *Linnaea*, 25 (1852), 401.

Type data: "In exposed clayey places near Crystal Brook and Cudnaka."

Lectotype, "*Cheiroloma* (n.g.) *hispidulum*, Ferd. Mueller, Crystal Brook and Cudnaka, Ferd. Mueller" (MEL).

Prostrate or ascending annuals from 1.5-27 cm. high, with many slender branching stems, and an indumentum of white septate hairs. *Cauline leaves* cuneate and distally 3-5 toothed or occasionally entire, up to 2 cm. long; the uppermost often clustered below the inflorescences. Lower cauline leaves not uncommonly smaller than those in a median position. *Inflorescences* greenish, up to several hundred on a large plant, forming rather dense cymose panicles, each slightly exceeded by the leaves immediately below. *Involucral bracts* 11-14, 3.5-4 mm. long, 1.1-1.4 mm. broad, lanceolate to spatulate, entire, subacute to acute, densely septate hairy on outer surface. *Ray florets* about 10, 0.8-1 mm. long, 0.2 mm. broad, filiform yellow. *Disc florets* fertile. *Receptacle*

0.8-1 mm. broad, 0.5-1 mm. high, conical, with prominent septa between the florets. *Fruits* very dark brown, the body cuneate, flattened, 2-2.5 mm. long, 1.5-2 mm. broad, shortly hairy on each face and woolly apically; awns 5-6, 1.5-2.5 mm. long, rigid, horizontally placed, distally barbed and proximally woolly, alternating with scales which are dissected into 2-8 soft marginally hairy processes.

Habitat: Grassland in dry situations on various types of soil.

Range: Throughout Australia.

Specimens examined:

Queensland: Georgina River, 1889, A. Henry (MEL); Hughenden, tufted, prostrate, 14.6.1934, S. T. Blake 6,203 (BRI); Bowen Downs, 1872, C. W. Birch (MEL); north of Ilfracombe, in open grassland on dark brown clay, erect or ascending, rather glaucous annual of 1-2 in., fls. pale greenish-yellow, 3.5.1936, S. T. Blake 11,355 (BRI); between Isis Downs and Portland Downs, prostrate herb, in heavy soils in river channels, 27.5.1936, S. L. Everist and C. T. White 73 (BRI); Blackall, small tufted plant on sandy loam near Barcoo River, leaves and flower heads pale green, 24.8.1935, S. L. Everist 1,210 (BRI); Blackall, common on sandy land and lighter soils throughout the district, 29.8.1935, S. L. Everist 1,349 (BRI); Albilbah Downs, on brown soil near eastern tank, alt. 750 ft., 11.7.1934, S. T. Blake 6,711 (BRI); Minnie Downs, L. Reese (JMB); Barcarolle, Jundah, a winter growing plant, 30.9.1930, F. L. Berney (BRI); Windorah, W. H. Rose (BRI); Mt. Howitt Station, 110 miles west of Eromanga, in open plain on grey silty clay, dense prostrate or ascending annual, 6.7.1936, S. T. Blake 12,004 (BRI); Nockatunga Station, between channels of Wilson River, on loamy sand "claypans", among Chenopodiaceae, 27.6.1936, S. T. Blake 11,830 (BRI); between Stokes Range and Coopers Creek, Wheeler (MEL); Emerald, P. A. O'Shanesy, (MEL); Gindie, 8.1916, C. T. White (BRI); Neerkool Creek, Rockhampton, 1857, E. Bowman (MEL); Gayndah, 8.1913, F. Kenny (BRI); Bungeworgorai, near Roma, very common in sandy soil, 25.10.1933, C. T. White 9,532 (BRI); 20 miles west of Bollon, in gutter on clay loam at foot of hard clay ridge, 7.8.1946, S. L. Everist (BRI); NNW of Bungunya, in Brigalow-Belah "scrub", compact brown soil, ca. 700 ft., more common in open places, 26.7.1945, S. T. Blake, 15,874 (BRI); Toowoomba 11.1916, G. Searle and Sons (BRI); near Brisbane, J. Lauterer (BRI).

New South Wales: Macintyre River, near Goondiwindi, 28.9.1944, C. T. White 12,620 (BRI); Gravesend, 5.1914, W. Carne (NSW 14,808); Bingara and Warialda, 9.1929, F. A. Rodway (FAR); Tamworth, 9.9.1938, E. R. Johnston (KI); Pilliga, 10.1932, H. M. R. Rupp (NSW 14,810); Gilgandra, 9.1915, J. D. Simon (NSW 14,819); Castlereagh River, Wools (MEL); Narromine, 9.1898, J. H. Maiden (NSW 14,832); Nyngan, on railway line, abundant (MEL); Nyngan, plains, prostrate plant, 11.9.1947, E. F. Constable (NSW 14,461); Boppy Mount, 6.1903, W. Bauerlen (NSW 14,845); Cobar, 1883, H. Andrae (MEL); Bourke to Cobar, 27.8.1926, C. S. Sutton (MEL); between the Bogan and Darling, 1877, L. Morton (MEL); Bourke district, 8.1896, J. H. Maiden (NSW 14,816); Warrego River, 9.1885, E. Betche (NSW 14,830); Wanaaring-Urisino, 10.1912, J. L. Boorman (NSW 14,831); Paroo River district, 9.1900, E. Betche (NSW 14,817); White Cliffs, 7.1906, E. P. O'Reilly (NSW 14,977); Tarella, 8.1887, W. Bauerlen (MEL); Silvertown, 24.8.1939, I. Pidgeon and J. Vickery (NSW 14,964); Broken Hill, 9.1918, E. C. Andrews (NSW 14,834); Stephen's Creek, 12.8.1928, A. Morris (MEL); Campbell's Creek, 4.8.1920, A. Morris (NSW 14,833); Broken Hill to Torrawangee, 8.1893, H. Deane (NSW 14,827); Wilcannia, 9.1884, D. A. Porter (MEL); 84 miles east of Wilcannia, 26.8.1939, I. Pidgeon and J. Vickery (NSW 14,836); Mossgiel, 1885, J. Bruckner (MEL); between the Darling and the Lachlan, 1877, Burkitt (MEL); between the upper Bogan and Lachlan, L. Morton (MEL); Lachlan River, L. Morton (MEL); Trundle, 1912, E. Breakwell (NSW 14,844); Lake Cargellico, 10.1906, J. L. Boorman (NSW 14,840); Tullibigeal, 20.9.1915, J. W. Dwyer (NSW 14,837); Ardliehan, 1.10.1916, R. H. Cambage (NSW 14,835); Temora, 9.1915, J. W. Dwyer (NSW 14,836); Scenic Hill, Griffith, 17.9.1938, D. O. Cross (NSW 14,822); Griffith, on dry hills, 7.1928, W. F. Blakely and D. W. C. Shiress (NSW 14,811); Yanco, 6.10.1912, J. B. Cleland (AD); Zara, via Hay, 9.1903, E. Officer (NSW 14,965); Wanganella, 1885, Kuentz (MEL); Hay, 22.9.1889, J. J.

Fletcher (NSW 14,828); Murrumbidgee River, 9.1878, F. Mueller (MEL); Balranald, 1878, Lucas (MEL); Edwards River, 10.1875, F. Mueller (MEL); junction of Darling and Murray Rivers, 1889, Holding (MEL); Tarcutta, 1.10.1947, F. J. Jeffery (NSW 14,823); Cemetery Reserve, Henty, in red sandy loam of more sparse grassland, in clumps, 2.9.1949, E. J. McBarron (NSW 14,824); Belmont, 9.1910, J. L. Boorman (NSW 14,963); Cowan, on railway line, ray flowers yellow, 10.1921, W. F. Blakely (NSW 14,813); between Richmond and Blacktown, grassland, 30.9.1910, C. T. Musson (NSW 14,843); Parramatta, 1887, Woolls (MEL).

Victoria: Mildura, 5.9.1912, H. B. Williamson (MEL); Wimmera, 1891, J. P. Eckert (MEL); Birchip, 11.9.1927, C. S. Sutton (MEL); Dumosa Road, near Wycheproof, 8.1918, W. W. Watts (NSW 14,850); Jeparit, 14.10.1912, W. R. Baker (MEL); Mallee, near Nhill, 1884, St. Eloy D'Alton (MEL); Antwerp, 10.905, C. S. Sutton (MEL); near Dimboola, F. Reader (MEL); Minyip, 1890, J. P. Eckert (MEL); Lake Boga, 11.1903, H. Bird (MEL); Skipton, W. Whan (MEL).

Northern Territory: Darwin, sheep paddock, herb on rocky hills, 7.1922, C. E. F. Allen (NSW 14,859); Tennant's Creek, 12.1896, Agric. Bureau, S.A. (NSW 14,853); near Hugh River, Macdonnell Ranges, 19.8.1929, J. B. Cleland (JBC); Hermannsburg, 9.8.1929, J. B. Cleland (JBC); Tempe Downs, 1889, Thornton (MEL); end of Gill's Range, 8.5.1894, R. Tate (AD); Finke River, 1879, H. Kempe (MEL); Charlotte Waters, 1875, C. Giles (MEL); 50 miles N.E. of Ayer's Rock, 9.6.1935, J. B. Cleland (JBC); N.W. of Petermann Range, 7.1926, H. Basedow (P).

South Australia: 2 miles west of Eriwanjawanja, Musgrave-Mann Ranges, 21.6.1933, Tindale and Hackett (AD); Ernabella, in low-lying hard soils, 1.7.1943, L. B. Young (MEL); halfway between Moorilyanna and Ernabella, 7.8.1933, J. B. Cleland (JBC); Everard Ranges, 11.4.1950, J. B. Cleland (JBC); Alberga Creek, 1.7.1920, H.W.A. (JMB); 20 miles west of Oodnadatta, 5.8.1933, J. B. Cleland (JBC); Minnie Downs, L. Reese (JMB); Diamantina, 8.1930, Morgan (JBC); flood plain of the Diamantina, Goyder's Lagoon, 14.8.1934, J. B. Cleland (JBC); Warburton River (AD); Lake Eyre, 9.1903, Baldwin Spencer (NSW 14,858); Kopperamanna, 7.10.1916, S. A. White (JMB); Beresford, 21.9.1945, J. B. Cleland (JBC); Finnis Springs, beyond Hergott, 5.9.1916, F. D. Warren (JMB); 5 miles north of Marree, 8.1931, J. B. Cleland (JBC); Marree, 5.8.1932, J. B. Cleland (JBC); Mt. Lyndhurst, 8.1899, M. Koch (AD); Mt. Flinders Gorge, Flinders Range, 30.5.1937, J. B. Cleland (JBC); between Flinders Range and Lake Torrens, T. P. Richards (MEL); Moolooloo, small prostrate plant, 29.9.1918 (JMB); Parachilna, 20.8.1921, J. B. Cleland (JBC); Wilpena Pound, 17.11.1881 (AD); between Wilpena and Oraparinna, 1.12.1930, J. B. Cleland (JBC); Koonamore Vegetation Reserve, 15.2.1930, T. B. Paltridge (AD); Gordon, 11.10.1917, J. M. Black (JMB); Woolshed Flat, near Quorn, 12.1914, J. Mills (JMB); Warren's Gorge, near Quorn, 1.10.1916, J. B. Cleland (JMB); Crystal Brook, F. Mueller (MEL); Cudnaka, 10.1851, F. Mueller (MEL); Yorke Penin., 1879, Tepper (MEL); Kinchina, 8.11.1924, 17.9.1927, J. B. Cleland (JBC); Arcoona, 18.9.1927, B. J. Murray (AD); in crabhole, tablelands, Andamooka, 4.11.1929, J. B. Cleland (JBC); 7 miles east of Iron Knob, 25.8.1928, J. B. Cleland (JBC); Middleback Sta., 5.11.1930, J. B. Cleland (JBC); between Spencer's Gulf and Mt. Elia, C. Giles (MEL); Gawler Ranges, Sullivan (MEL); Wudinna, 1941, C. W. Johns, Tarcoola, 19.9.1920, J. M. Black (JMB); Ooldea Soak, 17.8.1939, J. B. Cleland (JMB; JBC); Pidinga, 6.1880 (AD); Fowler's Bay, 10.1907, T. Brown (NSW 14,854); Hughes, 6.9.1920, E. H. Ising (BRI; MEL; NSW 14,848); Nullarbor Plains, 1891, J. D. Batt (MEL).

Western Australia: Port Hedland, 7.1906, W. V. Fitzgerald (P); Gascoyne River, near Jimta Jimta, common in sand or clay, 20.9.1941, C. A. Gardner, 6,050 (P); Champion Bay, Walcott (MEL); Parker Ranges, 1892, E. Merrall (MEL); Cue, 9.1903, W. V. Fitzgerald (NSW 14,853); Sandstone, 8.1937, N. Kniep (P); Mt. Fouracre, N.W. of Leonora, 8.1931, W. E. Blackall 341 (P); Mt. Fouracre, 28.7.1931, C. A. Gardner 2,430 (P); Glenorn Station, Malcolm, 8.1938, N. T. Burbidge (P); Laverton, 9.1909, J. H. Maiden (NSW 14,988); Victoria Desert, Camp 53, 15.9.1891, R. Helms (MEL); York, 19.10.1889, M. Heal (MEL); sources of the Swan River, 1889, A. Eaton (MEL); Yilgarn, 1892, Merrall (MEL); Kalgoorlie, 7.10.1914, C. H. Ostenfeld (P); Boulder,

s.1898, W. V. Fitzgerald (NSW 14,852); Nullarbor Plains, 1891, J. D. Batt (MEL); 100 miles N. of Eucla, J. D. Batt (MEL); Eucla, J. D. Batt (MEL).

The genus *Cheiroloma* was described by Mueller (1852) from specimens collected by himself at Cudnaka and Crystal Brook and which he named *Cheiroloma hispidulum*. In 1855, however, he incorporated this monotypic genus in *Calotis* with the note "the genus *Cheiroloma* may be referred as a fifth section to this genus" (i.e. *Calotis*).

The type series consists of several well preserved specimens in the Melbourne Herbarium from which a lectotype was selected.

Variation in the large series examined was found to be slight and was chiefly confined to the size of the plants. While the mean length of the branches was about 10 cm., dwarf fruiting specimens of 1.5-2.5 cm. in height were seen from all States, and in these the infructescences were hardly smaller than those of normal-sized plants. Plants in which the leaves were all entire were seen only from the Eucla and Nullarbor Plains areas.

Variation in leaf size was sometimes marked, but appeared to have no taxonomic significance.

The ray florets were always minute and often difficult to find in dried specimens owing to withering of the ligule, and it is chiefly the disc florets which give the yellow or yellowish-green colour to the inflorescences.

The number of infructescences varied with the size of the plant, some bearing many hundreds in tight cymose panicles.

As already noted, the points of resemblance between this species and *C. squamigera* are so many that close relationship is reasonably assumed. Comparison of vegetative features is most satisfactory when both species are growing together in the same situation and such was the case in a folder of specimens from Blackall. In these, *C. hispidula* possessed many slender branching stems arising from the base, with few or no radical leaves, whereas those of *C. squamigera* bore a solitary inflorescence at ground level from below which branches and radical leaves were given off. This distinction was also observed in specimens from other localities and is of use in field identification. Differences in the fruits of the two species have already been discussed in connection with *C. squamigera*.

S. CALOTIS ERINACEA Steetz in Lehmann, *Pl. Preiss.* (1845), 424. (Text-figs. 42-56.)

C. erinacea var. *parviflora* Benth., *Fl. Aust.*, III (1866), 503; *C. erinacea* var. *hirsutata* J. M. Black, *Fl. S.Aust.* (1929), 590.

Type data: "Only in rather muddy situations, Hay, November, 1840. Herb. Preiss No. 2427 (Drummond)".

Lectotype, "New Holland (Swan River Colony) in rather muddy situations, Hay, coll. Preiss (Herb. Preiss No. 2427), received 1843" (MEL).

Much branched erect or straggling glabrous perennials, up to 80 cm. high. *Leaves* cauline, sessile, the lower linear to broad-linear or linear-cuneate, occasionally elliptical, acutely toothed from the base or only distally, rarely entire, up to 6 cm. long, 7 mm. broad. *Upper leaves* acute or acuminate, usually entire. *Inflorescences* up to 70. 1.5-1.7 mm. diameter. *Involucral bracts* 10-22, 2.5-4.5 mm. long, 0.8-2.5 mm. broad, lanceolate to broad-elliptical, entire or microscopically serrulate, obtuse to subacute, glabrous. *Ray florets* 24-50, the rays 5-5.6 mm. long, 1.5-1.7 mm. broad, yellow. *Receptacle* hemispherical to conical, 1-2 mm. broad, 1-2 mm. high, with membranous septa between the florets produced into scale-like structures. *Fruits* light to dark brown, the body flattened and enclosed apically by the expanded bases of the awns forming a collar; exposed portion of body cuneate, 1.5-3 mm. long, 1.6-2.4 mm. broad. Awns commonly 2-4 or 7-9, barbed only distally or along their whole length, 0.5-3.5 mm. long, equal in length when only 2 or 4 present, otherwise variable.

Habitat: Sandy soil in low rainfall areas.

Range: Throughout Central and South Australia, extending into the western districts of Queensland, New South Wales and Victoria; south-west division of Western Australia.

Specimens examined:

Queensland: Between Tambo and Blackall, plentiful on sand ridges, 2-3 ft. high, 9.9.1937, L. J. Brass and C. T. White 29 (BRI); Tambo, densely branched subshrub, common in large patches on sandy hillside north of the town, florets yellow, 9.12.1935, S. L. Everist 1,452 (BRI); Currawilla, on deep loose red-brown sandhill, shrub about 2 ft., with numerous spreading intricately branched stems, leaves and stems dark green, with powerful smell of *Eugenia uniiflora*, 15.6.1949, S. L. Everist 4,017 (BRI); Arrabury, 25.5.1924, J. B. Cleland (JBC); near Kyabra, common, sandhills, 17.1.1937, S. L. Everist and L. S. Smith 79 (BRI); Mt. Howitt Sta., 80 miles west of Eromanga, on drift sand on lower part of sandhill, bushy deep green shrub of about 2 ft., 4.7.1936, S. T. Blake 11,925 (BRI); Charleville, in open places on sand, ca. 1000 ft., bushy, 2-3 ft. high, 4.4.1936, S. T. Blake 11,015 (BRI); Yappunya, near Thargomindah, 1885, Spencer (MEL); Offham, common on sand ridges, subwoody perennial, 28.3.1941, C. T. White 11,826 (BRI); Cunnamulla, on sand in cemetery enclosure, ca. 600 ft., dense bushy perennial, 29.4.1934, S. T. Blake 5,611 (BRI); Gilruth Plains, 17.9.1938, S. L. Everist 1,632 (BRI); between Stokes Range and Cooper's Creek, Wheeler (NSW 14,611; MEL); Wilson River, 4.9.1923, W. MacGillivray (BRI).

New South Wales: Grey Ranges (MEL); near Barrier Range, sand ridges, 19.8.1891, R. Helms (AD); 60 miles from Wentworth, 20.8.1946, J. Vickery (NSW 2,033); Zara, via Hay, 12.1913, E. Officer (NSW 14,995); Conargo, 19.12.1906, A. G. Mayne (NSW 14,612); Deniliquin (NSW 14,970); Mathoura, sand ridges, 5.1947, J. F. Feagan (NSW 14,616); Tocumwal, 9.1891 (NSW 14,613).

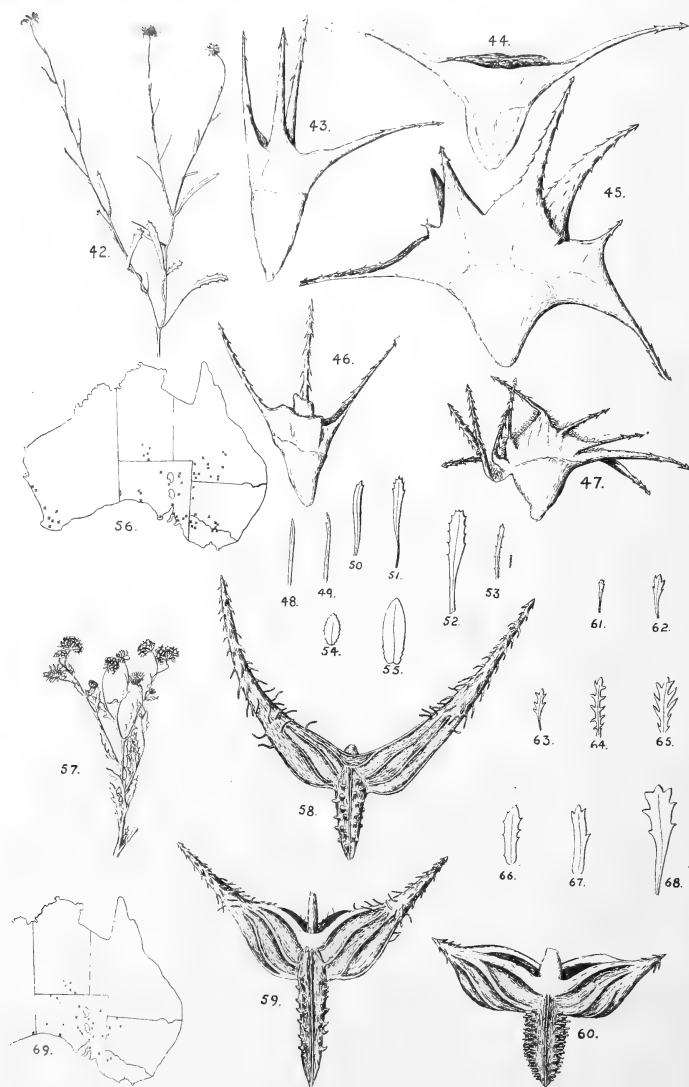
Victoria: Ouyen, 30.3.1911, G. McIntyre (MEL); Cow Plain, 1895, St. Eloy D'Alton (MEL); Lake Albacutya, 10.1907, C. S. Sutton (MEL); Hopetoun, 10.1897, Brymer (MEL); Echuca (MEL).

Northern Territory: Macdonnell Ranges, 1894, sand hills, subshrubby, 3 ft., R. Tate (AD); Alice Springs, 28.9.1939, B. A. Dale (NSW 14,609); Finke River, 8.8.1931, J. B. Cleland (JBC).

South Australia: Between Flinders Range and Charlotte Waters, 1885, H. Kempe (MEL), Cooper's Creek, 10.1920, W. MacGillivray (NSW 14,608); Warrina, 4.1891, R. Helms (AD); Stuart's Creek (MEL); Hamilton Bore, 7.1.1927, J. B. Cleland (JBC); Port Augusta, 1885, A. Richards (MEL); Port Augusta, 1.9.1941, J. B. Cleland (JBC); northern part of Yorke's Penin., 1869, Salmon (MEL); Pincry, Port River, 1.10.1927, J. B. Cleland (JBC); Holdfast Bay and Port Adelaide, F. Mueller (MEL); Berri, 1.1921, J. B. Cleland (JBC); Loxton, 21.8.1924, J. B. Cleland (JBC); River Murray Plain, 5.1.1884 (AD); near Spencer's Gulf, 1881, Lattorf (MEL); Boston Point, F. Mueller (MEL); north of Fowler's Bay, 1875, E. Giles (MEL); Pidinga, 1880, Richards (MEL); Ooldea, 11.9.1920, E. H. Ising (MEL; BRI; NSW 14,617); Ooldea Soak, 5.11.1934, N. B. Tindale (AD).

Western Australia: Greenough Flat, C. Gray (MEL); Moore River, Mogumber, 10.1903, W. V. Fitzgerald (NSW 14,614); Wickopin, 7.1915, W. J. Petticrew (P); Lake Wagin, 1890, M. Cronin (MEL); Stirling Range, 11.1881, J. Forrest (MEL); Gordon River, Oldfield (MEL); New Holland (Swan River Colony) in rather muddy situations, Hay, Preiss No. 2,427 (MEL).

The two type specimens from which the lectotype was selected are accompanied by an envelope of fruits, and attached to a herbarium sheet bearing the determination "*Calotis erinacea nobis*" and locality data in Steetz's handwriting, the date "1843" referring to receipt of the specimens by Steetz, and not to their collection. Their leaves are, unfortunately, rather fragmentary, but according to Steetz (1845) they are "sessile, slightly stem-clasping, linear-lanceolate or linear, acute, with a single vein which is prominent on the lower surface, entire or rarely with a single deep tooth, tapering distally, the lower ones 1-1½ inches, the upper shorter, narrower and more sparse". The only specimens examined by the present writer in which all the leaves were entire were also from Western Australia (Lake Wagin and Gordon River), which suggests that this condition is confined to the western portion of the range. In the eastern States it is quite common for only the lower leaves to be toothed and a fragment



Text-figures 42-69.

42-56, *C. erinacea*.—42, Habit $\times 0.3$; 43-47, Variation in fruits $\times 6.3$; 48-55, Variation in lower cauline leaves $\times 0.3$; 56, Distribution; 57-69, *C. cymbacantha*.—57, Habit $\times 0.3$; 58-60, Variation in fruits $\times 9$; 61-68, Variation in lower cauline leaves $\times 0.3$; 69, Distribution.

from the upper portion of such a plant gives an incorrect impression of the type of leaves present.

Leaf shape varies little throughout the range except for the occurrence of ovoid, almost stem-clasping, leaves on certain specimens from Queensland (Arrabury, Currawilla, Tambo, Kyabra) and South Australia (Eudunga, Hamilton Bore, Andado, Pidinga). This character, unsupported by others, was not considered sufficient to justify separate taxonomic status.

The fruits of this species are remarkable in their variability not only between those of different plants (Text-figs. 43-47), but within the same infructescence. When only two awns are present they are opposite, divaricate in the same plane as the flattened body of the fruit, and the united awn-bases form an entire and relatively deep collar-like structure. The presence of a third awn intermediate between the basic pair is a common variation. When four awns are present, as in the type series, they are equidistant from each other, and the junction of their expanded bases is marked by an indentation. An interesting series of fruits was seen in an infructescence from Erludurda in which some bore 2 or 3 awns and an entire collar, and in others the collar was regularly dissected into short projections between the three major awns. A further development of this condition was shown in specimens from Charleville, in the fruits of which there were four major awns, two of medium length, and three or four short acute projections of the collar with 2-5 barbs at their tips. An evolutionary series can be traced from the 2-awned condition to the 3-, 4- and more-awned state by the development of supernumeraries between the major awns. In their evolution, the supernumeraries progress from mere lobes of the collar, to barbed lobes, then to small but definite awns, and finally to the climax condition seen from a number of localities, in which 7-9 awns of approximately equal length are present and the collar lobed accordingly. It was on such fruits that Bentham (1866) described var. *parviflora* ("Durandoo, Victorian Expedition") for which a lectotype was selected but the variety was not confirmed since it appears to represent merely a variational peak.

On the basis of awn number, plants fall into two groups—those in which 2, 3, 4 or occasionally 5 awns are present, and those with 7, 8, 9 or, rarely, more. All Western Australian specimens belong to the first group, but in other States their occurrence is equal and both are found over the same range. Further collecting may well produce specimens which bridge this apparent discontinuity, and in view of the variation in awn number in the same infructescence, varieties based on this character alone are not upheld.

Bentham (1866) stated: "*Huenefeldia angustifolia* Walp. in *Linnaea*, XIV, 506, which I have not seen, is, from the description, most probably this species." Unfortunately Walpers' specimens have not been traced and the original description* conveys little idea of the plant in question. Should Bentham be correct in his supposition, Walpers' epithet must take priority over that of Steetz, but until such time as the specimens are located and examined the latter is retained.

9. *CALOTIS CYMBACANTHA* F. Muell., *Linnaea*, 25 (1852), 400. (Text-figs. 57-69.)

C. cymbacantha F. Muell., var. *pumila* Benth., *Fl. Aust.*, 3 (1866), 502.

Type data: "On barren slopes near Crystal Brook."

Lectotype, "On barren slopes near Crystal Brook, 10.1851, F. Mueller" (MEL).

Erect branching herbs up to 40 cm. in height, with a septate-hairy indumentum. *Radical leaves* 6-9 cm. long, spatulate, acutely toothed distally, tapering proximally into a long petiole, but only present on young plants. *Cauline leaves* up to 6.6 cm. long, sessile, broad-linear to spatulate in general outline, either with coarse teeth which are evenly distributed or distal in position or leaves may be pinnatifid to pinnatipartite. *Inflorescences* up to 60, 1.5-2 cm. diameter. *Involucral bracts* 15-20, 3.8-5 mm. long, narrow-elliptical, entire, acute to acuminate, densely septate-hairy on outer surface. *Ray florets* 18-30, the rays 4.6-5 mm. long, 1.2-1.5 mm. broad, yellow. *Receptacle*

* "Much-branched bush; branches erect, angular; leaves linear-lanceolate, entire, hardly pubescent; inflorescences terminal, solitary—growing in New Holland."

1.3-2 mm. broad, 0.6-1.5 mm. high, hemispherical, with a honeycombed appearance due to ciliate septa between the bases of the florets. *Fruits* brown, the exposed portion of the body cuneate, flattened, tuberculate on each face, 2.0-2.8 mm. long. Distal quarter to third of body enclosed in a boat-shaped structure formed by the united bases of the two rigid divaricate awns which are placed at right angles to the flattened face of the fruit. Awns 1.7-6 mm. long, bearing distally a number of backwardly directed barbs which are represented proximally by white unicellular hairs of the same length.

Habitat: No data available.

Range: Central and South Australia, extending into western New South Wales and the Wimmera district of Victoria.

Specimens examined:

New South Wales: Queensland border north and a little west of Broken Hill, 4.1917, MacGillivray (NSW 14,605; AD); Cobham Lake, 1887, W. Bauerlen (NSW 14,602; MEL); Barrier Range, 1889, Irvine (MEL); near Silverton, 7.1889, Irvine (MEL); Burke's Cave, Darling River, 1.8.1893, Tepper (MEL); Darling River, Dallachy (MEL).

Victoria: Murray River, F. Mueller (MEL); Cocamba to Ouyen, 9.1921, H. B. Williamson (MEL); Underpool, 9.1918, J. Malone (MEL).

Northern Territory: Ooraminna Pass (AD); Deep Well, 25.8.1931, J. B. Cleland (JBC); the Goyder, 1894, R. Tate (AD; NSW 14,597); between Youldeh and Charlotte Waters, E. Giles (MEL); south of Charlotte Waters, 9.1885, H. Kempe (MEL); about 30-80 miles east of Ernabella, 23.9.1945, J. B. Cleland (JBC); Ernabella, 13.7.1943, L. B. Young (MEL); half-way between Morrilyan and Ernabella; 7.8.1933, J. B. Cleland (JBC); between Ernabella and Echo Hill, 20.8.1933, J. B. Cleland (JBC); border of Northern Territory and South Australia, 7.1926, H. Basedow (NSW 14,598).

South Australia: Warrina, 1890, Richards (MEL); Strzelecki (AD); Stuart Range, C. French (MEL); N. of Marree, 26.8.1931, J. B. Cleland (JBC); Mt. Lyndhurst, 8.1898, M. Koch (AD; MEL; NSW 14,601); Bitter Well, Coondambo, 28.10.1929, J. B. Cleland (JBC); Parachilna, 20.8.1921, J. B. Cleland (JBC); Arcoona, west of Lake Torrens, sand, 2.8.1927, B. J. Murray (AD); south of Bookaloo, 5.11.1929, J. B. Cleland (JBC); between Flinders Range and Lake Torrens, T. P. Richards (MEL); Koonamore Vegetation Reserve, 31.7.1928, T. B. Paltridge (AD); Mingary, 14.8.1921, A. Morris (NSW 14,604; BRI); 25 miles north of Port Augusta, 28.10.1939, J. B. Cleland (JBC); Port Augusta, A. Richards (MEL); Spencer's Gulf, 1878, Felstead (MEL); towards Spencer's Gulf, Warburton (MEL); in clivis arenosis prope Crystal Brook, 10.1851, F. Mueller (MEL); Mantung district, 18.8.1924, J. B. Cleland (JBC); Hundred of Mantung, 1.1911, W. Gill (NSW 14,600); Wynbring, 20.9.1920, E. H. Ising (NSW 14,603); Ooldea (AD); Fowler's Bay, 10.1907, T. Brown (NSW 14,599).

Western Australia: Eucla, 1877, A. Richards (MEL).

Vegetative variation concerns the degree of dissection of the leaves and the amount of indumentum on stem and leaves. The type specimens have pinnatifid cauline leaves, becoming toothed and smaller on the upper parts of the plant, and the awns of the fruits are 2.5-3 mm. long, with the barbed portion equal in length to the expanded base.

Bentham (1866) described var. *pumila* on material collected by Dallachy from "the Darling River to Cooper's Creek", the fruits of which were slightly different from those of the type series in that their awns bore more barbs and their thin distal portions were longer. Measurement of the awns of all specimens examined by the present writer showed continuous variation from those of 6 mm. to the other extreme where they were represented by little more than the expanded bases (Text-figs. 58-60). These bases differed little in size throughout the series, and variation in awn length involved only the thin distal portion. Although a haptotype was selected, var. *pumila* is not regarded as representing a distinct population to the parent species.

The longevity of this species remains still to be established. Bentham (1866), following Mueller (1852), stated "apparently perennial", and for his var. *pumila*, "flowering the first year so as to appear annual". Black (1929), on the other hand, stated "probably always annual".

10. *CALOTIS LAPPULACEA* Benth., *Enum. Pl. Hueg.* (1837), 60. (Text-figs. 70-79.)
C. microphylla Benth. in *Enum. Pl. Hueg.* (1837), 60; *C. polyseta* Sond., *Linnæa*.
 25 (1852), 470; *C. suffruticosa* Domin., *Biblioth. Bot.*, 89 (1929), 655.

Type data: "Ferd. Bauer."

Haptotype, Australian Journey, 1802-5, R. Brown (MEL).

Much branched leafy perennials up to 47 cm. high, more or less septate-hairy all over, woody at the base with a thick tap root. *Radical leaves* present only on young plants, up to 6 cm. long, 8 mm. broad, cuneate, toothed or pinnatifid. *Cauline leaves* linear and entire or acutely toothed to pinnatifid, sessile, up to 2.5 cm. long, 4 mm. broad. *Inflorescences* over 200 on an established plant, 1.7-8 mm. diameter. *Involucral bracts* 14-22, 2-3 mm. long, 0.5-1.1 mm. broad, obtuse to subacute, linear, entire, sparsely hairy with ciliolate margins. *Ray florets* 44-60, the rays 2.5-3.5 mm. long, 0.5-0.7 mm. broad, yellow. *Receptacle* up to 1.2 mm. broad, 0.5 mm. high, truncate-conical with scale-like septa between the bases of the florets. *Fruits* light to dark brown, the body cuneate, flattened, minutely tuberculate, glabrous, 1.2-1.6 mm. long, 1-1.1 mm. broad; two erect or slightly diverging major awns pass off at right angles to the flattened face, and equal to or slightly exceed the body in length. Secondary awns are almost horizontal in position and seldom exceed 0.7 mm. in length; those facing the periphery of the capitulum form a group of 3-6, which are basally united and give the fruit a lipped appearance when seen from above; the opposite corner of the fruit summit is occupied by a single awn, and occasionally short supernumeraries are also present. All awns are barbed distally and bear septate hairs at the base.

Habitat: On various types of soil in open forest and cleared land.

Range: Widely spread throughout the eastern States with an occasional record in South Australia and Western Australia.

Specimens examined:

Queensland: Burdekin River, Suttor (MEL); Charters Towers (BRI); Oakley, on sparsely timbered low sandy ridge, ca. 600 ft., stems numerous, tufted, spreading to erect, ca. 6 in., 2.6.1936, S. T. Blake 11,649 (BRI); near Mueller River, 1881, C. W. Birch (MEL); Dunrobin, 1890, M. Walker (MEL); Jericho, 3.1946, M. S. Clemens (BRI); Yalleroi, in mixed open forest on reddish sand, ca. 1160 ft., 15.7.1934, S. T. Blake 6,774 (BRI); Blackall, very common on sandy aerodrome, 24.8.1935, S. L. Everist 1,230 (BRI); Peak Downs, G. Burkitt (MEL); Emerald, on open sandy ground, ca. 600 ft., fls. bright yellow, 19.7.1934, S. T. Blake 6,915 (BRI); Comet, in sandy soil, open *Eucalyptus* forest country beside railway trucking yards, 3.4.1946, S. L. Everist (BRI); Springsure, 1870, Wirth (MEL); Expedition Range, 1878, Thozet (MEL); Daringa, 3.1909, J. H. Maiden (NSW 14,747); Canal Creek, 1882, Hartmann (MEL); Rockhampton, scrubby open places, P. O'Shanesy (MEL); Marmon, 3.1920, W. D. Francis (BRI); Gladstone, A. Dietrich (MEL); Mt. Perry, 6.1929, C. S. Sutton (MEL); Gympie, F. H. Kenny (BRI); Boatman Station, in red-brown fine sandy loam with ringbarked Box and low mulga, shady situation, 21.3.1947, S. L. Everist (BRI); between Westgate and Myndetta, in railway enclosure, ca. 950 ft., 26.4.1934, S. T. Blake 5,526 (BRI); Mungallala, 8.1913, W. Dunn (NSW 14,754); Wandoan, in open *Eucalyptus populifolia* forest and *Aristida* sp. on heavy soil, about 900 ft., 5.11.1930, C. E. Hubbard 4,969 (BRI); Bungewin, 25.10.1933, C. T. White 9,535 (BRI); 21 miles west of Bollon, on clay loam at foot of hard red ridge, prostrate herb, 7.8.1946, S. L. Everist 2,599 (BRI); Roma to Surat, C. S. Sutton (MEL); Surat, 1892, H. Wehl (MEL); Condamine River (MEL); Dalby, 4.1916, C. T. White (BRI); Toowoomba, 1886, F. A. Hood (MEL); 2 miles south of Pittsworth, in shallow chocolate clay loam, basalt, in open parkland with *Eucalyptus melliodora*, *Stipa* spp., S. L. Everist and L. J. Webb 1,236 (BRI); Moreton Bay, C. Stuart (MEL); Ipswich, 12.1908, T. F. Hall (BRI); near Laidley, on railway bank amongst grasses, in sandy loam, ca. 335 ft., 5.7.1930, C. E. Hubbard 3,223 (BRI); between Laidley and Granchester, moderately common on railway embankment, 5.9.1930, C. T. White 6,830 (BRI); Forrest Hill, on railway station, 297 ft., 28.11.1930, C. E. Hubbard (BRI); Gatton College, in dark brown silty clay on top of creek bank, fls. pale yellow, 26.2.1947, S. L. Everist 2,731

(BRI); Goomburra to East Greenmount, 15.9.1930, M. Ramsay (BRI); Silverwood, 9.1922, C. T. White 1,750 (BRI); Noondoo Station, east of Dirranbandi, weed in sandy land, 15.12.1934, S. L. Everist 794 (BRI); Killawarra, Moonie River, common in red sandy soil, 4.1939, S. L. Everist 1,799 (BRI); Kindon Station, about 54 miles N.N.E. of Goondiwindi, 5.12.1938, L. S. Smith 519A (BRI); Texas, 9.1910, J. L. Boorman (NSW 14,746).

New South Wales: Angledool, red slightly sandy soil, 1.7.1913, C. T. Musson (NSW 14,764); Yetman, 2.1949, E. G. Jacobs (NSW 14,7712); Tenterfield, C. Stuart (MEL); Clarence River, Beckler (MEL); Emmaville Hill, 1.1911, J. L. Boorman (NSW 14,787); Wallangrah, w. of Inverell, 10.1929, N. J. Rodway (FAR); Mt. Russell, 1.2.1915, E. Breakwell (NSW 14,786); Gravesend, 5.1914, W. M. Carne (NSW 14,785); Ashley, 1.1925, E. H. Zeck (NSW 14,748); Baldersleigh, 25 miles west of Guyra, 6.11.1947, E. N. McKie (NSW 14,775); Baker's Creek, on Grafton road, 16 miles from Armidale, open Eucalypt forest, granite soil, 18.3.1951, G. L. Davis (NE); between Armidale and Uralla, roadside, 14.2.1940, G. L. Davis (FAR); Saumarez, 3500 ft., grassland, 14.2.1940, G. L. Davis (NE); George's Creek, Macleay River, 860 ft., grassland, 16.1.1941, C. Davis (NE); Barraba, 10.1912, H. M. Rupp (NSW 14,765); Narrabri, 1.1883, E. Betche (NSW 14,800); Boggabri, 11.1909, R. H. Cambage (NSW 14,799); Namoi, 1890, Musson (MEL); Gunnedah, 3.1914, W. L. Waterhouse (NSW 14,784); Tamworth, 20.10.1909, J. B. Cleland (AD); Walcha, 1884, A. R. Crawford (MEL); Baradine, 7.1947, K. Walton (NSW 14,782); Coonabarabran, 9.1916, J. L. Boorman (NSW 14,770); Binnaway, 5.1933, J. Rodway (FAR); Curlewis, 8.1913, E. Breakwell (NSW 14,760); Merriwa, 14.3.1924, E. Cheel (NSW 14,803); Wingen, 10.1909, R. H. Cambage (NSW 14,761); Scone, 8.1913, E. Breakwell (NSW 14,767); Belltrees, 2.1920, H. L. White (NSW 14,762); Bruschy Mts., 9.1897, J. H. Maiden (NSW 14,752); Clover Creek, Bourke, 1890, J. Mackay (MEL); Bourke to Cobar, 27.8.1926, C. S. Sutton (MEL); Cobar, 22.9.1924, A. Morris (NSW 14,792); Girilambone, 1.1917, J. L. Boorman (NSW 14,790); Nyngan, 5.1913, J. H. Maiden (NSW 14,776); Nevertire, 12.1923, A. Morris (NSW 14,789); Dubbo, 12.1907, J. L. Boorman (NSW 14,774); Gulgong, 4.1901, J. H. Maiden and J. L. Boorman (NSW 14,795); Wellington, 10.1883, E. Betche (NSW 14,791); Mudgee, 1870 (MEL); Euchareena, 6.1900, J. L. Boorman and C. Walter (MEL); 50 miles from Rylstone, near the Goulburn River, 10.1893, R. T. Baker (NSW 14,750); Capertee, 1.1.1900, J. L. Boorman (NSW 14,768); Manildra, 11.1907, J. L. Boorman (NSW 14,793); Bathurst, 1.1911, J. B. Cleland (AD); Newcastle, 1919, R. D. Rhone (MEL); Horse-shoe Bend, Grose Vale, 3.1910, W. M. Carne (NSW 14,758); Blackheath, 4.1909, J. H. Maiden (NSW 14,778); Hawkesbury Agricultural College, Richmond, 10.4.1910, W. Greenwood (NSW 14,766); Nepean River, 14.1.1888 (NSW 14,805); Penrith, 11.1912, E. Breakwell (NSW 14,757); Parramatta, 1871, W. Woolls (MEL); Cowan, 26.1.1918, W. F. Blakely (NSW 14,804); Asquith, on railway line, 6.1918, W. F. Blakely (NSW 14,797); Rookwood, 7.5.1881, J. J. Fletcher (NSW 14,802); Hurstville, 5.1901, J. H. Camfield (NSW 14,794); Como, 17.9.1881, J. J. Fletcher (NSW 14,806); Camden Park, 15.11.1949, L. A. S. Johnson (NSW 14,773); between Camden and Picton, 25.5.1930, F. A. Rodway (FAR); Shoalhaven River, at Nowra, roadside, 31.1.1943, F. A. Rodway (FAR); Cowra, E. Breakwell (NSW 14,753); Lachlan River, 9.1878, F. Mueller (MEL); Temora, 11.1915, J. W. Dwyer (NSW 14,781); Murrumbidgee River, 9.1878, F. Mueller (MEL); Wagga, 10.1881, J. J. Fletcher (NSW 14,801); junction of the Darling and Murray Rivers, 7.1889, Holding (MEL); on stony ridges near the Snowy River (MEL); Snowy River, 10.1851, F. Mueller (P); near the Snowy River, south of Jimenbuen, white Box-pine association, 23.11.1948, A. B. Costin (NSW 14,771); Kameruka, near Bega, dry roadside, 30.3.1937, F. A. Rodway (FAR); Mt. Imlay, near Eden, 12.1916, J. L. Boorman (NSW 14,763).

Victoria: Lower Hume's River and Mitta Mitta, 1.1874 (MEL); Neumerella, 28.5.1902, Grove (MEL); Orbost, 5.1902, J. Rowe (MEL); Tabberabbera, 11.1930, Birch (MEL); dryish stony walls of Deacock Creek, Jungle Gully, near Glendadale, 26.1.1946, J. H. Willis (MEL); Deddick Creek, growing with *Cymbopogon refractus* on dry

granitic slopes, 17.1.1948, J. H. Willis (MEL); Gippsland, 1882, Howitt (MEL); Bacchus Marsh, 3.11.1910, J. R. Tovey (MEL).

South Australia: Flinders Range, 10.1851, F. Mueller (MEL); Torrens River, 3.1847, F. Mueller (MEL); Cudnaka, F. Mueller (MEL); around the city of Adelaide, 28.12.1847, F. Mueller (MEL); Murray Pine Scrubs, 10.1886, C. French (MEL).

Western Australia: Between Esperance Bay and Fraser's Range, 1876, Bempster (MEL); south-west Australia (MEL).

Among Steetz's specimens in the Melbourne Herbarium is an envelope containing infructescences of this species, and labelled "e specimine Bauerianae herb. aulicae Vindobonn". These fragments were presumably removed by Steetz from the type specimen and have been used in the present work as a basis of comparison for fruit characters. Another folder is labelled "Iter Australiense, 1802-5, R. Brown", and contains three specimens, one of which bears mature fruits identical with those from Bauer's specimen. Since Bauer accompanied Brown on this expedition these specimens may be part of the type series.

C. polyseta is represented in the Melbourne Herbarium by the type specimen ("Cudnaka, F. Mueller") which, although it agrees vegetatively with this species, has fruits which differ slightly in that the 2-lipped appearance is less conspicuous, due to the secondary awns being little shorter than the two major ones. Bentham (1866) regarded this species as "a very slight variety of *C. lappulacea*, with rather larger flower heads", and since the fruits have not been matched with those of any other specimens this synonymy is followed.

C. suffruticosa was described by Domin from a specimen collected by himself in 1910 ("savannah woodland near Jericho, Q.") and the type material has not been traced. According to Domin (1929) this species is allied to *C. lappulacea*, but differs in the involucre, the fact that the capitula are twice the size, and that the fruits bear two elongate awns and many short ones. The original description does not state in what way the involucre is distinctive, and the size of the capitulum is of little significance when a number of specimens are compared, while the awn characters mentioned by Domin as points of difference from *C. lappulacea* are actually ones of resemblance. The question does arise as to whether the material with which Domin compared his specimen was actually *C. lappulacea*. According to White (1946) these two species are to be distinguished by *C. lappulacea* having a "pappus of 4-8 unequal free awns", whereas *C. suffruticosa* has a "pappus of two awns with a number of very reduced ones or setae united at the base". This distinction cannot be upheld since all the specimens listed above conformed to the second species and none were seen in which all the awns were free.

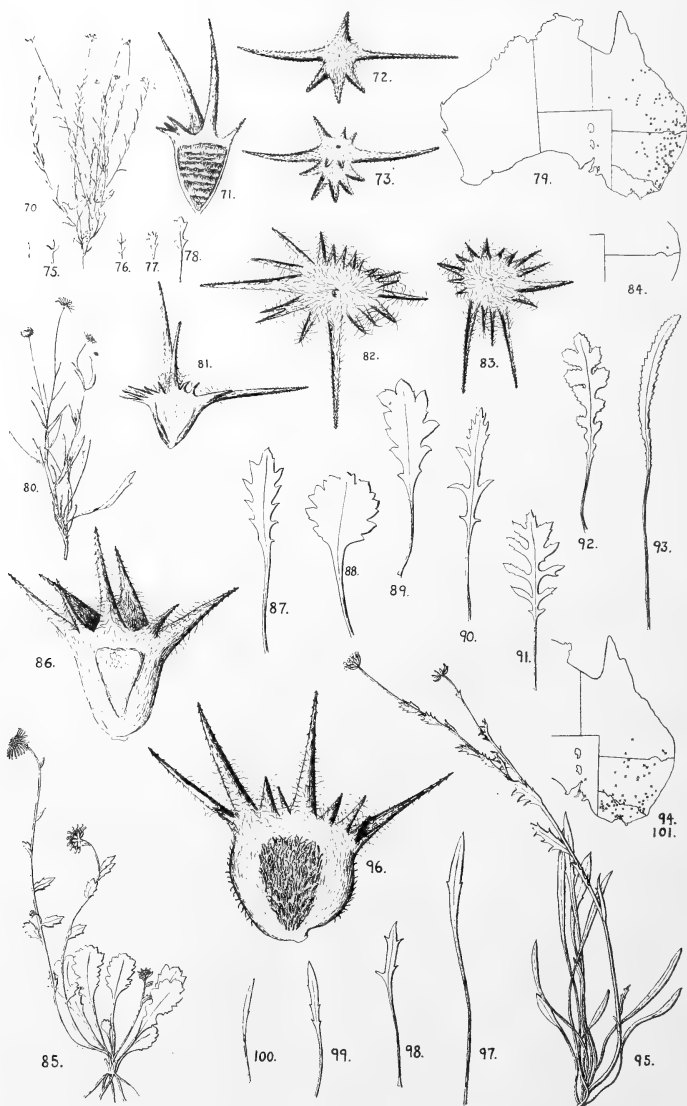
C. microphylla ("Ferd. Bauer") was described by Bentham at the same time as *C. lappulacea* from which he distinguished it as having "capitula a little smaller, more hispid, the awns shorter and less strong". These differences, however, are not taxonomically significant, and consequently *C. microphylla* is relegated to the synonymy implied by Bentham in not referring to it in "Flora Australiensis".

The general facies of *C. lappulacea* is very constant despite some slight variation in the shape of the lower cauline leaves, which, however, are usually obscured by the much-branched habit of the plant. Variation in the fruits is confined to the number of supernumerary spines and does not affect the characteristic 2-lipped appearance when seen from above. In certain specimens a second tier of very short awns is present (Text-fig. 73).

11. CALOTIS GLABRESCENS C. T. White, *Proc. Roy. Soc. Q.*, 57 (1946), 30. (Text-figs. 80-84.)

Holotype, Darling Downs: Bybera, between Inglewood and Milmerran, moderately common in open forestland, herb, fls. white, turning to purple when drying, 20.9.1944, C. T. White (BRI).

Slender erect perennials up to 15 cm. high, branching from the base and subsequently, with a few scattered septate hairs on the leaves and stems. *Leaves* cauline,



Text-figures 70-101.

70-79, *C. lappulacea*.—70, Habit $\times 0.3$; 71, Fruit $\times 9$; 72-73, Variation in fruits, apical view $\times 9$; 74-78, Variation in lower cauline leaves $\times 0.3$; 79, Distribution; 80-84, *C. glabrescens*.—80, Habit $\times 0.3$; 81, Fruit $\times 6.3$; 82-83, Variation in fruits, apical view $\times 6.3$; 84, Distribution; 85-94, *C. scabiosifolia* var. *scabiosifolia*.—85, Habit $\times 0.3$; 86, Fruit $\times 6.3$; 87-93, Variation in radical leaves $\times 0.3$; 94, Distribution (\times); 95-101, *C. scabiosifolia* var. *integrifolia*.—95, Habit $\times 0.3$; 96, Fruit $\times 6.3$; 97-100, Variation in radical leaves $\times 0.3$; 101, Distribution (\bullet).

up to 5.5 cm. long, 3 mm. broad, narrow-oblongate to linear, acute, entire or with a single lateral tooth. Upper leaves sessile, the lower basally attenuate. *Inflorescences* up to 16, 1.8 cm. diameter, on terminal or axillary naked peduncles. *Involucral bracts* about 16, 2.5-3.5 mm. long, 0.7-1 mm. broad, linear, obtuse, entire, septate-hairy. *Ray florets* about 30, the rays 6.5 mm. long, 1 mm. broad, white. *Fruits* dark brown, the body cuneate, 1.5-1.7 mm. long, 1.5-2 mm. broad, glabrous, with 2-3 rigid major awns 2-3.2 mm. long, distally barbed and proximally hairy, horizontal in position but not constant in arrangement and interspersed with very short awns which bear numerous long hairs and are not barbed.

Specimens examined: Type series only.

White (1946) expressed the opinion that this species was most closely allied to *C. suffruticosa*, but as has been pointed out above, all specimens of that species in the Brisbane herbarium fall well within the specific limits of *C. lappulacea*, and his statement must be modified accordingly. Although the type series is composed of seven specimens, only one of them bears fruits, and the wisdom of establishing a new species on such scanty material might well be questioned when such a close similarity exists to another species. The chief distinguishing feature from *C. lappulacea* is the awn arrangement which itself was found to vary within the head, some fruits being indistinguishable from those of *C. lappulacea*. Whether this is a valid species or not cannot be decided until further material is collected.

12. *CALOTIS SCABIOSIFOLIA* Sond. et F. Muell., *Linnaea*, 25 (1852), 471.

Erect septate-hairy stoloniferous perennials up to 44 cm. high, with a basal cluster of leaves. *Radical leaves* up to 18.5 cm. long, 7-40 mm. broad, petiolate, linear and entire or lanceolate to elliptical and toothed, pinnatifid or pinnatipartite, the segments sometimes again toothed. Upper cauline leaves sessile, entire or acutely toothed. *Inflorescences* up to 31, 1.7-3 cm. diameter. *Involucral bracts* 18-30, the outer 3.5-9 mm. long, 1.3-4 mm. broad, elliptical, subacute to acuminate. *Ray florets* 15-65, the rays 7.5-12 mm. long, 1.2-3 mm. broad, white or mauve. *Receptacle* 3.5-4 mm. broad, 1.5 mm. high, hemispherical, pitted, with long narrow scale-like septa between the bases of the florets. *Fruits* pale to dark reddish-brown, 2.7-4 mm. long, 1.6-3.5 mm. broad, cuneate, flattened. Major awns 5-6, stout, rigid, microscopically barbed distally, proximally hairy, 0.8-4 mm. long. Secondary awns, when present, 0.5-1 mm. long, hairy, without distal barbs, the smallest sometimes obscured by the long woolly hairs.

Key to the Varieties.

Radical leaves distally expanded, serrate or variously dissected.

Body of fruits glabrous on central area var. *α scabiosifolia*.

Radical leaves entire or occasionally with 2-5 linear distal lobes.

Body of fruits with many long appressed hairs on central area var. *β integrifolia*.

C. SCABIOSIFOLIA Sond. et F. Muell., var. *α SCABIOSIFOLIA* comb. et stat. nov. *Linnaea*, 25 (1852), 471. (Text-figs. 85-94.)

C. Muelleri Sond., *Linnaea*, 25 (1852), 470.

Type data: "In meadows near Wulpena, Octob. Murray."

Lectotype, "Wulpena, Nov. Holl. Austr., Ferd. Mueller" (MEL).

Radical leaves lanceolate to elliptical in gross outline, serrate, pinnatifid or pinnatipartite, the segments entire or serrate. The leaf blade tapers, often abruptly, into a petiole of approximately the same length as the blade. Fruits with 5-6 robust apically barbed and proximally hairy awns; body glabrous.

Habitat: No data.

Range: Southern Queensland, western New South Wales and Victoria, Spencer's Gulf district of South Australia.

Specimens examined:

Queensland: Charleville, 1869, E. Giles (MEL); Goomburra, 15.9.1930, M. Ramsay (BRI); Darling Downs district, about three miles S.E. of Blaxland, 13.10.1940, L. S. Smith, S. L. Everist 803 (BRI; MEL).

New South Wales: Warrego River, 9.1885, E. Betche (NSW 14,916); near Queensland border north of Bourke, 9.1884, L. Henry (MEL); Bourke district, O. C. McDougall (NSW 14,926); Warialda, 10.1914, J. L. Boorman (NSW 14,927); Curriwillinghi Walgett, T. C. Dalton (MEL); Namoi River, 3.1887, A. Carson (MEL); Liverpool Plains, Leichhardt (MEL); Coolabah, 10.1900, R. W. Peacock (NSW 14,917); Gular-gambone, 9.1886, Cardell (NSW 14,951); Nyngan and Nevertire, 23.9.1924, A. Morris (NSW 14,925); near Cobar, 9.1910, L. Abrahams (NSW 14,922); near Wilcannia, 27.1.1924, W. MacGillivray (NSW 14,920); Mossgiel, 1885, J. Bruckner (MEL); Condobolin flats, 8.1897, J. H. Maiden (NSW 14,918); Wentworth, 10.1887, J. Minchin (MEL); Darling River, junction with Murray, Dallachy and Goodwin (MEL); Balranald, 1878, Lucas (MEL); Murrumbidgee River, 9.1878, F. Mueller (MEL); Zara, Wanganella, near Hay, 10.1917, E. Officer (MEL; NSW 14,919); Jerilderie, 10.1920, J. W. Dwyer (NSW 14,953); Berrigan, 29.10.1920, J. L. Sones (MEL).

Victoria: Swan Hill, 1890, J. G. Luckmann (MEL); Kerang, 10.1887, J. Minchin (MEL); Prairie, 22.8.1928, C. S. Sutton (MEL); Campaspe River, 10.1875 (MEL); north-west of Lake Albacutya, 9.1887, C. French (MEL); north of Lake Hindmarsh, 10.1892, St. Eloy D'Alton (MEL); Birchip, 11.9.1927, C. S. Sutton (MEL); Jarklin, 9.10.1925, A. Morris (MEL); near Rifle Range, Wycheproof, 9.1917, W. W. Watts (MEL); Jeparit, 16.9.1916, W. R. Baker (MEL); Nhill, 10.1922, J. B. Williamson (MEL); Dimboola, 16.9.1898, F. M. Reader (MEL); Donald, Curdie (MEL); Minyip, 1890, J. P. Eckert (MEL); Horsham, 11.1904, M. Thurman (MEL); Wimmera, Dallachy (MEL); Avoca, 1.12.1853, F. Mueller (MEL); Werribee, Fullagher (MEL); Little River, 1.11.1904, P. R. H. St. John (MEL); between Geelong and Station Peak, 1.1853, F. Mueller (MEL); dry places about Station Peak (MEL); Sydenham, 26.9.1912, P. R. H. St. John (MEL).

South Australia: Wilpena, F. Mueller (MEL); near upper end of Spencer's Gulf, 1887, L. Wehl (MEL); Yorke's Penin., 1888, E. Beythieu (MEL); Cudnaka, 10.1851 (MEL).

Five specimens collected by Mueller at the type locality are in the Melbourne Herbarium, and although three of these are in rather a fragmentary state, the remainder are sufficiently intact to be nominated lectotype and lectoparatype respectively. Both the original description and the label accompanying these specimens cite the locality as "Wulpena", but as no place of that name has been traced, it is thought to refer to "Wilpena".

Sonder described *C. Muelleri* ("Cudnaka") from specimens which differed from *C. scabiosifolia* in the possession of lanceolate, toothed leaves and small tubercles on the flattened faces of the fruits. In the absence of further similar specimens the present writer regards this species as a local variant of *C. scabiosifolia*, thereby following Bentham (1866).

Vegetative variation within var. *scabiosifolia* is very marked in the radical leaves, in which the degree of dissection of the blade is sometimes extreme. Specimens from the Warrego River and Gungerwarildi bear serrate leaves (Text-fig. 92) while those from Coolabah, Nevertire, Nyngan and Hay (Text-figs. 86-88) are coarsely and regularly toothed. Deepening of the indentations between the teeth leads to the pinnatipartite and pinnatisect conditions seen in specimens from Lake Cargellico and Condobolin in which the leaf lobes are commonly themselves serrate (Text-figs. 89-92).

The body of the fruit shows little variation except in size, and long woolly hairs are always present within the circlet of awns. Fruits of the type series bear 5-6 major awns and 2-3 secondary ones, but in the specimens examined by the writer an interesting series was found which may have a bearing on awn phylogeny. At one end of the series are the specimens from the Campaspe River, Jarklin and Darling River, whose fruits bear 6-11 very short awns which are little more than teeth and the barbs are few in number or absent; at the other are those with fruits whose awns equal or exceed the body in length and are provided with numerous backwardly directed barbs. Between these two extremes all intermediate conditions have been found with no correlation in vegetative characters.

C. SCABIOSIFOLIA VAR. β *INTEGRIFOLIA* F. Muell. ex Benth., *Fl. Aust.*, 3 (1866), 503. (Text-figs. 95-101.)

C. scabiosifolia var. *lasiocarpa* F. Muell. ex Benth., *Fl. Aust.*, 3 (1866), 503.

Type data: "Blue Mts., A. Cunningham and others; grassy mountains on the Macalister River and Black Forest, F. Mueller."

Lectotype, "Grassy mountains on the M'Allister River, Gippsland, F. Mueller" (MEL).

Sturdy perennials up to 35 cm. high, with 1-3 main stems. The middle and upper *cauline leaves* are sessile and acutely toothed or lobed, while the radical and lowest *cauline leaves* form a basal cluster, and are up to 15 cm. long, 8 mm. broad, linear to oblanceolate, acute, entire or occasionally with a few narrow acute lobes. *Fruits* bear 4-6 robust major awns which are distally barbed, hairy proximally, and equal to, or exceeding, the body in length, as well as a number of short unbarbed secondaries. The central area of each fruit face is provided with many appressed hairs, and long woolly hairs cover the apex of the fruit and may obscure the bases of the awns.

Habitat: Grassland and open forest.

Range: Central highlands and middle-western districts of New South Wales, to highlands of Victoria.

Specimens examined:

New South Wales: Orange, 11.1907, W. F. Blakely (NSW 14,952); Wallerawang, 11.1899, J. H. Maiden (NSW 14,937); Wingello, 12.1913, J. L. Boorman (NSW 14,938); Cavan, near Yass, I. L. Calvert (MEL); Gudgenby, Queanbeyan, 14.1.1912, R. H. Cabbage (NSW 14,941); near Wagga, 11.1897, J. H. Maiden (NSW 14,940); Yarrangobilly Caves, 2.1897, E. Betche (NSW 14,939); Yarrangobilly Mt., near summit, 12.1.1940, J. Vickery (NSW 14,935); Kiandra, 12.1901, W. Forsyth (NSW 14,946); Monaro, on the mountains, in grass, F. Mueller (MEL); Cooma, widespread in *Stipa* savannah, *E. pauciflora* woodland, *E. melliodora* woodland, dry sclerophyll forest and *E. pauciflora-E. Dalrympleana* forest, 17.11.1948, A. B. Costin (NSW 14,943); Nimity-belle to Tantawango Mts., 12.1896 (AD); Tumberumba, 11.1926, J. W. Dwyer (NSW 14,942); Mt. Kosciusko, gully, among *E. gigantea*, 4.1947, A. B. Costin (MEL).

Victoria: Mitta Mitta, 1.1920, S. F. Clinton (MEL); grassy mountains on the Snowy River, 1.1853, F. Mueller (MEL); Strathbogrie, 11.1901, A. W. Vroland (NSW 14,930); Upper Loddon, 1874, F. Mueller (MEL); Ranges on the Macalister River, 500-3000 ft., F. Mueller (MEL); grassy mountains on the Macalister River (MEL); Upper Yarra, 9.1892, C. Walter (NSW 14,933); Dandenong Ranges, 11.1901, C. Walter (NSW 14,934); Mt. Dandenong, near Devil's Elbow, 1.10.1902, P. R. H. St. John (MEL); Ringwood, 11.1922, A. J. Tadgell (MEL); Dromana, 11.1902, G. Weindorfer (MEL).

Mueller (1866) described var. *lasiocarpa* ("Snowy and Macalister Rivers and Maneroo, F. Mueller") as differing from the species proper by "leaves more rigid, less toothed. Flower heads and achenes larger". Comparison of the type specimens of this and var. *integrifolia*, however, showed that they were not sufficiently distinct to merit separate status. In each case a lectotype was selected and the epithet "*integrifolia*" retained.

Vegetative variation is limited to the occasional presence of a few narrow acute lobes on some of the radial leaves and the degree of dissection of the *cauline leaves*. Some dwarf specimens from Queanbeyan bore radical leaves 2 cm. long and 2.5 mm. broad, but usually these plants are robust and the radical leaves are approximately half the length of the mature scapes.

13. *CALOTIS CUNEATA* (F. Muell. ex Benth.), n. comb.

Stoloniferous perennials up to 30 cm. high. *Radical leaves* up to 10.5 cm. long, 1.8 cm. broad oblanceolate, coarsely toothed to the base or only distally and forming a basal cluster. *Cauline leaves* cuneate to ovate-cuneate, toothed. *Inflorescences* 16, up to 2.5 cm. diameter. *Involucral bracts* 18-30, 3.5-4.5 mm. long, 1.2-4 mm. broad, elliptical, acute, entire. *Ray florets* about 40, the rays 9 mm. long, 1.5 mm. broad, usually white but occasionally pale lavender. *Receptacle* about 1.5 mm. high, 1.5 mm.

broad, hemispherical, with long forked filiform septa between the bases of the florets. *Fruits* 1.6-3.8 mm. long, 1.5-3.7 mm. broad, cuneate, with 4-6 proximally woolly major awns; secondary awns numerous and hairy. An inner ring of about 12 fine awns is present which have an almost plumose appearance due to long straight hairs at right angles to the axis.

Key to the Varieties.

Radical leaves cuneate, coarsely toothed distally, sparsely septate-hairy. Body of fruits glabrous with no demarcated central area var. *α cuneata*.

Radical leaves usually 3-toothed distally, woolly hairy. Body of fruits with many long appressed hairs on central area var. *β pubescens*.

C. CUNEATA (F. Muell. ex Benth.), n. comb. var. *α CUNEATA*, comb. et stat. nov. (Text-figs. 102-104.)

C. scabiosifolia Sond. et F. Muell., var. *cuneata* F. Muell. ex Benth., *Fl. Aust.*, 3 (1866), 503.

Type data: "Rockhampton and Keppel Bay, Thozet, Burdekin River and desert on the Suttor, F. Mueller."

Lectotype. Rockhampton, Thozet (MEL).

Weakly erect and often tufted plants, up to 44 cm. high, with several, usually branched, stems with ovate-cuneate to elliptical, sessile, entire or shortly toothed leaves. *Radical leaves* up to 14 cm. long, 1.8 cm. broad, cuneate, obtuse, toothed distally or along the whole margin, and forming a basal cluster. *Ray florets* white, occasionally pale lavender. *Fruits* glabrous with no specially demarcated central area on the body. Major awns 4-6, the distal half barbed and woolly proximally. Secondary and super-numerary awns about 12, with no or few barbs and many woolly hairs. Inner awns fine, not rigid, about 11, with a plumose appearance due to the presence of long straight hairs at right angles to the awn axis.

Habitat: On various soils in grassland or open country.

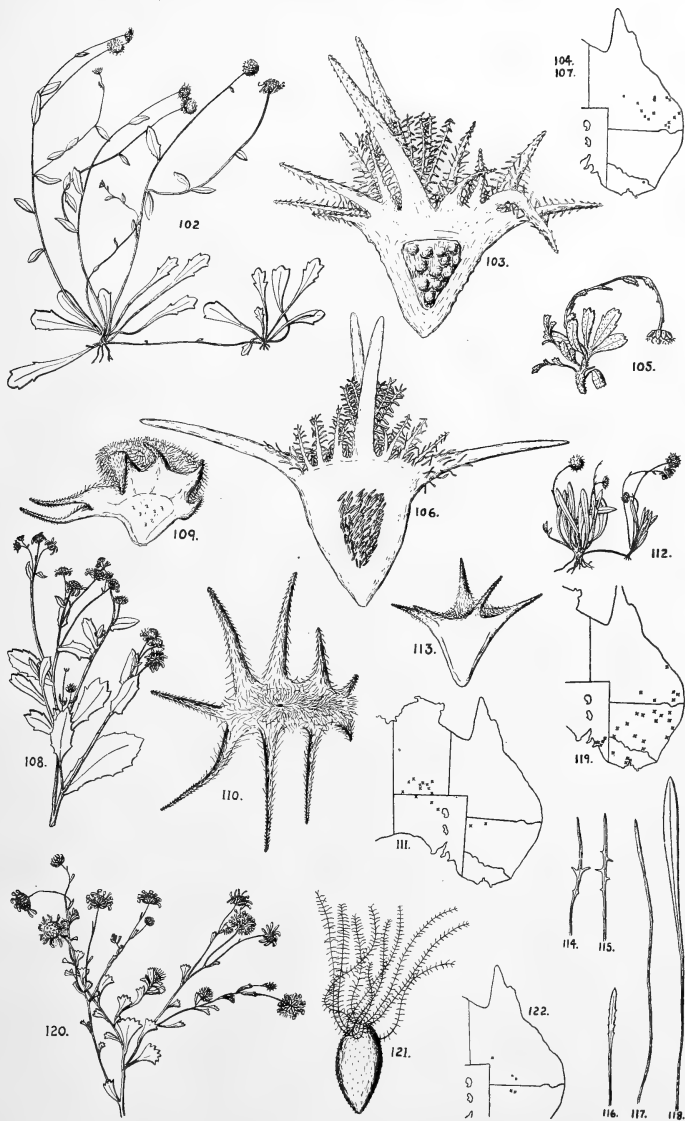
Range: Widely spread in Queensland.

Specimens examined:

Queensland: Rockhampton, Thozet (MEL); Rockhampton, grassy bank of Fitzroy River, ca. 18 ft. alt., 27.2.1931, C. E. Hubbard 8,029 (BRI); Keppel's Bay, Thozet (MEL); Port Curtis district, Serpentine Water Reserve, 14.3.1948, L. J. Webb (BRI); Wood End, Rockhampton district, 3.1920, W. D. Francis (BRI); between Capella and Clermont, 5.1929, Sutton (MEL); Emerald, 8.1912, J. L. Boorman (NSW 14,929); between Emerald and Longreach, 10.1913, E. Jarvis (BRI); Blackall, "in damper more or less shady places on bank of Barcoo River, ca. 900 ft., leaves tufted, dark green above, paler beneath, ray white, 14.7.1934, S. T. Blake 6,753 (BRI); Blackall-Northampton Downs, tufted plant very close to the ground, ray florets white or pale lavender, on heavy chocolate soil near edge of clay pan, 26.8.1935, S. L. Everist 1,283 (BRI); Augathella, common on black soil plains, flowers white, 15.12.1941, C. T. White 11,648 (BRI); Wandoan, in open *Eucalyptus populifolia* forest with *Aristida*, heavy soil, ca. 900 ft., 15.11.1930, C. E. Hubbard 4,968 (BRI); Mitchell, in grassland on dark greenish-brown silty clay, ca. 1100 ft., leaves prostrate, ray white, 3.5.1934, S. T. Blake 5,717 (BRI); Roma, in open grassy places on clayey soils, ca. 1000 ft., leaves tufted, ray white, 29.3.1936, S. T. Blake 10,887 (BRI); Rosedale, common on gravelly loam, Ironbark forests, 25.2.1931, L. G. Dovey (BRI); Gayndah, 9.1913, F. H. Kenny (BRI); Chinchilla, on brown sandy soil in grassland, 992 ft., 7.1.1931, C. E. Hubbard and C. W. Winders 6,438 (BRI); Forest Hill, 11.1921, F. Coleman (BRI); Laidley, 3.1920, C. T. White (BRI);

The type series is represented in Australia by specimens collected by Thozet at Rockhampton and Keppel's Bay, one from the former locality being selected as lectotype.

Collector's notes indicate that the radical leaves form a conspicuous basal cluster and are commonly closely appressed to the ground; this is not always apparent from herbarium specimens.



Text-figures 102-122.

102-104, *C. cuneata* var. *cuneata*.—102, Habit $\times 0.3$; 103, Fruit $\times 9$; 104, Distribution (x); 105-107, *C. cuneata* var. *pubescens*.—105, Habit $\times 0.3$; 106, Fruit $\times 6.3$; 107, Distribution (•); 108-111, *C. latiuscula*.—108, Habit $\times 0.3$; 109, Fruit $\times 6.3$; 110, Fruit, apical view $\times 6.3$; 111, Distribution; 112-119, *C. scapigera*.—112, Habit $\times 0.3$; 113, Fruit $\times 6.3$; 114-118, Variation in radical leaves $\times 0.3$; 119, Distribution; 120-122, *C. incermis*.—120, Habit $\times 0.3$; 121, Fruit $\times 6.3$; 122, Distribution.

Mueller, in preceding the varietal name by a question mark in the original description, appears to have been in doubt as to the status of the specimens he examined. As in the other varieties of *C. scabiosifolia* described at the same time, he confined himself to vegetative characters such as leaf shape and margin, which are unsatisfactory criteria in such a variable species. However, the presence of an inner row of awns in the fruits separates this population as a separate entity of specific status.

C. CUNEATA (F. Muell. ex Benth.), n. comb. var. β PUBESCENS (F. Muell. ex Benth.), n. comb. (Text-figs. 105-107.)

C. scabiosifolia Sond. et F. Muell. var. *pubescens* F. Muell. ex Benth., *Fl. Aust.*, 3 (1866), 503.

Type data: "Mountains on the Mitta Mitta River, F. Mueller."

Lectotype, "Grassy mountains on the Mitta Mitta. F. Mueller" (MEL).

Densely septate-hairy perennials 9 cm. high, with cuneate, apically toothed *cauline leaves*. *Fruits* 3.8 mm. long, 3.8 mm. broad, hairy on central area of each face and with 4-5 major awns between which are numerous supernumeraries with long hairs. Major awns not barbed and are proximally hairy. A second inner ring of plumose awns is present.

This variety is known only from the type specimen which is rather fragmentary, and is apparently extremely rare.

The body of the fruit most resembles that of var. *integrifolia* and the second ring of awns is a character shared with var. *cuneata*, but the unbarbed major awns is a unique feature.

14. CALOTIS LATIUSCULA F. Muell. et Tate, *Trans. Proc. Roy. Soc. S. Aust.*, 13 (1890), 107. (Text-figs. 108-111.)

Type data: "Central Australia. This plant has also been gathered near the Finke River by the Rev. H. Kempe."

Lectotype, Finke River, 1882, H. Kempe (MEL).

Erect branching septate-hairy perennials (?), up to 40 cm. high with a long tap root. *Radical leaves* up to 7 cm. long, 1.5 cm. broad, oblanceolate, the serrate blade tapering into a petiole of equal length, but only present on young plants. *Cauline leaves* up to 6 cm. long, 1.1 cm. broad, oblanceolate to cuneate, dentate or entire, acute, sessile. *Inflorescences* about 50, 1.5 cm. diameter, in a terminal cymose panicle. *Involucral bracts* 16-18, 2.5-3.7 mm. long, 0.7-1.1 mm. broad, linear, acuminate, entire, septate-hairy. *Ray florets* 10-21, the rays 4.5 mm. long, 1.6 mm. broad, yellow. *Receptacle* steeply conical, 1.5 mm. broad, 1-1.5 mm. high, the septa between the florets dissected into long scale-like processes. *Fruits* light brown, flattened, about 2 mm. long, 1 mm. broad, glabrous, the body not sharply defined. Awns 6-10, up to 3 mm. long, unequal, distally barbed, rigid, united basally, and passing off from the fruit at right angles; apex of fruit projects above the bases of the awns as a hairy central cone.

Habitat: No data.

Range: Central Australia and extending into the northern portion of South Australia and north-western New South Wales, with a single record from Western Australia.

Specimens examined:

New South Wales: Evelyn Creek, north of Barrier Range, 1887, A. King (MEL); near Mt. Wanaaring, 1.1941, A. B. Chislett (NSW 14,961).

Northern Territory: Macdonnell Range East, 5.1875, E. Giles (MEL); south side of Gill's Range, 1884, R. Tate (AD); Tempe Downs, 1888, R. F. Thornton (MEL); Mt. Sonder, W. Tietkins (MEL); Arltunga goldfield, 7.1922, C. G. F. Allen (NSW 14,865); Alice Springs, 7.1922, C. G. F. Allen (NSW 14,868); Finke River, 1882, H. Kempe (MEL); near the Finke River, Gosse's Range, Swartz and Schultz (MEL); Charlotte Waters, 1887, P. M. Byrne (MEL); Ernabella, in open country, 13.12.1943, L. B. Young (MEL); between the Alberga and Mt. Olga, 1873-4, Giles (MEL).

South Australia: North of Lake Eyre, 6.1887, H. Newland (MEL); Upper Arkaringa Valley, 22.5.1891, R. Helms (AD; NSW 14,864).

Western Australia: Murrin, 4.1907, F. A. Rodway (MEL).

A number of specimens are extant which were collected in the Finke River area by H. Kempe and a lectotype was selected from these.

The species shows little variation of any type and is easily recognized by its rather compact cymose panicles and large sessile cauline leaves. The fruits are very distinctive in their possession of robust horizontal awns and the extreme development of the central cone which exceeds the length of the body and the shorter awns.

15. *CALOTIS SCAPIGERA* Hook. in Mitch., *Journ. Trop. Austral.* (1848), 75. (Text-figs. 112-119.)

C. scapigera Hook. in Mitch. var. *dentata* Sond., *Linnaea*, 25 (1852), 472; *C. scabiosifolia* Sond. et F. Muell. var. *elongata* F. Muell. ex Benth., *Fl. Aust.*, 3 (1866), 503.

Type data: None.

Hapotype, Subtropical New Holland, 1846, T. L. Mitchell (NSW 14,641).

Stoloniferous perennials, 7-38 cm. high, with a basal cluster of radical leaves up to 24.5 cm. long, 8 mm. broad. *Leaves* linear to linear-lanceolate, acute, entire or sparsely toothed, occasionally with a few linear lobes, almost glabrous. *Stems* 1-5, usually unbranched and scape-like, exceeding the leaves, and bearing a few bract-like or small leaves. *Inflorescences* up to 10, 1.5 cm. diameter. *Involucral bracts* about 15, 3.5 mm. long, 1.5 mm. broad, oblanceolate, obtuse and entire. *Ray florets* 22-40, the rays 2.5-5 mm. long, 0.5-1 mm. broad, white or lavender. *Receptacle* hemispherical, 1.3 mm. broad, 0.5-1 mm. high. *Fruits* brown, the body cuneate, flattened, glabrous, 1.7-2.5 mm. long, 1.2-2.4 mm. broad. *Awns*, 4-6, rigid, diverging, straight or subulate, more or less equal, 1-4 mm. long, microscopically barbed distally and woolly proximally.

Habitat: On rather heavy soils.

Range: Eastern States and south-eastern portion of South Australia.

Specimens examined:

Queensland: Canal Creek, 1882, Hartmann (MEL); Dingwall, on grey clay flat with much gypsum, ray florets yellow, white or pale mauve, 19.7.1948, S. L. Everist 3,489 (BRI); Dalby, 30.9.1950, H. J. Anderson (BRI); Toowoomba, H. G. Longman (BRI); Noondoo, near Dirranbandi, at edge of tank on grey heavy soil, ca. 550 ft., ray white, 1.3.1936, S. T. Blake 10,627 (BRI).

New South Wales: Glen Innes, 9.1910, F.H.R. (AD); Armidale, rays white, gravelly loam soil, 20.1.1941, G. L. Davis (NE); West Maitland 11.1908, S. Brewster (NSW 14,640); Concord, Woollys (NSW 14,960); Burwood, 1890, Woollys (MEL); Narrabri, 10.1933 (NSW 14,630); Euralah, via Walgett, 9.1912, L. K. Clank (NSW 14,629); Macquarie River (NSW 14,632); Bourke, 8.1896, J. H. Maiden (AD); Bourke, flowers white, 5.1918, J. L. Boorman (NSW 14,636); Warrego River, 9.1885, E. Betche (NSW 14,637); Sub-tropical New Holland, 1846, T. L. Mitchell (NSW 14,641); Wilcannia, 6.1893, Tepper (MEL); 20 miles from Menindie, clay, 14.10.1860, Victorian Expedition (MEL); Wentworth, Ford (MEL); Booberoi, Lachlan River, swampy land, 2.1941, N. C. Beadle (NSW 14,634); Murrumbidgee River, 2.1893, E. Betche (NSW 14,959; MEL); Narrandera, 4.1932, B. J. Shadbolt (NSW 14,635); Howlong, Community Park, white rays turning pink on drying, fairly common but inconspicuous among tall herbage, mixed with *Hemarthria*, *Mentha*, *Pulegium* and *Paspalum distichum*, 8.2.1950, E. J. McBarron (NSW 14,633).

Victoria: Shire of Dimboola, 1891, F. M. Reader (MEL); near Mt. Macedon, 1873, D.S. (MEL); Stordley Park, Melbourne, 3.9.1883, F. Reader (MEL); Port Phillip, F. Mueller (MEL); Geelong, 3.1906, H. B. Williamson (MEL).

South Australia: Renmark, rays white in two irregular rows, rare, 4.10.1915, J. M. Black (JMB); Swan Reach, 19.3.1927, J. B. Cleland (JBC); Murray Bridge, ray pink turning white, 16.10.1918, J. M. Black (JMB); between North Arm and Hindmarsh, rays pinkish lilac, 4.1849, Wirth (MEL); Port Adelaide, 22.6.1910, H.H.D.G. (JMB); Mannum river flats, J. B. Cleland (JMB).

The original description gives no locality data as such, though from the title of the book, it is to be supposed that the specimens were collected between Sydney and the Gulf of Carpentaria, probably in New South Wales. In the National Herbarium, Sydney, there is a folder of specimens accompanied by a printed label "Sub-tropical New Holland, 1846, Col. Sir T. L. Mitchell", which presumably form part of the type series. The material consists of one plant with flowering and fruiting heads (haptotype) and four others, without heads, connected by stolons. All conform to the original description except that instead of the scapes being naked, as stated by Mitchell, they bear small and inconspicuous bracts. The majority of specimens examined agree with the haptotype in the possession of scapes, but in some (Geelong, Port Phillip, Melbourne and Dingwall) a lateral branch is present and in one from Glen Innes, each so-called scape is branched twice. Although entire leaf margins is the usual condition in this species, in the specimens from Dingwall most of the leaves are finely serrate. A further variation was seen, chiefly in Queensland specimens, in which among the usual entire leaves were a few bearing 3-6 linear acute lobes up to 7 mm. long, at right angles to the mid-vein of the leaf. This last condition was seen in Mueller's type specimen of *C. scabiosifolia* var. *elongata* (Port Phillip), in which the leaves are 22 cm. long, 2.5 mm. broad, but whose fruits are identical with those of *C. scapigera*. Sonder's type specimen of *C. scapigera* var. *dentata* (Australia. Herb. Aulic. Vindob. ec Mus. Paris n. 397) has not been examined by the present writer, but his description ("leaves equal to the scapes, basally narrowed, entire or dentate with 3-4 lanceolate teeth") suggests that this also is an example of the last-named variation.

16. *CALOTIS INERMIS* Maiden et Betche, PROC. LINN. SOC. N.S.W., 26 (1901), 84. (Text-figs. 120-122.)

Type data: "Urisino, 20 miles west of Wanaaring, on the Paroo River, Sept. 1900, E. Betche."

Lectotype, Urisino, Paroo River district, 9.1900, E. Betche (NSW 14,869).

Herbaceous branching annuals up to 16 cm. high, more or less septate hairy. *Cauline leaves* numerous, up to 2.5 cm. long, 1.5 cm. broad, cuneate, sessile, 5-7 toothed distally, tapering rather abruptly into a narrow basal portion which is slightly stem-clasping. *Radical leaves* lanceolate, serrate, up to 4.5 cm. long, 0.8 cm. broad, only present on young plants. *Inflorescences* up to 26, 2.5 cm. diameter. *Involucral bracts* about 20, 3.5-4 mm. long, 1.2-1.5 mm. broad, lanceolate, acuminate, entire, densely hairy. *Ray florets* 18-23, the rays up to 7 mm. long, 2.5 mm. broad, purple. *Receptacle* 1-2 mm. broad, 1-2 mm. high, hemispherical, slightly pitted. *Fruits* 2.5 mm. long, 1.2 mm. broad, elliptical, flattened, pale brown, microscopically hairy; awns 12-15, 10-15 mm. long, fine and flexible, without barbs but with numerous fine straight hairs given off at right angles.

Habitat: On red-brown clay or loam soils.

Range: Western Queensland to Paroo River district of New South Wales.

Specimens examined:

Queensland: Currawilla, near Moncarbey Creek, in hard bare pebbly red-brown loam, annual with numerous erect stems, ray florets bright purple, 13.6.1949, S. L. Everist 4,010 (BRI); Currawilla, Stallion paddock, in red-brown clay loam with *Cassia phyllodinea*, annual with rosette of leaves and several short flowering stems, 9.6.1949, S. L. Everist 3,914 (BRI); Dynevor Downs, on hard stony ridges, flowers deep mauve, 2.4.1941, C. T. White 11,827 (BRI; NSW 14,870); Goonamurra, near Eulo, small erect herb on hard red soil flats; ray florets purple, 20.9.1938, S. L. Everist 1,656 (BRI).

New South Wales: Wanaaring-Urisino, 10.1900, J. L. Boorman (NSW 14,871); Urisino, Paroo River district, 9.1900, E. Betche (NSW 14,869; MEL).

The fruits of *C. inermis* are unique in that the awns are long, soft and feathery and consequently do not possess the burr-like properties of most other species. It is possibly due to this that it occupies such a limited range compared with others whose rigid barbed awns become readily attached to passing animals.

C. inermis appears to be a rare plant and no variation was shown in the short series of specimens available. Its very limited distribution may perhaps be attributed to the absence of rigid awns as a means of mechanical distribution by animals.

17. *CALOTIS BREVISETA* Benth., *Enum. Pl. Hueg.* (1837), 60. (Text-figs. 123-125.)

C. tropica F. Muell. in *Trans. Phil. Inst. Vict.*, 3 (1859), 58; *C. pterosperma* R.Br. ex Benth., *Fl. Aust.*, 3 (1866), 505.

Type data: "Ferd. Bauer."

Erect perennials up to 35 cm. high, branching from the base and subsequently, glabrous or sparsely septate-hairy. *Leaves* cauline, linear to narrow-oblongate, up to 3.5 cm. long, 6 mm. broad, acute, entire or occasionally with 1-2 small lateral teeth. *Inflorescences* over 100 on an established plant, 5-7 mm. diameter. *Involucral bracts* 30-40, 2.5 mm. long, 0.5 mm. broad, narrow lanceolate, acuminate, entire, very sparsely septate hairy. *Ray florets* 26-34, the rays 2-3 mm. long, 0.5 mm. broad, white. *Receptacle* 0.8 mm. broad, 0.8-1 mm. high, conical, pointed, shallowly pitted. *Fruits* reddish to dark brown, 1.4-2 mm. long, 1.2-1.5 mm. broad, slightly flattened, the body cuneate with a few white or straw-coloured simple hairs, and a conspicuous hairy apex forming a central cone; wings rather thick and narrow with simple marginal hairs; awns 7-10, stout, barbed, the same length or slightly exceeding the central cone.

Habitat: "Dry beds of rivers" (Mueller, 1859) and barren country.

Range: North and North-western Australia from Arnhem Land to the Kimberleys.

Specimens examined:

Northern Territory: Port Darwin, ray white, 10.1888, M. Holtze (MEL); Spring Vale, Port Darwin, Giles (BRI); Telegraph Line, 200 miles south of Port Darwin, A. Giles (MEL); Edith Creek, 7-8.1911, W. B. Spencer (NSW 14,985); Albert River, Henne (MEL); Driffield Creek, 7-8.1911, W. B. Spencer (NSW 14,983); Maude's Creek, 7-8.1911, W. B. Spencer (NSW 14,901; 14,984); Katherine River, 12.1886, A. Giles (MEL); low barren country towards the Fitzmaurice River and McAdams Range, 10.1885, F. Mueller (MEL); Upper Victorian River, rays white, 12.1885, F. Mueller (MEL).

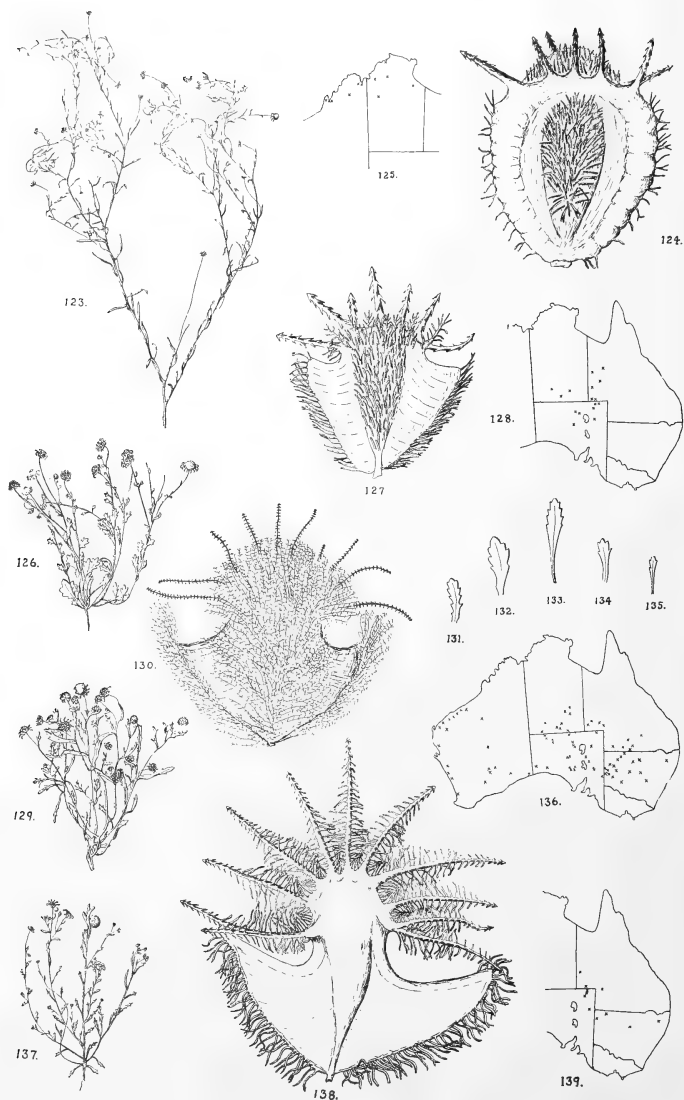
Western Australia: near Cambridge Gulf, 1887, W. J. O'Donnell (MEL); west of Cambridge Gulf, 1887, A. J. Keiller (MEL); King Sound, 1888, Froggatt (NSW 14,900; MEL); Fitzroy River, 8.1906, W. V. Fitzgerald (NSW 14,902); Beagle Bay, 1879, A. Forrest (MEL).

According to Bentham (1863) the types of the species described in "Enumeratio Plantarum" were deposited in Vienna, although duplicates of those collected by Bauer were in Robert Brown's collection. It is of interest that in the National Herbarium, Melbourne, there is a specimen accompanied by an envelope, with a single fruit, labelled in Sonder's handwriting "*C. breviseta* Benth. ex herb. Vindobonnensis", which presumably was removed by Sonder from the type material and has been used as a basis of comparison in the present work.

Mueller did not quote an exact locality for *C. tropica* ("In North-West Australia, generally in dry beds of rivers") but two specimens have been examined ("Towards the Fitzmaurice River and McAdam's Range" and "Upper Victoria River") which are accompanied by labels bearing Mueller's identification "*C. tropica*". Since these were collected four years prior to the date of publication of this species they are presumably at least part of the type series. A specimen from the last-named locality has been nominated lectotype, but Bentham (1866) is followed in regarding this species as synonymous with *C. breviseta*.

Type specimens of *C. pterosperma* ("Islands of the Gulf of Carpentaria, R. Brown") have not been examined, unless a specimen in the National Herbarium, Melbourne, labelled "*C. pterosperma* R.Br., North Coast, 1802-5, R. Brown" can be considered such. Since this and the original description agree with *C. breviseta*, this species is relegated to synonymy.

All the specimens examined were very similar in every respect, the small differences of the plants and their fruits being of no taxonomic significance.



Text-figures 123-139.

123-125, *C. breviseta*.—123, Habit $\times 0.3$; 124, Fruit $\times 18$; 125, Distribution; 126-128, *C. porphyroglossa*.—126, Habit $\times 0.3$; 127, Fruit $\times 18$; 128, Distribution; 129-136, *C. multicaulis*.—129, Habit $\times 0.3$; 130, Fruit $\times 18$; 131-135, Variation in radical leaves $\times 0.3$; 136, Distribution; 137-139, *C. ancyrocarpa*.—137, Habit $\times 0.3$; 138, Fruit $\times 18$; 139, Distribution.

18. *CALOTIS PORPHYROGLOSSA* F. Muell. ex Benth., *Fl. Aust.*, 3 (1866), 505. (Text-figs. 126-128.)

C. microcephala F. Muell. ex Benth., *Fl. Aust.*, 3 (1866), 504.

Type data: "Cooper's Creek, Murray."

Lectotype, Cooper's Creek, 1862, Dr. Murray (MEL).

Septate-hairy annuals up to 40 cm. high, branching from the base and subsequently. *Cauline leaves* up to 4 cm. long, 1.2 cm. broad, narrow cuneate to cuneate, toothed or acutely lobed distally, sessile. *Radical leaves* of the same type, but petiolate, only present on young plants. *Inflorescences* about 1 cm. diameter, up to 100 present on a bushy plant. *Involucral bracts* about 30, 2.2-3.2 mm. long, 0.8-1 mm. broad, lanceolate, acute, entire and septate-hairy on the outer surface. *Ray florets* about 65, 3-4 mm. long, 0.6 mm. broad, bluish. *Receptacle* 1.6 mm. broad, 1.2-1.5 mm. high, steeply conical, moderately pitted. *Fruits* light to golden or reddish brown, 1.2-1.5 mm. long, 1.5-1.7 mm. broad, cuneate, flattened, body and wing margins bear white forked hairs; awns 6-11, rather unequal, 0.5-1 mm. long, rigid and barbed along their whole length.

Habitat: Grassland.

Range: Western Queensland and Central Australia.

Specimens examined:

Queensland: Cloncurry, herb among grass on the plains, eaten by stock, 1882, Palmer (NSW 14,911); Georgina River, E. J. Whelan (BRI); Boulia, in river channels, ca. 500 ft., tufted spreading annual, rays mauve, 28.6.1934, S. T. Blake 6,476 (BRI); Mulligan River, 2.1904, H. Clarke (NSW 14,910); 40 miles south of Birdsville, water-hole, Diamantina, 14.8.1934, J. B. Cleland (JBC).

Northern Territory: Stevenson, McDonald Ranges, 7.5.1894, R. Tate (AD); Ryan's Well, North of Alice Springs, 7.1922, C. E. F. Allen (NSW 14,908); Finke River, 1885-6, Dittrich (MEL).

South Australia: Near Eyre Creek, 1862, Murray (MEL); Pandie, Diamantina, 19.8.1934, J. B. Cleland (JBC; JMB); Minnie Downs, 1927, L. Reece (JMB); Alberga Creek, near Todmorden Station, 1.7.1920, H. W. Andrews (JMB); Ross' Waterhole, Macumba River, 5.1.1927, J. B. Cleland (JBC; JMB); Coober Pedy, 9.1935, C. French Jr. (MEL); Cooper's Creek 1862, Murray (MEL).

A haptotype of *C. microcephala* ("Murray and Darling Rivers, Herb. F. Mueller") has been selected which agrees with the original description in all particulars. The fruits are identical with those of *C. porphyroglossa*, but since only the small upper leaves are present an erroneous impression is created as to leaf size (Bentham: "leaves under $\frac{1}{2}$ inch long").

Mueller (1866), in describing this species, commented on its resemblance to *C. plumulifera* (i.e. *C. multicaulis*), to which it is undoubtedly closely related. The fruits of the two species can be distinguished by the forked, rather than plumose, hairs on those of *C. porphyroglossa*, and the more robust and comparatively fewer awns. Vegetatively the resemblance is even closer, though the leaves of *C. porphyroglossa* tend to be more lobed than in *C. multicaulis*. It is always difficult to compare vegetative characters of specimens from different localities since the environment plays a large part in their development. In this instance, a folder from Coober Pedy was of considerable interest, since it contained a number of plants of both these species, which as they were intertwined, were apparently growing in close association. In this collection the two species were almost identical vegetatively, but easily separable on fruit characters, indicating that a genetic barrier to their crossing exists and that *C. porphyroglossa* is correctly regarded as a full species and is not, as suggested by Mueller (1866), a variety of *C. multicaulis*.

19. *CALOTIS MULTICAULIS* (Turczaninow) Druce, *Rep. Bot. Exch. Cl. Brit. Isles*. 1916 (1917), 611. (Text-figs. 129-136.)

Goniopogon multicaule Turcz., *Bull. Soc. Nat. Mosc.*, 24 (1851), 173; *Calotis plumulifera* F. Muell., *Trans. Phil. Inst. Vict.*, 3 (1859), 57.

Type data: "New Holland, Drum. IV.n.115."

Septate hairy annuals up to 47 cm. high, branching from the base and subsequently. *Radical leaves* oblanceolate and distally toothed, up to 4.5 cm. long, 8 mm. broad, petiolate, only present on young plants. *Cauline leaves* up to 4 cm. long, 1 cm. broad, narrow-cuneate to cuneate, distally toothed or with short acute lobes, sessile. *Inflorescences* 1.5 cm. diameter, over 200 on bushy plants. *Involucral bracts* 15-19, 2.5-3.6 mm. long, 0.6-1 mm. broad, narrow-lanceolate, acute to acuminate, margins microscopically serrulate, septate hairy on outer surface. *Ray florets* 12-20, the rays 3-4 mm. long, 0.6-1.1 mm. broad, bluish or white. *Receptacle* slightly taller than broad, 0.8-2 mm., narrow conical, moderately pitted. *Fruits* light to dark brown, 1.4-2 mm. long, 1.5-2.7 mm. broad, body cuneate, slightly flattened, usually densely covered with white plumose hairs which intermingle with those of the summit of the fruit forming a thick felt; wings rigid and thick with white plumose hairs along the margins, otherwise glabrous, but often obscured by the long hairs from the body; awns up to 24, but usually 12-14, of unequal length, 0.5-2.5 mm. long, frequently exceeding the length of the body, fine and flexible, with short straight hairs or barbed. Bases of the awns obscured by the white plumose hairs of the fruit apex.

Habitat: Flat, rather bare, areas of silty sand or loam, particularly on areas liable to flooding.

Range: Throughout inland areas of Australia with the exception of Victoria.

Specimens examined:

Queensland: Chatsworth, 13.9.1939, Hunt (BRI); Breadalbane Station, north of Bedourie, on silt beds, flooded ground, tufted dull green annual up to 4 inches, ray white, 23.7.1936, S. T. Blake, 12,339 (BRI); Mulligan River, 1885, W. H. Cornish (MEL); Monkira Station, 8.1891, G. L. Debney (BRI); Currawilla, stallion paddock, in hard, pebbly, red-brown loam on bare patch, annual with several branched stems, 10.6.1949, S. L. Everist 3,939 (BRI); Nockatunga Station, between channels of the Wilson River, on loamy sand "clay pans" among Chenopodiaceae, ray white, 27.6.1936, S. T. Blake 11,829 (BRI); near Charleville, 9.1949, H. Harkin (MEL); Yowah Creek, near Toompine, slender herb in red alluvium, 21.9.1938, S. L. Everist 1687 (BRI); Thargomindah, 3.1885, L. Spencer (MEL); Goonamurra, slender herb very common on red soil flats, florets yellow, 20.9.1938, S. L. Everist 1,670 (BRI); Caiwarro, 1886, J. Cotter (MEL).

New South Wales: Glen Innes, 29.10.1886 (MEL); Hungerford, 9.1910, Bucknell (NSW 14,894); Thurloo Downs-Berawinia Downs, 10.1912, J. L. Boorman (NSW 14,888); Tarcoon, 11.1903, J. L. Boorman (NSW 14,958); Bourke district, 8.1896, J. H. Maiden (NSW 14,892; MEL); Bourke district, 5.1950, W. E. Darley (NSW 14,893), 29 miles east of Nyngan, 19.8.1939, I. Pidgeon and J. Vickery (NSW 14,897); Cobar, 8.1911, L. Abrahams (NSW 14,980); Yandanlo, 1886, B. Kennedy (MEL); Tarella, 4.1887, W. Bauerlen (MEL); Wilcannia, 8.1887, W. Bauerlen (NSW 14,886); Paldrumatta bore, Wilcannia, 4.1900, F. Corbett (NSW 14,891); Barrier Range, 1890, Irvine (MEL); Silverton, 11.1884, Harris (MEL); Broken Hill, white, 4.10.1920, A. Morris (NSW 14,896); Broken Hill, 21.5.1921, A. Morris (BRI); 90 miles east of Broken Hill, 20.8.1939, I. Pidgeon and J. Vickery (NSW 14,899); Menindee, Beckler (MEL); between the Lachlan and the Darling Rivers, 1885, J. Bruckner (MEL); Mossgiel, 1885, J. Bruckner (MEL); Parkes 22.9.1947, E. Constable (NSW 14,898).

Northern Territory: MacDonald Downs 22.8.1930, J. B. Cleland (JBC); Deering Creek, 1894, R. Tate (AD); near Henbury Craters, 19.6.1935, J. B. Cleland (JBC); 12 miles south-west of Henbury, 4.6.1935, J. B. Cleland (JBC); near Finke River, 1880, R. E. Warburton (MEL); between Angas Downs and Ayer's Rock, 9.6.1935, J. B. Cleland (JBC); between Charlotte Waters and Alice Springs, 5.1875, C. Giles (MEL).

South Australia: Abminga, 22.9.1945, J. B. Cleland (JBC); north of Musgrave Ranges, 7.1926, H. Basedow (NSW 14,874); Ernabella, 25.9.1945, J. B. Cleland (JBC); near Mt. Everard, 1882, E. Giles (MEL); between Ernabella and Echo Hill, 20.8.1933, J. B. Cleland (JBC; JMB); between Ernabella and Moorilyanna, 20.8.1933, J. B. Cleland (JBC); Alberga Creek, 1.7.1920, H. W. Andrews (JMB); 15 miles north-west of Oodnadatta, 22.8.1933, J. B. Cleland (JBC); 50 miles west of Oodnadatta, 5.8.1933, S. Neales (JBC); Warrina, 1890, Richards (MEL); Diamantina at Pandie, 20.8.1934,

J. B. Cleland (JBC); Waterhole, Diamantina, 14.8.1934, J. B. Cleland (JBC); Cooper's Creek, J. McLeod (AD); Cooper's Creek, A. C. Gregory (MEL); Lake Eyre, 9.1903, B. Spencer (NSW 14,877); between Hergott and Innanious Range, 6.1916 (JMB); Mt. Lyndhurst, annual, fodder plant, M. Koch (AD; MEL; BRI; NSW 14,884); Lake Torrens plain 28.8.1883, R. Tate (MEL); Curnamona, 2.12.1930, J. B. Cleland (JBC); Black Hill Wells, Koonamore, 15.8.1928, T. B. Paltridge (AD); Koonamore, 13.11.1924, T. G. B. Osborn (JMB); Mingary, 14.8.1921, A. Morris (JMB); Coober Pedy, 9.1935, C. French Jr. (MEL); between Kingoonya and Mt. Eba, 5.1917, H.B. (JMB); Tarcoola, 21.9.1920, E. H. Ising (BRI); east of Wingena, 30.10.1929, J. B. Cleland (JBC); Ooldea, 7.1921, J. A. Kershaw (MEL); Nullabor Plains, 1891, J. D. Batt (MEL).

Western Australia: Mulyie Station, De Grey River, spreading annual growing abundantly on flats liable to flooding, 3.8.1941, N. T. Burbidge (P); Rabbit Proof Fence, east of Gregory Range, rays blue, small annual, in sandy soil in depressions, 2.1.1947, R. D. Royce (P); Sherlock and Yule Rivers, 1878, J. Forrest (MEL); Nickol River, 1878, J. Forrest (MEL); Fortescue River, 10.1941, C. A. Gardner (P); Roy Hill, Fortescue River, 150 miles from coast, 14.5.1943, C. Davis (FAR); Cane and Ashburton Rivers, 1878, J. Forrest (MEL); Minderoo, Ashburton River, 9.10.1905, A. Morrison (P); Parker Range, 1892, E. Merrall (MEL); Gascoyne River, 1882, J. Forrest (MEL); Murchison River, 1892, I. Tyson (MEL); 91 miles east of Meekathana, 3-4", ray florets violet-lilac, in clay soil in depressions, 16.10.1945, C. A. Gardner 7,893 (P); Champion's Bay, 1871, Guerin (MEL); Irwin River, Oldfield (MEL); upper Swan River, 1888, M. Eaton (MEL); Laverton, 9.1900, J. H. Maiden (NSW 14,989); Glenom Station, Malcolm, 9.1938, N. T. Burbidge (P); Coolgardie, 7.1899, R. Helms (NSW 14,991); Victoria Desert, 16.9.1891, R. Helms (MEL); Eucla, 1889, Batt (MEL).

Although Turczaninow's type material was not examined, the identity of this species is quite clear. The monotypic genus *Goniopogon* was short-lived, as such, for its description was shortly followed by Mueller's description of *Calotis plumulifera* under which name Bentham (1866) listed this population, listing *Goniopogon multicaule* as a synonym. From 1917 to 1928 no less than four authors pointed out the priority of Turczaninow's epithet, Druce's publication of the new combination preceding that of Black by a few months. Among the specimens cited by Bentham (1866) is "Cooper's Creek, Gregory", a duplicate of which is in the National Herbarium, Melbourne. Since this specimen agrees well with both the original and Mueller's descriptions, it has been used as a basis of comparison by the present writer.

This species is usually easily identified by the densely woolly fruits with long fine awns, but certain specimens have been examined from Western Australia (Sherlock R., Fortescue River, Wongawal Sta., and Nickol River) and Queensland (Currawilla) in which the shorter plumose hairs exposed the glabrous portions of the wings, and those awns were not as long as usual. On this account these fruits approached those of *C. porphyroglossa* but were nevertheless quite distinct.

The wings of the fruits are each of an equal breadth to the body and more or less abruptly terminated distally below the awns, but some variation was noticed, notably in two records from Western Australia (Meekathana, Lake Violet) in which they approached the typical anchor-shape of *C. ancyrocarpa*. Variation was also observed in the armature of the awns in specimens from Nullabor Plains in which they were microscopically barbed along their entire length and glabrous, while in a specimen from Warrina, the barbs were so minute they were hard to detect even microscopically.

20. *CALOTIS ANCYROCARPA* J. M. Black, *Trans. Proc. Roy. Soc. S. Aust.*, 45 (1921), 18. (Text-figs. 137-139.)

Type data: "Murteree, Strzelecki Creek, 9.1916, S. A. White."

Lectotype, Murteree, Strzelecki Creek, 25.9.1916, S. A. White (JMB).

An almost glabrous annual up to 22 cm. high, branching from the base and subsequently. *Leaves* cauline, up to 5-7 cm. long, 4 mm. broad, broad-linear to oblanceolate, with a few linear acute lobes. Upper leaves commonly entire. *Inflorescences* up to 100 on a much-branched plant, 1-1.5 mm. diameter, terminal and axillary. *Involucral bracts*

18-20, 1.6-3.6 mm. long, 0.5-0.9 mm. broad, linear to narrow-elliptical, subacute to acute. *Ray florets* 20-30, the rays up to 10 mm. long, 1.5 mm. broad, white. *Receptacle* hemispherical, 1 mm. broad, 1.2 mm. high, pitted. *Fruits* 1.2-2 mm. long, 2-2.5 mm. broad, light brown, glabrous except for the long simple hairs fringing the broad anchor-shaped wings. Pappus of 15-25 awns, 1-1.7 mm. long, stiff, with a few distal barbs with long simple hairs proximally.

Habitat: "Growing in tufts on the flooded ground" (field note of S. A. White).

Range: Western Queensland, north-western New South Wales and north-eastern corner of South Australia.

Specimens examined:

Queensland: Mulligan River, 2.1904, H. Clarke (NSW 14,905); Birdsville, on alluvial flats, annual to 6 in., ray white, 19.7.1936, S. T. Blake, 12,230 (BRI); Cuddapan, in grey clay near edge of melon hole, annual with numerous erect stems, ray florets white, 26.8.1949, S. L. Everist 4,060 (BRI).

New South Wales: Glen Innes, 29.10.1886, E. Betche (NSW 14,885); near Cobar, 9.1910, L. Abrahams (NSW 14,906); between the Paroo River and Grey Range, 1881, L. Morton (MEL).

South Australia: Flood plain of the Diamantina at Pandie Pandie, 18.8.1934, J. B. Cleland (JBC); Goyder's Lagoon, 15.8.1924, J. B. Cleland (JBC); Diamantina, 8.1930, Morgan (JBC; JMB); Murteree, Strzelecki Creek, 25.9.1916, S. A. White (JMB).

Variation is confined to the size of the plant and its leaves. All fruits examined were very similar, although in some the sinus at the apex of each wing was a little more pronounced than in that figured.

This is a very distinct species which, in awn arrangement and wing shape, most closely resembles *C. multicaulis*, which is found over the same area.

21. *CALOTIS BREVI-RADIATA* (E. H. Ising), n. comb. (Text-figs. 140-142.)

C. multicaulis (Turcz.) Domin var. *breviradiata* E. H. Ising, *Trans. Roy. Soc. S. Aust.*, 46 (1922), 608.

Type data: "1552."

Lectotype, Hughes, N.P., 8.9.1920, E. H. Ising 1,552 (MEL).

Erect ? annuals up to 15 cm. high, branching from the base and subsequently, with an indumentum of white septate hairs. *Leaves cauline*, up to 2.5 cm. long, 4 mm. broad, cuneate, sessile, distally toothed or acutely lobed. *Inflorescences* about 50, 7 mm. diameter, axillary and terminal. *Involucral bracts* up to 36, 2-3 mm. long, 0.5-0.6 mm. broad, linear, entire, acuminate, with white septate hairs on margins and outer surface. *Ray florets* about 100, 1 mm. long, 0.5 mm. broad, apparently yellow. *Receptacle* 1.5-2.3 mm. broad, 1-2 mm. high, conical, moderately pitted. *Fruits* reddish-brown, 1.8-2 mm. long, 1.5 mm. broad, flattened; body oval, microscopically tuberculate, distal half obscured by straight white hairs; wings rather thick and rigid, distally convex and bearing long straight hairs along the outer margins. Awns about 20, 0.5-1.3 mm. long, unbarbed and provided with numerous hairs so as to appear plumose.

Habitat: No data.

Range: Nullabor Plains.

Specimens examined:

South Australia: Watson, 31.8.1950, J. B. Cleland (JBC); Hughes, 8.9.1920, E. H. Ising, 1,552 (MEL; NSW 14,904).

Western Australia: Eucla, 1889, Batt (MEL).

22. *CALOTIS ANTHEMOIDES* F. Muell., *Trans. Phil. Soc. Vict.*, 1 (1855), 44. (Text-figs. 143-145.)

Type data: "In muddy localities in the neighbourhood of Station Peak."

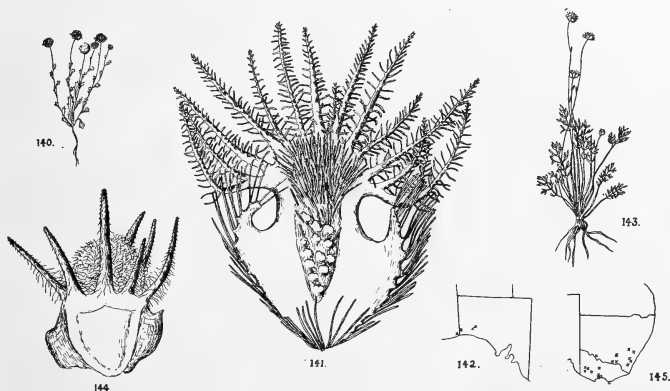
Lectotype, near Station Peak, in muddy places, F. Mueller (MEL).

Glabrous stoloniferous perennials with one to seven scapes arising from a basal rosette of radical leaves. *Leaves* up to 11.5 cm. long, bipinnatisect, the ultimate segments linear, acute, petioles almost as long as the dissected blade. *Scapes* up to 19.5 cm. high, slender, exceeding the leaves and provided with a few small entire or toothed bract-like

leaves. *Inflorescences* up to 1.5 cm. diameter. *Involucral bracts* 10-14, 3.5-4.2 mm. long, 1.2-3.5 mm. broad, ovate-lanceolate to orbicular, subacute to obtuse, entire with ciliolate margins but otherwise glabrous. *Ray florets* 50-70, 4.5-6 mm. long, 0.8-1 mm. broad, white. *Receptacle* 2 mm. broad, 1.5 mm. high, hemispherical with septa which enclose the base of each floret. *Fruits* reddish-brown to black, 2.5 mm. long, 1.7-2 mm. broad, the body cuneate, flattened, with rigid wing-like margins; awns 7-14, of unequal length, 0.2-2 mm. long, microscopically barbed distally, woolly proximally on inner surface. The apex of the body is covered with white hairs and forms a central cone which is usually exceeded by the longest awns.

Habitat: Swampy situations.

Range: Central and southern districts of New South Wales, western half of Victoria.



Text-figures 140-145.

140-142, *C. breviradiata*.—140, Habit $\times 0.9$; 141, Fruit $\times 18$; 142, Distribution; 143-145, *C. anthemoides*.—143, Habit $\times 0.3$; 144, Fruit $\times 9$; 145, Distribution.

Specimens examined:

New South Wales: Grenfell, 23.2.1947, H. F. McCarthy (NSW 3,086); Crookwell, 12.11.1937, W. A. Cady (NSW 14,627); Tarago to Braidwood, 29.10.1908, R. H. Cambage (NSW 14,625); Braidwood district, 3,000 ft., 11.1886, W. Bauerlen (MEL); Colinton, savannah, 31.10.1948, A. B. Costin (NSW 14,622); Wagga, 11.1885, R. Thom (MEL); Walbundie, white and yellow florets, common roadside weed, 17.9.1948, E. J. McBarron (NSW 14,621); Holbrook, 2 mile reserve, white-flowered swamp plant, 11.10.1947, E. J. McBarron (NSW 14,623); Edward's River, 1875 (MEL; NSW 14,624).

Victoria: Raywood, 26.8.1928, C. S. Sutton (MEL); Moyston, stiff clay, wet soil, D. Sullivan (MEL); Grampians, 11.1898, C. Walter (NSW 14,628); Dunkeld, pastures, 11.1901, H. B. Williamson (MEL; NSW 14,627); Skipton, W. T. Whan (MEL; NSW 14,982); Lara, 22.8.1923, H. B. Williamson (MEL); near Station Peak, in muddy places, F. Mueller (MEL); Geelong, H. B. Williamson (MEL).

Mueller's type series consists of six well-preserved specimens accompanied by his own label with the type data, and from these the lectotype was selected. All agree satisfactorily with the original description except that the disc florets are not hermaphrodite, as claimed by Mueller.

In a very variable genus this species is remarkable in its homogeneity in vegetative features as well as fruits.

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NOTES ON PHLEBOTOMUS FROM THE AUSTRALASIAN REGION
(DIPT. PSYCHODIDAE).

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(Communicated by D. J. Lee.)

(Seventy-seven Text-figures.)

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Synopsis.

The present paper outlines the results of a study of more than 300 specimens of *Phlebotomus*, most of which were collected in New Guinea during the last war and a few from New South Wales and Queensland. Methods of study are detailed and following this is a systematic review of the species. The only earlier paper on this group in Australia (Tonnoir, 1935) described the first species of this genus to be recorded from Australia, comprising three species and one subspecies. These are discussed herein and in addition three new species from the Australian Mainland together with eight new species and one new subspecies from New Guinea. Notes are also given on the characters of other specimens from New Guinea which, owing to the fragmentary nature of the material, must await further collections before description. The paper includes keys to both sexes of these flies for both Australian and New Guinea species.

The material on which this study is based consists of 326 specimens mounted in balsam on microscope slides. The bulk of the material is from various localities in New Guinea and was collected by personnel of the 5th Malaria Survey Unit, U.S. Army, under the direction of Maj. M. S. Ferguson and Maj. Owen H. Graham, who have already published a preliminary note on the field aspects of their work (Ferguson and Graham, 1948). Some of this material was sent us for study in 1945, the rest being sent to Mr. D. J. Lee, of the School of Public Health and Tropical Medicine, Sydney, Australia. In 1948 Mr. Lee very generously sent us not only his part of the Ferguson and Graham material, but also some material from various parts of Australia collected by Miss K. English and Col. C. B. Philip. Subsequently we received some further New Guinea material collected by Lt. H. Hoogstraal and Dr. L. E. Rozeboom.

Some of the material had been stored dry in pill boxes, but much of it was preserved in alcohol. The dry material has made satisfactory mounts, though in many cases the specimens were somewhat broken or damaged by mites. The alcoholic material has been impossible to clear satisfactorily and has made very poor mounts, though in most cases comparison with the dry preserved specimens has enabled identification to be made.

Since so little collecting of these interesting insects appears to have been done in Australia, some brief notes upon their habits and habitats, and methods of collection and preservation may be useful.

Sandflies are small hairy midges 2 or 3 millimetres long, with a characteristic way of holding their wings out from the body and slightly tilted upwards. Their flight is short and hopping, and when walking they progress in a jerky, erratic manner. Most species are quite strictly nocturnal, hiding away during the day in holes and crevices which are reasonably dark and relatively humid. Holes and crevices in ruined masonry, stone walls, hollow trees and crevices between the buttressed roots of large trees, animal burrows and deep crevices in the soil, especially in arid regions, provide favoured daytime resting places. From these habitats the sandflies may be flushed with tobacco smoke and collected by the use of a suction tube. Some species are attracted to lights and may be taken in various types of light traps. Sheets of paper coated with castor oil and placed near likely looking habitats will often catch numbers of specimens.

Sandflies should not be stored in alcohol for more than a short time, as the tissues become altered so that subsequent clearing in KOH becomes difficult or impossible. Dry storage in small cotton-plugged vials with naphthalene or para-dichlorobenzene is more satisfactory, but it is best to clear and mount specimens as soon as possible.

Since most of the taxonomic characters are internal, sandflies must be cleared and in many cases mounted. For preliminary clearing, wet the specimens with alcohol and place in liquid phenol, made by adding a little water to phenol crystals, or in a moist atmosphere, allowing the crystals to deliquesce in an open watch glass. Specimens will usually be sufficiently cleared to allow the spermathecae to be made out in 15-30 minutes. Such cleared material should be further processed by treatment in 20% KOH solution without heat for about an hour, or by brief boiling, followed by thorough rinsing in water to remove all muscle and tissue fragments that may remain. The cleaned "skeletons" resulting may be stored indefinitely in 70% alcohol, or mounted on slides.

Due to the tenuous nature of some structures, especially the spermathecae, satisfactory permanent mounts in resinous media are somewhat difficult to make. The procedure devised by us (Fairchild and Hertig, 1948) has proved relatively reliable and consists essentially in the use of liquid phenol (carbolic acid) as the clearing and dehydrating agent throughout the process. Material previously treated with KOH and washed is placed directly into a weak solution of acid fuchsin in phenol, where it is allowed to stain for about fifteen minutes and the excess stain washed off in clear phenol. The specimens are then placed in a weak solution of gum copal in phenol which is allowed to thicken gradually over a period of days, thus infiltrating the specimens gradually with the resinous medium and avoiding shrinkage and collapse of the spermathecae. When the medium has become sufficiently thick, the specimen is dissected on a cover glass in a small drop of the copal-phenol, the wings, head, thorax and abdomen arranged in a uniform manner, and the preparation allowed to dry gradually. Chips of cover slip should be stuck to the corners of the cover glass to prevent crushing, and the whole preparation turned over onto a drop of thick xylol balsam on a slide. The finished mount should be thoroughly dried with moderate heat to drive off any remaining phenol which might otherwise crystallize in the preparation.

We have had no difficulty with this technique in Panama, where temperature and humidity are always relatively high. In cool or dry climates, however, crystallization of the phenol occurs quite rapidly. The use of beechwood creosote or lacto-phenol may solve this difficulty, though we have made no tests along these lines. The use of aqueous mounting media or those containing water-soluble gums or sugars we have found totally unsatisfactory under our conditions, no specimen so preserved having lasted more than two years.

The technique outlined above yields permanent mounts with each part of the insect in the same relative position on the slides, thus greatly facilitating the examination of long series of specimens. Being first mounted on the cover slip, the specimens are close to the glass and may be examined with the oil immersion lens. The use of glass chips at the corners prevents crushing and distortion, and the arrangement is such that the various parts are right side up when viewed through the microscope. We do not find that the removal of the cibarium and pharynx or the spermathecae is necessary if the specimens are properly cleared of tissue, as they are quite adequately seen through the posterior wall of the head capsule or the abdominal wall. In some cases it is useful to split the male genitalia sagittally to enable a clear view of the inner aspect of the coxite and paramere, but some specimens should also be mounted undissected.

The terminology adopted here is that used in a previous paper (Fairchild and Hertig, 1947). It is essentially that used by Tonnoir (1935), with slight modifications. The "cibarium" is the buccal cavity of Tonnoir. The "chitinous arch" is a thickening of the ventral surface of the cibarium, forming a more or less complete curved band across the cibarium between the armature and the base of the proboscis. It is believed to be the attachment of the salivary muscle. The detailed measurements of palpi, antennae, wing veins, etc., so much a part of earlier work on *Phlebotomus*, are believed to be largely unnecessary. By themselves they are seldom of much use in separating closely related species or in associating the sexes. Certain proportions, however, seem to be

valuable supplementary characters, such as the relative lengths of certain sectors of wing veins, the first flagellar segment (segment III) of the antennae relative to the palpi, and the length of the genital filaments relative to the genital pump in the male. It is felt that figures give a better idea than tables of measurements in any case.

The holotype, allotype and a series of paratypes, where available, of the new species described here are to be deposited in the collections of the School of Public Health and Tropical Medicine, University of Sydney, Sydney, Australia. A set of paratypes, where available, will be deposited in the U.S. National Museum, Washington, D.C.

1. THE AUSTRALIAN SPECIES.

No work on the Australian species seems to have been published since Tonnoir's paper (1935) in which three species and one subspecies were recorded from Australia. The present material consists of 10 specimens collected by Miss K. English at Yass, New South Wales, and 9 specimens collected by Dr. C. B. Philip at Cairns, Queensland. No information as to habits or habitats accompanied this material.

The 10 specimens from Yass consisted of 1 ♀ *brevifilis* Tonn., 1 ♂, 1 ♀ *englishi* Tonn., 1 ♀ *queenslandi meridionalis* Tonn., and 6 ♀ *brevifiloides*, n. sp. The 9 specimens from Cairns consisted of 1 ♀ *queenslandi* Hill, 1 ♀ *pezopharynx*, n. sp., 4 ♂ *buccinator*, n. sp., and 2 ♂, 1 ♀ undetermined. One or both of the undetermined males may be *queenslandi*. They differ somewhat in structure of the cibarium, but whether these differences are specific or not, only additional material will tell. We have refrained from placing them under *queenslandi* due largely to the greater number of cibarial teeth in our material, about 20 in one and about 30 in the other, whereas *queenslandi* is said to have from 15 to 17 teeth. Also the pharynges of our specimens do not agree well with Tonnoir's description in having "a comparatively small number of shallow scales arranged so as to give the impression of a loose and slender net". The undetermined female is represented by only the abdomen and a wing. The spermathecae are thin-walled elliptical capsules, much like those of *queenslandi*, which the specimen may be. Unfortunately the spermatheca of our single complete *queenslandi* was not drawn before mounting, so that detailed comparisons are not possible. We deem it better to leave these specimens undescribed until adequate material becomes available.

Keys to the Australian Species.

Males.

1. Style with three strong spines. Genital pump large, filaments short, less than twice as long as pump, heavily sclerotized. Abdominal hairs mostly erect. A few setae on lower border of mesanepisternum 2.
Style with four strong spines all very close to the apex and a single fine seta beyond the middle of the segment. Genital pump small and slender, the slender filaments more than twice as long as the pump. Abdominal hairs recumbent. No pleural setae 3.
2. Aedeagus a pair of short truncated cones, poorly sclerotized. Plunger of genital pump slender. Style with basal spine longest, widely separated from the two closely approximated terminal spines *brevifilis*.
Aedeagus long, tubular, the tips up-turned, heavily sclerotized. Plunger of genital pump stout, the apex trumpet-shaped. Basal spine of style not longer than others, separated from the subterminal spine by about twice the distance between the subterminal and terminal spines *buccinator*.
3. Pharynx hairy *meridionalis*.
Pharynx scaly 4.
4. Cibarium with about 16 teeth *queenslandi*.
Cibarium with about 43 teeth *englishi*.

Females.

1. Pharynx rather heavily sclerotized and pigmented on basal two-thirds, apex densely beset with spines in a rather characteristic fan-shaped whorl. Cibarium with five to ten well-separated horizontal teeth and often small fine lateral teeth. Spermathecae thick-walled or annulated. A few small setae on lower border of mesanepisternum 2.
Pharynx less heavily sclerotized and pigmented; apical armature very much less prominent, consisting of scarcely pigmented slender scales or hair-like spines not arranged in a fan-like whorl. Cibarium with much more numerous, fine, closely set horizontal teeth in a comb. Spermathecae oval, very thin walled. No pleural setae 4.

2. Pharynx shaped like an inverted flask, the anterior plate densely beset with small pigmented spines in a fan-shaped whorl; posterior plates with numerous longer spines. Cibarium with about 10 short stout horizontal teeth. Spermathecae with subspherical thick-walled heads and very long smooth ducts which join to form a common duct of appreciable length *pexopharynx*.
Pharynx less widened posteriorly. Spermathecae irregularly annulate, opening separately or with a very short common duct 3.
3. Pharynx similar to *pexopharynx*, but the spines on anterior plate fewer and larger, on posterior plates longer and hair-like. Cibarium with five small well-separated horizontal teeth. Spermathecae with the anterior third irregularly annulate, the terminal knob sunk in a conical pit *brevifilis*.
Pharynx less strongly pigmented, the terminal armature of the same pattern as the preceding species, but much reduced as to both number and size of the teeth. Cibarium with six to eight pointed horizontal teeth and a number of fine lateral teeth. Spermathecae as in *brevifilis* *brevifiloides*.
4. Pharynx beset with rather broad-based denticulate scales. Cibarium with a comb of very fine long horizontal teeth, 77 to about 85 in number, and a few small erect teeth below *englishi*.
Pharynx beset with long slender spines. Cibarium with numerous well marked erect teeth below 5.
5. Cibarium with a comb of about 45 moderately long horizontal teeth and with one and part of a second transverse row of well marked erect teeth below *queenslandi*.
Cibarium with a comb of about 75-80 very fine horizontal teeth and erect teeth below as in *queenslandi* *meridionalis*.

PHLEBOTOMUS BREVIFILIS Tonnoir. (Figs. 3, 4, 9, 44, 47.)

1935, *Bull. Ent. Res.*, 26:145-147, figs. 2c, d and 3d. (♂, ♀; Canberra and Yass, N.S.W., Australia.)

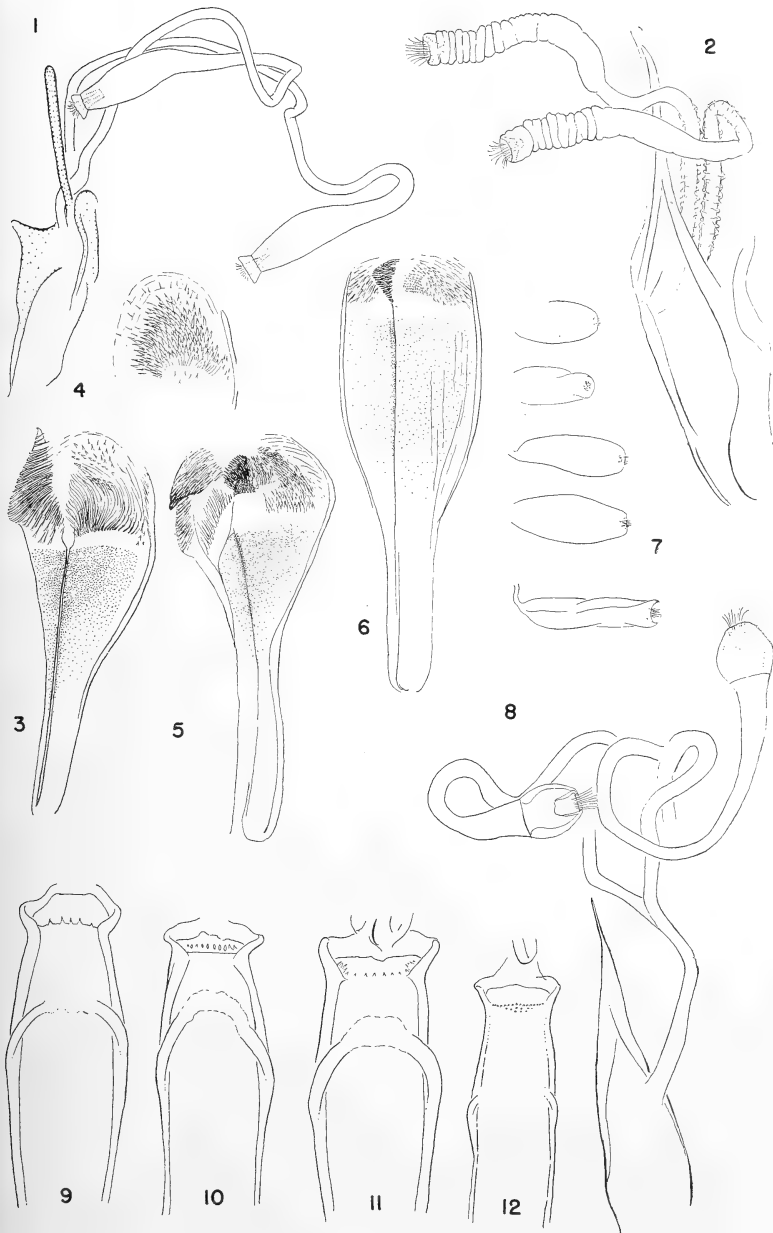
Phlebotomus (Australophlebotomus) brevifilis, Theodor, 1948, *Bull. Ent. Res.*, 39 (1): 99-100, 105, 108; fig. 8.

A single female specimen, slide 1420, lacking the palpi, is in the collection. It was taken at Yass, N.S.W., in March 1946, by Miss K. English and is thus topotypical. We give here figures of wing, antennae, cibarium and pharynx. The spermathecae are visible but too distorted and shrunken to be worth figuring; they agree with Tonnoir's and Theodor's figures as far as can be made out. The ascoids appear to be broken, and are probably a little longer than shown in the figure. The specimen is quite pale, the mesonotum but slightly infuscated. The wing measures 2.05 mm. in length and is indistinguishable from the wing of *brevifiloides*. The proboscis is long, equaling the head height, there are no post-spiracular setae, and the abdominal hairs appear from their insertions to have been erect.

Theodor (1948) has erected the subgenus *Australophlebotomus* for *brevifilis* Tonnoir, placing it in the genus *Phlebotomus*. The characters used to distinguish the group are the presence of erect abdominal hairs, lack of, or rudimentary, cibarial armature, presence of but three spines on the style, rudimentary aedeagus and incompletely annulated spermathecae. The finding of other obviously related species in Australia and New Guinea necessitates a re-evaluation of *Australophlebotomus*. If *brevifiloides*, n. sp., *buccinator*, n. sp., and *pexopharynx*, n. sp., be considered to be closely related to *brevifilis*, as I believe they are, then but one of the characters cited by Theodor is shared by all the group, the presence of erect abdominal hairs. While it is true that *buccinator* and an as yet undescribed species from New Guinea have three-spined

Text-figs. 1-12.

Fig. 1, *P. hoogstraali* holotype, spermathecae, drawn in phenol before mounting, the junction of individual ducts not visible.—Fig. 2, *P. brevifiloides* paratype, spermathecae drawn in phenol before mounting; individual ducts probably separate to vagina.—Figs. 3 and 4, *P. brevifilis* female, whole pharynx and anterior plate only.—Fig. 5, *P. pexopharynx* holotype female, pharynx.—Fig. 6, *P. brevifiloides* holotype female, pharynx.—Fig. 7, spermathecae of, from top to bottom, *P. brachycornutus* holotype, *P. sansapovens* holotype, *P. fergusoni* paratype and holotype, and *P. dolichobysus* holotype, all drawn from mounted specimens.—Fig. 8, *P. pexopharynx* holotype, spermathecae drawn in phenol, parts of the ducts not visible.—Fig. 9, *P. brevifilis* female, cibarium.—Fig. 10, *P. pexopharynx* holotype female, cibarium.—Fig. 11, *P. brevifiloides* holotype female, cibarium.—Fig. 12, *P. papuensis* paratype male, cibarium. All figures drawn to the same scale with camera lucida, approximately $\times 290$.



styles, the males of *brevifloides* and *pezopharynx* are unknown. All three species in which the females are known, *brevifilis*, *brevifloides* and *pezopharynx* have definite teeth in the cibarium, not, in my opinion, rudimentary, while the male from New Guinea also has small horizontal and erect teeth. Both *buccinator* and the New Guinea species have a well-developed aedeagus or penis sheath, while the spermathecae of *pezopharynx* are quite unlike those of *brevifilis* and *brevifloides*. Except for the erect abdominal hairs, these species could fit as well into *Sergentomyia* sensu Theodor as into *Phlebotomus*. The parameres of the males, the cibarial teeth, type of pharyngeal armature and the two types of spermathecae can nearly all be matched among various species placed by Theodor in *Sergentomyia*. It seems best, therefore, at least for the time being, to refrain from placing these species in any definite restricted category.

PHLEBOTOMUS BREVILOIDES, sp. nov. (Figs. 2, 6, 11, 67.)

Female. Wing length 2.1 to 2.2 mm. Abdominal hairs apparently erect. No post-spiracular setae on thorax. Mesonotum very slightly infuscated. Antennae lacking in all the specimens and only the basal palpal segments present. Proboscis long, greater than head height. Pharynx as figured, broad and well sclerotized. Cibarium as figured, the lateral teeth slender and transparent. Wing as figured. Spermathecae as figured, their posterior terminations not certainly visible, but probably opening separately into the vagina, at most with a very short common duct. Gonapophyses of the eighth sternite small and slender. Cerci short, moderately pointed.

Holotype female, slide 1414, and five female paratypes, slides 1412, 1413 and 1415 to 1417, Yass, New South Wales, Australia, March 1933, K. English coll.

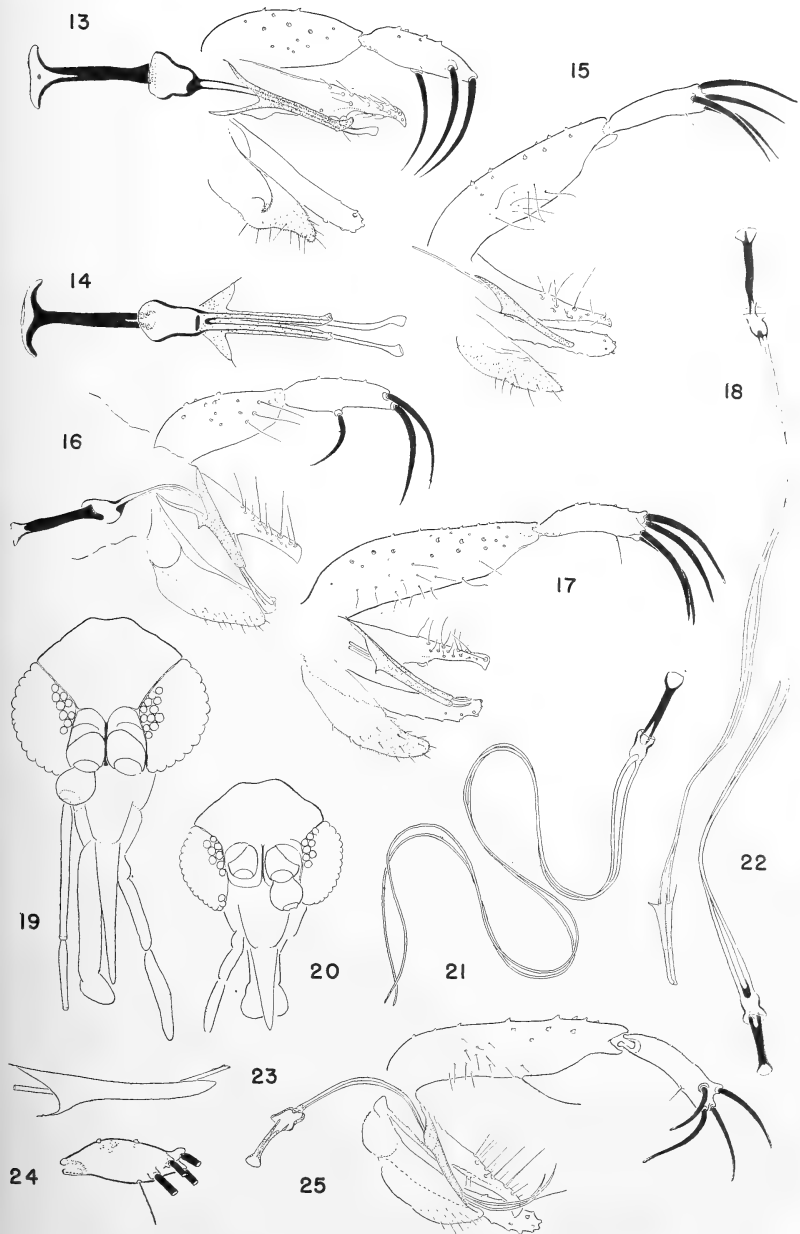
This species differs from *brevifilis* Tonn. only in the structure of the cibarium and pharynx, *brevifilis* having a much greater development of the spinose area in the pharynx but fewer horizontal teeth and no lateral teeth in the cibarium. The spermathecae of our single specimen of *brevifilis* are somewhat shrunken and distorted, so that detailed comparisons are not possible, though they appear to have been very similar to those of *brevifloides*. The finding of two such closely related females at Yass raises some question as to the status of the male described by Tonnoir. It is very probable that he correctly associated the sexes, as his figure of the male pharynx shows it to be more spinose than would be expected of the male of the present species. Further intensive collecting may turn up the male of *brevifloides* and indicate that the species are ecologically separated.

PHLEBOTOMUS BUCCINATOR, sp. nov. (Figs. 13, 14, 48, 66.)

Male. Wing length 1.5 to 1.6 mm. Abdominal hairs apparently erect. No setae on the upper margin of the anepisternum (post-spiracular setae). Mesonotum very slightly infuscated. Ascoids simple, shorter than their respective segments, paired on all segments where it has been possible to see them, at least to segment IX. Proboscis as long as head height. Pharynx slender, not strongly pigmented, armed only with weak denticulate ridges and short digitate processes. Cibarium as figured, without horizontal or vertical teeth, but with a few fine transparent lateral teeth. Wing, palpi and basal antennal segments as figured. Genitalia as figured, the style with three strong spines but no accessory setae, parameres hooked, aedeagus long, cylindrical, the apices up-turned, heavily sclerotized. Genital filaments short, only a little longer

Text-figs. 13-25.

Fig. 13, *P. buccinator* holotype, genitalia, lateral aspect.—Fig. 14, same, genital pump, dorsal aspect.—Fig. 15, *P. sansaporensis* allotype, genitalia.—Fig. 16, *P. papuensis* paratype, genitalia.—Fig. 17, *P. fergusonii*, genitalia of specimen with short delta wing.—Fig. 18, *P. hoogstraali*, allotype, genital pump and filaments.—Fig. 19, *P. pezopharynx* holotype, head in frontal aspect.—Fig. 20, *P. quevianandi* female, head in frontal aspect.—Fig. 21, *P. dolichobysus* allotype, pump and genital filaments, the latter drawn from measurements.—Fig. 22, *P. fergusonii*, pump and genital filaments of same specimen as Fig. 17.—Fig. 23, *P. dolichobysus* allotype, aedeagus $\times 290$.—Fig. 24, *P. hoogstraali* allotype, style.—Fig. 25, *P. quintus* paratype, genitalia. All figures except Fig. 23 and the two heads are drawn to the same scale, approximately $\times 215$. The heads are about $\times 72$.



than the pump, their tips expanded. Pump very large and heavy, the plunger with its anterior end greatly expanded, trumpet-shaped. Lateral lobes simple, unarmed, straight, but little longer than the cerci which are rather acutely pointed.

Holotype male, slide 1407, and three paratype males, slides 1404 to 1406, Cairns, North Queensland, Australia, no date, C. B. Philip coll.

This species differs from *brevifilis* in having a long and heavily sclerotized aedeagus, a larger and stouter genital pump, and in having the spines on the style rather differently arranged. It is possible that this is the male of *P. pexopharynx*, n. sp., but the reduced lateral teeth in the cibarium of that species and the lack of spines in the pharynx of *buccinator* coupled with the long spermathecal ducts of *pexopharynx* and the short genital filaments of *buccinator* make it seem inadvisable to pair them without further evidence.

PHLEBOTOMUS PEXOPHARYNX, sp. nov. (Figs. 5, 8, 10, 19, 46, 65.)

Female. Wing length 2.01 mm. Abdominal hairs apparently erect. No post-spiracular setae on thorax. Mesonotum very slightly infuscated. Palpi and basal antennal segments as figured. Ascoids apparently paired on the flagellar segments, but collapsed and distorted in the single available specimen. Proboscis long, greater than head height. Pharynx and cibarium as figured, the latter with scarcely visible vestiges of lateral teeth, not shown in the figure. Spermathecae as figured, the ducts not visible in their entirety but probably little longer than shown.

Holotype female, slide 1410, Cairns, N. Queensland, Australia, no date. C. B. Philip coll.

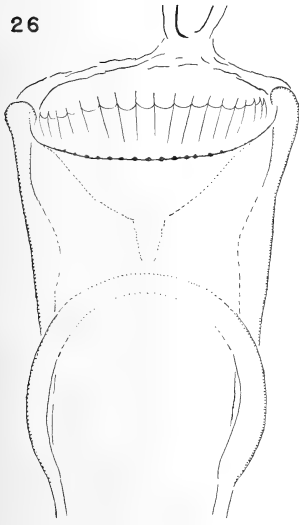
This species differs from *brevifilis* and *brevifloides* externally in having a somewhat broader wing and relatively longer delta. The cibarium has more, about 10, and stouter teeth, and the lateral fine teeth are vestigial. The pharynx is somewhat like that of *brevifilis*, but the spines on the ventral or posterior plates are shorter and more numerous, less hair-like, while those on the dorsal or anterior plate are smaller and more closely set. The whole pharynx is more abruptly widened posteriorly, almost racquet-shaped. The spermathecae are of a quite different type from the other species, globular, apparently thick-walled, and with long smooth ducts.

The following three species are all rather closely related and are placed by Theodor (1948) in the genus *Sergentomyia*. This group is the "minutus group" or *Prophlebotomus* of previous workers and has usually been considered of no more than subgeneric rank. The species differ from the other Australian species considered in having the abdominal hairs mostly recumbent, the style of the male genitalia with four spines grouped near the apex, and a single more basal accessory seta. The spermathecae of the known Australian species are thin-walled oval or elliptical capsules with the terminal "knob" very small and sunk in a pit. The cibaria are provided with a comb-like series of fine horizontal teeth in both sexes, and the pharynges are armed with denticulate scales or slender hair-like spines. The Australian species are all small, generally markedly smaller than the *brevifilis* group, and usually with narrower wings. The proboscides are also relatively shorter, not or scarcely equaling the head

Text-figs. 26-43.

Fig. 26, *P. noemforensis* female paratype, cibarium $\times 650$.—Fig. 27, *P. quintus* male paratype, cibarium, upper $\times 650$, lower $\times 290$.—Fig. 28, *P. hoogstraali* female holotype, cibarium $\times 650$.—Fig. 29, *P. englishi moresbyi* female holotype, cibarium $\times 290$.—Fig. 30, *P. hoogstraali* female holotype, cibarium $\times 290$.—Fig. 31, *P. fergusonii* male allotype, cibarium $\times 650$.—Fig. 32, *P. fergusonii* female paratype, cibarium $\times 650$.—Fig. 33, *P. fergusonii* female, cibarium showing common appearance of teeth at other than critical focus, $\times 650$.—Fig. 34, *P. fergusonii* female, holotype, cibarium $\times 290$.—Fig. 35, *P. sansaporensis* female paratype, cibarium $\times 290$.—Fig. 36, *P. sansaporensis* male paratype, cibarium $\times 650$.—Fig. 37, *P. sansaporensis* female paratype, cibarium $\times 650$.—Fig. 38, same, at other than critical focus, the usual appearance in poorly cleared specimens, $\times 650$.—Fig. 39, *P. dolichobysus* female holotype, segment of cibarial tooth row $\times 1300$.—Fig. 40, *P. queenslandi* female, apex of pharynx $\times 650$.—Fig. 41, *P. englishi* female, apex of pharynx $\times 650$.—Fig. 42, *P. brachycornutus* female holotype, cibarium $\times 290$.—Fig. 43, *P. dolichobysus* female holotype, cibarium $\times 290$.

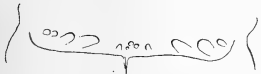
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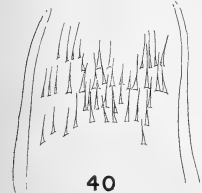
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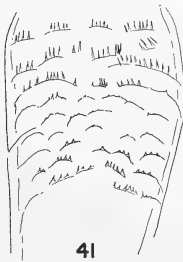
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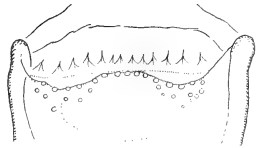
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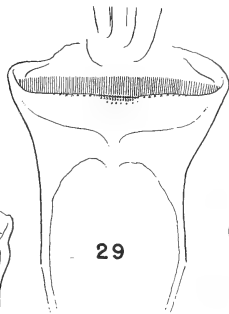
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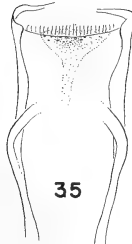
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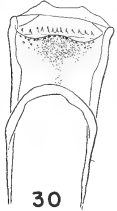
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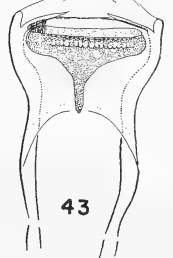
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height. Most species of the group do not bite man, but are believed to feed mainly on cold-blooded vertebrates. Tonnoir recorded (1935) Miss English's observations on *englishi* and *queenslandi meridionalis*, which fed readily on lizards but refused human blood, while *brevifilis* would bite both man and lizards.

PHLEBOTOMUS ENGLISHI Tonnoir. (Fig. 41.)

1935, *Bull. Ent. Res.*, 26:144-145, fig. 3, Plate I, figs. f, g. (♂, ♀; Yass, New South Wales, Australia.)

Sergentomyia (Sergentomyia) englishi Theodor, 1948, *Bull. Ent. Res.*, 39 (1):111.

One male and one female, Yass, New South Wales, March 1933, K. English coll. There is little to add to Tonnoir's description of the species, but we give here figures of the pharyngeal armature of the female, as his photographs are not very clear on this point. The male armature is difficult to see in the single specimen, but appears to consist of groups of longer and more slender spines arising from similar, but less clearly marked, ridges or scales like those in the female.

PHLEBOTOMUS QUEENSLANDI Hill. (Figs. 20, 40.)

1923, *Bull. Ent. Res.*, 14:83-86, 6 figs. (♂, ♀; Townsville, N. Queensland.) Tonnoir, 1935, *Bull. Ent. Res.*, 26:140-142, figs. 2A, B, 3C (re-described from the type series).

Sergentomyia (Sergentomyia) queenslandi Theodor, 1948, *Bull. Ent. Res.*, 39 (1):111.

One female, Cairns, N. Queensland, C. B. Philip coll., agrees with Tonnoir's description and figures. We give here a figure of the pharyngeal armature for comparison with *englishi*, but have nothing to add to Tonnoir's full description except to note the presence of fairly numerous erect teeth in the cibarium below the comb of horizontal teeth.

PHLEBOTOMUS QUEENSLANDI MERIDIONALIS Tonnoir.

1935, *Bull. Ent. Res.*, 26, 142-143, fig. 3A, a, Pl. I, fig. c. (♂, ♀; Yass, New South Wales.)

Sergentomyia (Sergentomyia) queenslandi var. *meridionalis* Theodor, 1948, *Bull. Ent. Res.*, 39 (1):111.

One female, Yass, New South Wales, March 1933, K. English coll. The specimen agrees with Tonnoir's description. The pharyngeal armature is essentially like *queenslandi*, though the teeth seem somewhat shorter. The pharynx is not in the best position, however, and this may be an illusion. The cibarial teeth are quite different: longer and more numerous. I count 77 on this specimen, which agrees fairly well with Tonnoir's "about 80". There is also a single complete transverse row and part of a second row of stout erect teeth below the fine comb of horizontal teeth, as in *queenslandi*. Only further careful study of good series of these two forms from intermediate localities will show whether they are good species or geographical races.

2. THE NEW GUINEA SPECIES.

Aside from the mention by Tonnoir (1935) of a single specimen from Port Moresby, no *Phlebotomus* have been hitherto known from New Guinea, although they appear to be fairly abundant and widespread there. The 300 odd specimens taken by Ferguson and Graham appear to be separable into not more than 19 species, none of which agree with previously described forms from elsewhere. Of these, 9 species are represented by sufficiently well preserved material to warrant description. The remainder can be seen to be distinct but are too poorly preserved for figures to be made or complete descriptions to be drawn up, and a residue of about 25 specimens are quite indeterminate, though probably belonging to one or another of the describable species.

The fauna is like that of Australia in lacking any representatives of the more typical groups of *Phlebotomus*, with one exception the species all belonging to the *minutus* group (*Sergentomyia*). Only two species, however, *papuensis*, n. sp., and *englishi moresbyi*, n. subsp., appear to be at all closely related to Australian species, the former being the only representative of the *brevifilis* group (*Australophlebotomus*) known outside of Australia. Of the remaining species, all have unarmed pharynges and oval or elliptical unsegmented spermathecae, but only a few can be placed with confidence in any of Theodor's (1948) groups of the genus *Sergentomyia*.

The relative paucity and lack of diversity in the Australasian fauna is of considerable interest, as it seems to indicate that the group had its origins elsewhere. Except for the *brevisfilis* group, which seems to be a local Australian development, the species are similar in general to the other Old World Sargentomyias, failing to show either any marked "primitive" characteristics or any marked local modifications. There is no such wealth of bizarre developments as is found in the Neotropics, for example. It is interesting to note that no *Phlebotomus* are so far known from Chile, whose insect fauna in many groups shows such close affinity with that of Australia.

In the following list those species of which material is too fragmentary or too poorly preserved to warrant description are noted. All the species belong to the *minutus* group, and are to be separated very largely on small characters of the cibarium, antennae, etc. With two exceptions they are represented by single specimens and nearly all are very inadequate mounts, having been long in alcohol. The series from Biak and Owi Islands might have been described, but there is not a single really good specimen in the lot and the species is very close indeed to *sansaporensis*. These insects are difficult enough to separate at best, and I do not wish to add to the difficulty by perpetuating any names based on inadequate type material.

1 ♂. Dobadura, 22 Sept. 1944. Slide 2809. Cibarium with a comb of about 15 teeth. Genital filaments about 4 times as long as pump. Segment III of antennae about as long as first three palpal segments. Delta short, less than half alpha. This and the following males all have genitalia of the same type, like *sansaporensis*.

1 ♂. Aitape, 16 Sept. 1944. Slide 2654. Cibarium not visible. Genital filaments about 2.5 times as long as pump. Segment III of antennae slightly longer than first three palpal segments. Delta short, less than half alpha.

1 ♂. Dobadura, 21 Sept. 1944. Slide 2700. Cibarium broad, with a comb of at least 12 long teeth. Genital filaments about 7 times as long as pump. Segment III of antennae about equal to first three palpal segments. Delta short.

1 ♂. Sansapor, 11 Sept. 1944. Slide 2830. Cibarium broad, teeth indistinct, though apparently short and numerous. Genital filaments about 7 times as long as pump. Segment III of antennae very long, at least one-quarter longer than first three palpal segments. Delta short.

1 ♂. Dobadura, 7 Aug. 1944. Slide 1141. Cibarial teeth not visible, chitinous arch present. Genital filaments about 4 times as long as pump. Segment III of antennae about as long as first three palpal segments. Delta short. This may be same as Slide 2809.

14 ♂, 8 ♀. Biak and Owi Islands, 13 Sept. 1944, and 1 ♂ without data. The males have a faint comb of small teeth, while the cibarium of the female is similar in appearance to that of *sansaporensis*, though it appears to have fewer teeth. Genital filaments 3 to 3.5 times as long as pump. Segment III of antennae a little shorter than first three palpal segments. Delta short or minus.

1 ♀. Dobadura, 18 Aug. 1944. Slide 3517. Cibarium of about 22 teeth. Chitinous arch discernible at sides. Segment III of antennae about equal to first three palpal segments. Delta short.

2 ♀. Sansapor, 11 Sept. 1944. Slides 1149, 1152. Cibarium of about 26 teeth. Chitinous arch not visible. Spermatheca oval, thin walled, the terminal knob sunk in a pit. Antennae and palps missing. Delta long, half or more alpha.

1 ♀. Dobadura, 21 Sept. 1944. Slide 2713. Cibarium very broad with about 39 slender teeth, no chitinous arch. Segment III of antennae about three-fourths as long as first three palpal segments. Delta short.

1 ♀. Hollandia, 6 Sept. 1944. Slide 2824. Cibarium with fairly numerous very short teeth, not clear enough to count. No chitinous arch. Segment III of antennae shorter than first three palpal segments. Delta short. Mesonotum quite strongly infuscated.

Key to Males.

1. Style with 3 well-developed spines, 2 apical and 1 median. Genital filaments less than twice as long as pump. No post-spiracular setae, but a few small setae on lower border of mesonepisternum. Wing quite broad *papuensis*
Style with 4 well-developed spines, all beyond middle, and an accessory seta proximal to the spines. Genital filaments at least twice length of pump. No pleural setae on thorax. Wing very narrow 2.
2. Style rather short, hardly 3 times as long as wide, with one of the more basal pair of spines quite widely separated from the other and the accessory seta at about middle of segment. Genital filaments about 6 times as long as pump *hoogstraali*.
Style longer, more cylindrical, about 4 times as long as wide, with all spines grouped close to the apex and the accessory seta inserted beyond middle of segment 3.
1. Genital filaments at least 9 times as long as pump. Aedeagus rather long and broad. Cibarium with numerous short teeth in a straight row and a strong chitinous arch *dolichobyssus*.
Genital filaments less than 5 times as long as pump 4.
1. Cibarium with rather irregular, large, triangular teeth, about 12 in number. Chitinous arch fairly well marked. Genital filaments about 4 times as long as pump *fergusoni*.
Cibarium with small slender teeth in a fairly regular row 5.
5. Chitinous arch well developed, the whole cibarium heavily sclerotized. Genital filaments about 4 times as long as pump *quintus*.
Chitinous arch weak, obsolete in the middle. Genital filaments less than 4 times as long as pump 6.
3. Genital filaments about 3 times as long as pump. Cibarial teeth fine, comb-like *sansaporensis*.
Genital filaments about twice as long as pump. Cibarial teeth more triangular, somewhat divergent from the centre *noemforensis*.

Key to Females.

1. Cibarial teeth irregular in size and position 2.
Cibarial teeth in a regular comb of even subequal teeth 3.
2. Cibarium with 4 large triangular teeth and a variable number of more slender teeth in the middle and at sides. Chitinous arch practically absent. Spermathecae oval, thin-walled, the terminal knob sunk in a pit. Delta at least half alpha *fergusoni*.
Cibarium with two large blunt teeth in the middle and a variable number of smaller teeth at the sides. Chitinous arch very prominent. Delta short, less than half the short alpha. Segment III of antennae very short, about equalling fourth palpal segment. Spermathecae as above *brachycornutus*.
1. Cibarium with very numerous, 70 or more, fine teeth 4.
Cibarium with less than 30 teeth 5.
4. Cibarium exceedingly broad, with about 80 long slender teeth. Pharynx broad, armed with groups of short spines. Chitinous arch absent. Segment III of antennae shorter than fourth palpal segment *moresbyi*.
Cibarium narrower, but with about 125 long hair-like teeth and a strong broad pigment patch. Chitinous arch weakly developed. Pharynx slender, unarmed. Segment III of antennae considerably longer than fourth palpal segment *dolichobyssus*.
5. Cibarium with about 24 slender peg-like teeth. Chitinous arch obsolete in the middle *sansaporensis*.
Cibarium with less than 20 spine-like teeth 6.
3. Cibarium with about 18 long slender teeth joined nearly to their tips. Erect teeth small, in a single transverse row. Pigment patch more or less triangular. Chitinous arch faint in the middle *noemforensis*.
Cibarium with about 13 short triangular teeth. Erect teeth large and numerous, not in an even row. Pigment patch oval, with a slender tail. Chitinous arch well sclerotized throughout *hoogstraali*.

PHLEBOTOMUS PAPUENSIS, sp. nov. (Figs. 12, 16, 50, 63.)

Male. Wing length 1.53 to 1.67 mm. Dorsal abdominal hairs erect, as are those on the sternites. No post-spiracular setae. Mesonotum very slightly infuscated. Proboscis, from level of base of palpi to apex, about one-quarter less than head height from base of clypeus to vertex. Palpi and basal antennal segments as figured. Newstead's scales in a loose patch a little proximal to the middle of the third segment. Ascoids simple, long, paired at least to segment X and probably further. Pharynx slender, weakly sclerotized, not obviously spinose, but with faint indications of numerous small denticles at its posterior end, hardly visible in the poorly stained mounts. Cibarium as figured. Genitalia as figured, with two nearly terminal and one median spine but no accessory seta on the style. Aedeagus well sclerotized, slender, with a

triangular ventral extension near the base, not visible in all specimens, and probably representing a sclerotized area extending onto the base of the paramere. Paramere simple, with a small internal ventral triangular excrescence, not shown in the figure, as it lies behind the aedeagus. Genital pump large, with flaring plunger, the filaments rather stout, simple, their apices finely and faintly annulate, less than twice as long as the pump.

Holotype male, slide 1254, and 5 male paratypes, slides 1251-1253, 1255-1256, Dobadura, Oro Bay, Papua, 7 Aug. 1944, Ferguson and Graham colls. Taken in tree holes. One male paratype, slide 1128, same locality, 18 Aug. 1944, and 1 male paratype, slide 2666, same locality, 21 Sept. 1944.

There seem to be no females which can be associated with these males with certainty. The relatively very long antennal segments, especially the first flagellar, and the long palpi, combined with the broad wing and presence of setae on the lower border of mesanepisternum would seem to make the recognition of the female comparatively simple. This species seems clearly related to the Australian species with similar genitalia, *brevifilis* and *buccinator*, differing from the former in the long aedeagus, and from the latter in the less sclerotized aedeagus, more slender genital pump, arrangement of the spines on the style, and arrangement of the teeth in the cibarium.

PHLEBOTOMUS ENGLISHI subsp. *MORESBYI*, subsp. nov. (Figs. 29, 53, 71.)

Female. Wing length 1.56 mm. Dorsal abdominal hairs recumbent, those on the sternites possibly semi-erect on the margins. Mesonotum slightly infuscated. Pleural area not well preserved, probably without setae. Proboscis less than head height from vertex to base of clypeus. Palpi and basal antennal segments as figured. The very short antennal segments are noteworthy. Newstead's scales in a large dense patch on the proximal third of the third palpal segment. Ascoids simple, rather stout and relatively long, paired on all segments except the terminal one. Pharynx lamp-glass shaped, armed with short spines set in groups on short arcs, exactly as in *englishi*. Cibarium very broad, armed with a comb of very numerous fine horizontal teeth, about 80, and with a considerable number of not very distinct small vertical teeth. Spermathecae not visible in the single mount.

Holotype female, slide 1048, Port Moresby, 12-mile swamp, Papua, 13 Aug. 1944, Ferguson and Graham colls., taken in a tree hole or buttress.

This species is exceedingly close to *P. englishi* Tonn. from New South Wales, differing only in having an even shorter antennal segment III, .112 mm. as against a minimum of .134 given by Tonnoir for *englishi*; in a shorter alpha, .240 mm., and delta, .088 mm. as against minimum measurements of .252 and .091 respectively for *englishi*; in shorter wing-length, 1.56 mm. as against 1.70 mm. for *englishi*, and in having fewer teeth in the cibarial comb, 80 instead of 85. These differences are hardly sufficient grounds for erecting a species, yet the great differences in locality seem to call for some sort of recognition, hence the subspecific status. Further material from Papua and Australia may well make the name superfluous.

There is a single male, slide 3522, Port Moresby, 12-mile swamp, 12 Aug. 1944, which may be the male of *moresbyi*. It has similar wing measurements, length 1.35 mm., alpha .184, delta .036, and a short third antennal segment, .120 mm. The pharynx bears spines set on short arcs, as in *moresbyi*, but the cibarium has but 12 rather broad-based triangular horizontal teeth. The genitalia lie in dorso-ventral position, but appear to have a style with four nearly terminal spines and the usual accessory seta. The genital filaments are twisted about the aedeagus, but appear to be at least three and possibly more times as long as the pump. The aedeagus is slender, hardly half as long as the parameres. The parameres do not appear to have the terminal ventral beak found in most species of this group, but this may be due to the position in which they are mounted. If this is truly the male of *moresbyi*, it is very different from male *englishi* and indicates that the two forms are distinct. However, the only available specimen is not adequate for accurate description and the association must remain tentative for the present.

PHLEBOTOMUS HOOGSTRAALI, sp. nov. (Figs. 1, 18, 24, 28, 30, 59, 60, 75.)

Female. Wing length 1.63 to 1.75 mm. Dorsal abdominal hairs mostly recumbent, but with a few erect hairs on the posterior margins of all tergites and the margins of all sternites. No post-spiracular or other pleural setae. Mesonotum very slightly infuscated. Proboscis short, less than head height from vertex to base of clypeus. Palpi and basal antennal segments as figured. Ascoids apparently paired on at least the basal flagellar segments, though only their bases seen with certainty. Newstead's scales in a small dense patch on the proximal third of the third palpal segment. Cibarium and pharynx as figured, the latter without visible armature of spines or scales. Wing as figured. Spermathecae as figured. Gonapophyses of eighth sternite short and slender.

Male. Wing length 1.44 mm. Externally like the female except that delta is relatively shorter and there appears to be but a single ascoid on each of the antennal segments. Cibarium with about eight small horizontal teeth. Male genitalia of the usual type for this group, but the style with one of the spines considerably more proximal than the others, as figured. Inner aspect of coxites with rather numerous fine setae. Aedeagus slender and pointed. Pump and genital filaments as figured, the filaments about 6 times as long as the pump.

Holotype female, slide No. 1446, Hollandia, Dutch New Guinea, January 1945. Taken at light. H. Hoogstraal coll.

Allotype male, slide 1445, and 1 paratype female, slide 1447, same data as holotype.

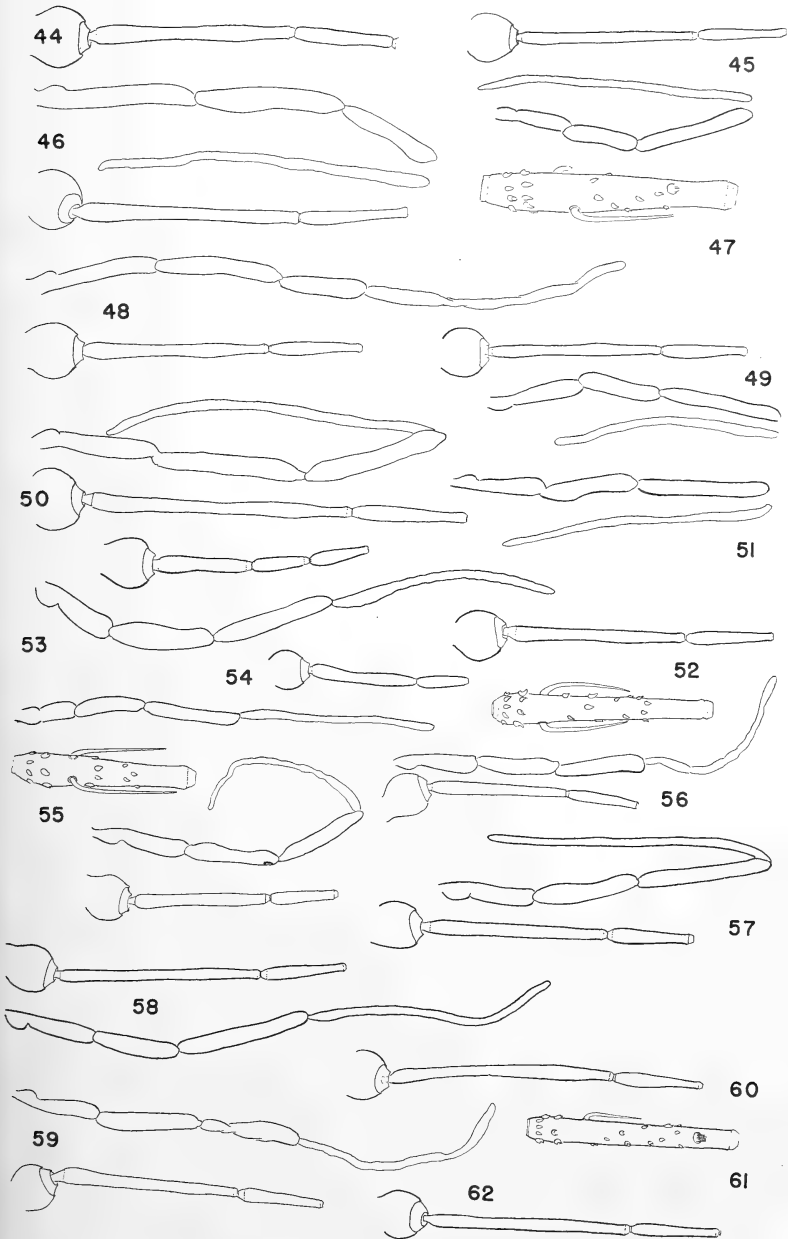
The sexes of this species are associated on the basis of the collecting data, the general similarity of external structures, and the long genital filaments and long spermathecal ducts, not conclusive evidence, but the best that can be done at present. This species will go into Theodor's "group *africana*" of the genus *Sergentomyia*, subgenus *Sergentomyia*, except that the cibarial armature is of the type found in *P. zeylanicus* with erect teeth as well as pointed horizontal teeth. The pharynx is lamp-glass shaped, but bears no visible teeth or spines.

PHLEBOTOMUS DOLICHOBYSSUS, sp. nov. (Figs. 7, 21, 23, 39, 43, 55, 56, 68, 70.)

Female. Wing length 1.26 to 1.33 mm. Dorsal abdominal hairs recumbent, except for a patch of erect setae on the first tergite and a few scattered erect setae on the posterior margins of the succeeding tergites. Sternites with semi-recumbent setae. Mesonotum moderately infuscated. No pleural setae. Proboscis longer than head height from vertex to base of clypeus. Palpi and basal antennal segments as figured. Newstead's scales in a dense patch on proximal third of third palpal segment. Ascoids as figured, long and slender, paired on all but the terminal segment, from which they appear to be absent. Pharynx unarmed, fairly well sclerotized, as figured. Cibarium broad and heavily sclerotized, no chitinous arch, a very large and dense pigmented area and a comb of exceedingly fine and numerous hair-like horizontal teeth and what appear to be several rows of erect or semi-erect teeth below, much obscured by the pigment patch. The teeth in the comb are so fine and numerous that it has not been possible to count

Text-figs. 44-62.

Fig. 44, *P. brevifilis* female, basal antennal segments.—Fig. 45, *P. fergusoni* male, short delta wing, basal antennal segments and palpus.—Fig. 46, *P. pexopharynx* female holotype, antenna and palp.—Fig. 47, *P. brevifilis* female, antennal segment showing ascoids.—Fig. 48, *P. buccinator* male holotype, antenna and palp.—Fig. 49, *P. sansaporensis* female paratype, antenna and palp.—Fig. 50, *P. papuensis* male paratype, antenna and palp.—Fig. 51, *P. noemforensis* female holotype, antenna.—Fig. 52, same, palp and antennal segment VII showing ascoids.—Fig. 53, *P. englishi moresbyi* female holotype, antenna and palp.—Fig. 54, *P. brachycornutus* female holotype, antenna and palp.—Fig. 55, *P. dolichobyssus* female holotype, ascoids, antenna and palp.—Fig. 56, same, male allotype, antenna and palp.—Fig. 57, *P. fergusoni* female holotype, antenna and palp.—Fig. 58, *P. quintus* male paratype, antenna and palp.—Fig. 59, *P. hoogstraali* female holotype, palp and antenna.—Fig. 60, same, male allotype, antenna.—Fig. 61, *P. sansaporensis* male allotype, antennal segment IV showing ascoid.—Fig. 62, *P. fergusoni* male allotype, antenna. All figures of basal antennal segments and palpi are to the same scale, approximately $\times 145$. Figures of single antennal segments to show ascoids are at greater magnification, about $\times 290$.



them accurately, but they are estimated to number about 125. Spermathecae somewhat distorted, as figured, the ducts long, at least five and probably more times as long as the spermathecae and apparently opening separately into the vagina, although they are visible with great difficulty in the available material.

Male. Wing length 1.11 to 1.20 mm. Abdominal setae and colour as in the female. Proboscis slightly less than head height. Palpi and basal antennal segments as figured. Newstead's scales as in female, though fewer. Ascoids small and slender, apparently single on segments III to VII, paired on IX to XIII, remaining segments missing. Where paired, one ascoid is larger than the other. Cibarium as figured. Pharynx as in the female, but more slender. Genitalia characteristic of the group, but the genital filaments exceedingly long, between 9 and 10 times as long as the pump, as figured.

Holotype female, slide 1209, Hollandia, Dutch New Guinea, 6 Sept. 1944, in buttresses of forest trees. Ferguson and Graham coll.

Allotype male, slide 1208, same data as holotype.

Paratypes, 2 males, slides 2820, 2821 and 2 females, slides 2823, 2825, same data as holotype; 1 male, slide 2793, Hollandia, 16 Oct. 1944, in buttresses, 24th Malaria Survey Unit colls.; 1 male, slide 1449, and 1 female, slide 1448, Hollandia, Jan. 1945, at light, H. Hoogstraal coll.; 1 male, Hollandia, Feb. 1945, 1 female, no data, L. E. Rozeboom coll., 1 female, slide 2655, Aitape, 16 Sept. 1944, in buttress, 5th Malaria Survey Unit.

On the basis of the cibarial structure, this species would go into Theodor's "group *minuta*" of the genus *Sergentomyia*, but the type of spermatheca, unarmed pharynx and slender aedeagus indicate closer relationships with his "group *africana*". It is to be distinguished from *hoogstraali* on the structure of the style, longer genital filaments, shorter third antennal segment and very different cibarium. From *englishi moresbyi* it can be separated by the more numerous cibarial teeth and the longer third antennal segment.

PHLEBOTOMUS BRACHYCORNUTUS, sp. nov. (Figs. 7, 42, 54, 64.)

Female. Wing length about 1.17 mm., though both wings are somewhat distorted. Dorsal abdominal hairs mostly recumbent, though some erect hairs present on the posterior margins of tergites I, VI and VII. Sternites mostly with erect hairs and a few semi-recumbent lorate scales. Mesonotum apparently pale, though much broken and distorted. Proboscis greater than head height from vertex to base of clypeus. Third antennal segment and basal palpal segments unusually short, as figured. Ascoids simple, short, paired on at least the first five flagellar segments. Newstead's scales in a dense patch on the proximal third of the third palpal segment. Pharynx moderately well sclerotized and somewhat expanded posteriorly, without visible teeth, hairs, scales or spines, obscurely ridged. Cibarium as figured, the high and heavily sclerotized chitinous arch being especially characteristic. Spermathecae simple thin-walled oval structures, the ducts not discernible in the single specimen.

Holotype female, slide 1195. Toem, Dutch New Guinea, 9 Sept. 1944. Taken in buttress of forest tree.

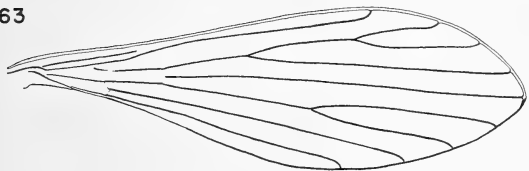
PHLEBOTOMUS FERGUSONI, sp. nov. (Figs. 7, 17, 22, 31-34, 45, 57, 62, 69, 72, 77.)

Female. Wing length 1.386 to 1.710. Dorsal abdominal hairs recumbent, hairs on lateral and posterior margins of sternites apparently semi-erect. No post-spiracular or other pleural setae. Mesonotum very slightly infuscated. Proboscis less than height of head from vertex to base of clypeus. Palpi and basal segments of antennae as figured.

Text-figs. 63-77.

Fig. 63, *P. papuensis* male paratype.—Fig. 64, *P. brachycornutus* female holotype.—Fig. 65, *P. pexopharynx* female holotype.—Fig. 66, *P. buccinator* male holotype.—Fig. 67, *P. brevifiloides* female holotype.—Fig. 68, *P. dolichobysus* female holotype.—Fig. 69, *P. fergusonii* female holotype.—Fig. 70, *P. dolichobysus* male paratype.—Fig. 71, *P. englishi moresbyi* female holotype.—Fig. 72, *P. fergusonii* short delta male.—Fig. 73, *P. noemforensis* female holotype.—Fig. 74, *P. sansaporensis* male paratype.—Fig. 75, *P. hoogstraali* female holotype.—Fig. 76, *P. quintus* male paratype.—Fig. 77, *P. fergusonii* male allotype. All figures are of wings and are to the same scale, $\times 52.5$, except Figs. 65 and 67, which are to a somewhat smaller scale, $\times 34.5$. Both the latter are considerably larger than *P. papuensis*.

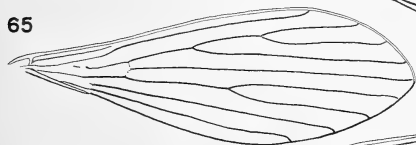
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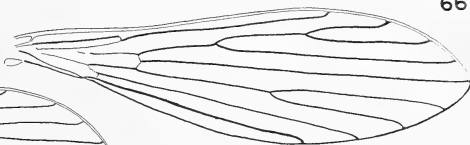
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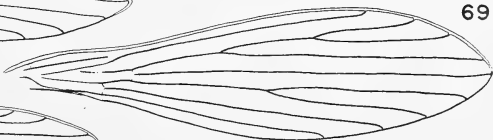
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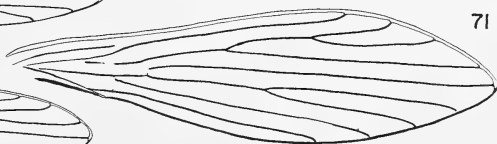
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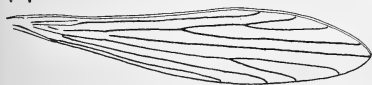
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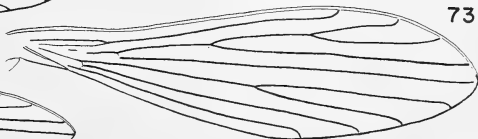
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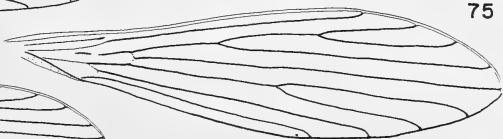
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Ascoids apparently paired on at least the basal antennal segments, short, thin-walled and impossible to see on the majority of specimens. Newstead's scales in a dense patch on the proximal third of the third palpal segment. Pharynx slender, poorly sclerotized, the proximal end with very weakly sclerotized denticulate ridges only visible under optimum conditions. Cibarium as figured, usually with four large teeth and a group of small slender teeth in the middle and at each side. The apparent number, shape and position of the teeth vary considerably, as shown in the figures. The appearance indicated by Figure 33 is often seen and appears to be due to the teeth being bent down into the lumen of the cibarium, i.e. away from the observer. Wing as figured, the length of delta relative to alpha varying considerably. Spermathecae as figured, the ducts not visible. Gonapophyses of eighth sternite short and slender. Cerci short and blunt.

Male. Wing length 1.29 to 1.44 mm. Externally similar to the female. Wing, basal antennal segments and palpi as figured. Ascoids apparently single on at least the basal segments, thin-walled and difficult to see. Cibarium similar to that of the female but narrower and the teeth smaller, as figured. Wing as figured, delta relatively shorter than in the female. Genitalia not distinguishable from other members of the group, the filaments a little more than four times as long as the pump.

Holotype female, slide 1192, Toem, Dutch New Guinea, 9 Sept. 1944, in tree buttresses. Ferguson and Graham colls.

Allotype male, slide 1317, Lae, North-east New Guinea, 16 Aug. 1944, in tree buttresses. Ferguson coll.

Paratypes, 56 females and 17 males from the following localities: Dobadura, Oro Bay, Papua, 26 July, 7, 8, 13, 18 August, and 21 and 22 September 1944 (29 ♀, 3 ♂); Lae, North-east New Guinea, 16 Aug. 1944 (1 ♂); Popendetta, Oro Bay, Papua, 7 October 1944 (3 ♀); Nadzab, North-east New Guinea, 15 August and 1 October 1944 (6 ♀, 6 ♂); Finschhafen, North-east New Guinea, 29 August 1944 (3 ♀, 4 ♂); Tumleo Island, off Aitape, 16 September 1944 (4 ♀, 1 ♂); Toem, Dutch New Guinea, 9 September 1944 (6 ♀); New Guinea, no other data (5 ♀, 2 ♂). All were collected from tree holes or the crevices between the buttressed roots of large forest trees by Majors Ferguson and Graham or members of the 5th Malaria Survey Unit, U.S. Army.

In addition to the above specimens, there is a long series of males (37) and a single female which agree with the above in what can be seen of the cibarium, in the male genitalia and in palpal and antennal lengths, but which differ in having a consistently smaller delta and alpha and shorter average wing length, though there is an overlap of about 10% in this measurement. The pertinent measurements in mm. are given below, taken from all available specimens.

Paratypes:

	15 Males.			56 Females.		
	Alpha.	Delta.	Wing Length.	Alpha.	Delta.	Wing Length.
Max. ..	.280	.144	1.440	.420	.256	1.710
Min. ..	.184	.060	1.260	.220	.080	1.386

Other specimens:

	37 Males.			1 Female.		
	Alpha.	Delta.	Wing Length.	Alpha.	Delta.	Wing Length.
Max. ..	.176	.044	1.314	.168	.044	1.404
Min. ..	.080	.040	1.134			

Whether this material represents another species or is merely a subjective segregate cannot be decided, as most of the specimens with short wing measurements were among those long preserved in alcohol and the mounts are very unsatisfactory. The cibaria of only a few of these can be seen clearly enough to make out the presence of several large teeth similar to those of the paratypes. The localities of these specimens are listed here: 20 males, Dobadura, 18 Aug. and 21 Sept.; 6 males, 1 female, Aitape, 16 Sept.; 3 males, Nadzab, October; 1 male, Tumleo Id., 16 Sept.; 1 male, Hollandia, 6 Sept.; 2 males, Port Moresby, 12, 13 Aug.; 16 males, Toem, 9 Sept.; 5 males, New

Guinea, no other data. Except for the material from Hollandia and Port Moresby, these specimens were taken mainly together with typical *fergusoni*. This species seems to be quite abundant in the eastern part of New Guinea, specimens having been taken in most of the localities where collecting was done from Toem in Dutch New Guinea to Dobadura in Papua. No specimens have been identified in the fairly abundant material from Sansapor on the north-western tip of Dutch New Guinea nor from the islands in Geelvink Bay. The species does not seem to be very closely related to any previously described, though it bears certain resemblances to *P. iyengari* Sint. and its various forms, sharing with them the unarmed pharynx and long delta. It differs, however, in having considerably fewer and more irregularly arranged teeth in the cibarium and in the simple, thin-walled spermathecae.

PHLEBOTOMUS QUINTUS, sp. nov. (Figs. 25, 27, 58, 76.)

Male. Wing length 1.29-1.42 mm. Dorsal abdominal hairs recumbent. No pleural setae. Mesonotum slightly infuscated. Proboscis short, a little less than head height. Palpi and basal antennal segments as figured. Ascoids short and slender, apparently single, on all segments except the terminal three, which are nearly globular. Newstead's scales in a small dense patch on proximal third of third palpal segment. Cibarium as figured, quite heavily sclerotized. Pharynx slender, weakly sclerotized, the apex unarmed but with faint irregular transverse ridges. Wing as figured. Genitalia as figured.

Holotype male, slide No. 1206, Hollandia, Dutch New Guinea, 6 Sept. 1944, in tree buttress.

Paratypes, 1 male, slide 1207, same data as holotype, and 3 males, slides 1044, 2683 and 2685, Finschhafen, at Mape River, North-east New Guinea, 29 Aug. 1944, in tree buttresses. All collected by personnel of the 5th Malaria Survey Unit, U.S. Army, in honour of which the species is named.

PHLEBOTOMUS SANSAPORENSIS, sp. nov. (Figs. 7, 15, 35-38, 49, 61, 74.)

Female. Wing length 1.45 to 1.53 mm. Mesonotum rather strongly infuscated. Dorsal abdominal hairs recumbent. Ventral hairs semi-recumbent. Proboscis less than head height. Third antennal segment and palpi as figured. Newstead's scales in a dense patch on the basal third of third palpal segment. Ascoids short and slender, paired on all segments except the last three, which are abruptly shortened. Pharynx not widened posteriorly, unarmed, with weak ridges and digitate processes. Cibarium as figured, with about 24 relatively short teeth whose apices appear to be bent down into the lumen of the cibarial cavity. It is possible that these teeth represent thickenings on an otherwise tenuous membrane. At other than critical focus the refractive pattern shows a series of broad blunt contiguous structures quite characteristic for the species and easily seen in even the poorest mounts. Spermathecae distorted, apparently simple oval thin-walled capsules, as figured.

Male. Wing length 1.20 to 1.22 mm. Similar to female but alpha and especially delta relatively shorter than in female. Ascoids shorter and more slender than in female, single on all segments but the terminal three. Genitalia as figured. Genital filaments a little more than three times as long as pump. Cibarium as figured, probably with a complete row of smaller and finer teeth of similar type to those in the female, but only those figured visible in the available material.

Holotype female, slide 1151, Sansapor, Dutch New Guinea, 11 Sept. 1944, in tree buttresses at Mar village.

Allotype male, slide 1145, same data as holotype.

Paratypes, 13 males and 14 females, same locality, 11 Sept. and 28 Aug. 1944; 1 female, New Guinea, no other data.

PHLEBOTOMUS NOEMFORENSIS, sp. nov. (Figs. 26, 51-52, 73.)

Female. Wing length 1.40 to 1.53 mm. Mesonotum slightly infuscated. Dorsal abdominal hairs recumbent, at most with occasional erect hairs on the posterior margins of some tergites. Ventral hairs larger, semi-recumbent. Proboscis about equal to head height from vertex to base of clypeus. Third antennal segment and palpi as figured.

Newstead's scales in a small dense patch on proximal third of third palpal segment. Ascoids paired on all but the terminal three flagellar segments (which are abruptly shorter than the preceding segments), slender, short and subequal, as figured. Pharynx not widened posteriorly, unarmed, with faint ridges and obscure digitate processes. Cibarium broad, bearing a comb of about 18 pointed teeth, as figured. Spermathecae not well preserved, apparently thin-walled ovoid structures with the terminal knob sunk in a pit.

Male. Wing length 1.13 to 1.20 mm. Similar to the female, but delta and alpha relatively shorter and wing narrower. Ascoids more slender and shorter, single on each flagellar segment except the last three, from which they appear to be absent. Genitalia of the *Sergentomyia* type, all spines of the style close to apex and aedeagus long and slender. Genital filaments a little more than twice as long as pump. Cibarium much like that of female, but narrower, the teeth smaller, about 13 in number. Pharynx as in female.

Holotype female, slide 1167, Kornosoren, Noemfor Island, Geelvink Bay, Dutch New Guinea, 12 Sept. 1944. Ferguson and Graham colls.

Allotype male, slide 1174, same data as holotype.

Paratypes, 34 males, 11 females, same data as holotype.

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NOTE.—For the sake of those who may be stimulated to follow the lead of Dr. Fairchild's work, it is worth recording that the range of distribution of *Phlebotomus* in Australia is quite wide. Mr. K. R. Norris has recently drawn attention to the existence of specimens, collected by himself, from both Western Australia and South Australia. These specimens were originally examined by Mr. Tonnoir, who determined the one from Crawley, W.A., as *Phlebotomus* near *queenlandi* Hill, and the one from the Waite Institute, Adelaide, S. Aust., as *Phlebotomus englisi* Tonn.? These are now in the C.S.I.R.O. collection at Canberra. During the present year Mr. A. L. Dyce has recovered *Phlebotomus* in a light trap he has been operating at Moree, N.S.W.—Ed.

AUSTRALIAN RUST STUDIES.

IX. PHYSIOLOGIC RACE DETERMINATIONS AND SURVEYS OF CEREAL RUSTS.

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(Plate ix.)

[Read 30th July, 1952.]

Synopsis.

In continuation of earlier work, studies of the life histories and specialization phenomena have been made of the stem and leaf rusts of wheat, oats, barley, and rye. The host range has had to be extended to other grasses in many cases.

In general the aecidial stages of the pathogens are unimportant here. The carry-over of the rust takes place in the uredospore stage on self-sown plants of the cereal host or sometimes on susceptible grasses.

The physiologic races and, in certain cases, the biotypes of these rusts, have been determined during a long period of years and their occurrence surveyed for Australia and New Zealand. The bearing of this work on breeding programmes is emphasized.

General.

Cereal rusts do enormous damage throughout the world. In Australia, studies have been in progress for a number of years, and although results of earlier work have been published (Waterhouse, 1929, 1930, 1933, 1934, 1935, 1936, 1938, 1939, 1951; Waterhouse and Watson, 1941; Watson and Waterhouse, 1949), a detailed account of the later investigations has not been given for some time. This paper is designed to bring up to date the results that have been obtained with the following rusts: stem and leaf rust of wheat, stem and leaf rust of oats, leaf rust of rye, and leaf rust of barley. Results of work on certain grass rusts are not included here.

STEM RUST OF WHEAT.

INTRODUCTION.

Weather conditions in recent years have again been responsible for heavy crop losses from disease attack, and these have directed attention to the continuing importance of the wheat rust problem. Butler (1948) estimated that the New South Wales losses caused by stem rust in the 1947-1948 season amounted to £7,000,000, and pointed out that this would have been much greater had it not been for the cultivation of several resistant varieties in some areas. Further heavy losses have occurred since. Apart altogether from rust, other organisms have done much damage under the favourable conditions. It is difficult to give a true assessment of particular losses: some put down to stem rust may well have been due to other causes.

LIFE HISTORY.

Aecidial Stage.

Earlier work with *Puccinia graminis tritici* E. & H. (Waterhouse, 1929, 1936, 1938) has shown that the Australian position is unique in many ways. For example, the rust does not regularly develop the aecidial stage on the barberry. To date only one record of the natural occurrence of this stage has been made (Waterhouse, 1934). Nevertheless controlled work in the plant house has shown that the barberry is a potential source of danger, and the growing of susceptible species is rightly proscribed.

Material sent from other countries for examination has consistently given good germinations of teleutospores which have been over-wintered abroad before being forwarded by air mail in the spring. There have been a few cases, e.g., wheat straw from Greece, in which all attempts have failed to break the dormancy, either by exposing to winter conditions on the Tablelands, or by artificial freezing and thawing, material

which had not been thus treated. Year after year Australian material has been exposed to winter conditions on the Tablelands of New South Wales, and also treated in the refrigerator, but very rarely has it been possible to get the spores to germinate. Failures have occurred with spores formed in the spring and in the autumn and therefore not subjected to the high summer temperatures, as well as with rust produced at the usual times. There is a clear need for a fuller investigation of this happening: proper control of teleutospore germination is essential for studies dealing with the genetics of the rust fungi.

Teleutospores on wheat straw from India have yielded cultures from barberries which proved to be races 16 and 21.

Wheat rust sent for determination from Burma in 1947 showed the presence of races 14, 17 and 78. Reference is made elsewhere (p. 235) to the leaf rusts also present in this material.

British material has given many different races. It has already been stated (Waterhouse, 1938) that races 23, 24, 27, 33, 35, 51, 53, 69, 83, 109, 117 and 122 have been sorted out. In more recent work, the following additional races have been determined from teleutospore and uredospore material: 10, 11, 16, 21, 34, 48, 56, 75, 95, 100, 107, 148, 151, 194, 222 and 228.

This is a very wide range of races. Relatively few isolates have been available for examination, but the number of races found is very much greater than in comparable studies of Australian material. The greater diversity is probably due to the presence of the barberry in parts of Britain, and the production on it of new races by hybridization.

It has been the practice to test the overseas races for their reactions on useful extra-differential varieties—viz., "Yalta", "Celebration", and "Eureka". Uniformly resistant reactions have been given on "Yalta", this being in sharp contrast with the susceptibility shown to the common Australian rust. On "Celebration", instead of resistance, susceptibility is usual. There have been cases—e.g., with r. 34—in which isolates giving the normal reactions on the differential set have behaved quite differently on "Celebration", one biotype giving fully susceptible and another completely resistant reactions. "Eureka" is resistant to some but susceptible to others of these races. This again emphasizes the fact that varieties useful as resistant parents in one area may be quite worthless in another where different physiologic races occur. At the same time it is important to have the greatest possible number of races on hand for work designed to classify the genes that are concerned with resistance, as well as to enable tests for wide resistance to be made of new crossbred wheats. The more genes for resistance that are present, the more likely is such a variety to remain resistant under changes that take place in the races present in that area.

Uredospore Stage.

Evidence has mounted to show that the uredospore stage carries the rust over from season to season on "volunteer" wheat, barley, rye, and on certain grasses. During the period under consideration the occurrences on common grasses in time and space are shown in Tables 1 and 2.

It is clear that with the exception of 1945, which was a drought year, rusted grasses came to hand in each of the years. The significance of the widely distributed *Hordeum leporinum* and *Agropyron scabrum* is shown by the fact that they provided more than 90% of the isolates. By reason of its perennial habit, the latter is particularly important. The relative paucity of rusts from the other grasses does not mean that they are therefore unimportant. Thus the other two species of *Hordeum* and the three of *Agropyron* listed have a limited distribution only, but where they do occur they may serve as foci for the spread of the rust. It should not be taken that the grasses listed are the only ones capable of being attacked by wheat stem rust. Further investigation may well bring others to light.

Apart from its occurrence on wheat and grasses, stem rust has commonly been found on rye and barley, sometimes on plants growing out of season. Details of these isolates are set out in Tables 3 and 4.

TABLE 1.

Summary of the Number of Isolations of Physiologic Races of *P. graminis tritici* Found on Grasses, Grouped According to Time of Collection.

Race.	Season of Collection, Ending 31st March of the Year Named.											Totals.		
	1939.	1940.	1941.	1942.	1943.	1944.	1945.	1946.	1947.	1948.	1949.		1950.	1951.
21										1				1
45		1												1
59	1													1
126	13	11	8	5	2	8		1	2	6	2	3		61
126B								8	2	11	2	10	2	35
222BB												20	5	25
222AB												13	2	15
Totals	14	12	8	5	2	8		9	4	18	4	46	9	139

TABLE 2.

Summary of the Number of Isolations of Physiologic Races of *P. graminis tritici* Found on Grasses, Grouped According to Their Source.

Grass Host.	Total No. of Isolates.	Source of Material and Number of Each Race Found.										Totals of Races.									
		A.C.T.			N.S.W.				Qld.		S.A.								W.A.		
		Races.			Races.				Races.		Races.	Race.									
		126.	45.	21.	59.	126.	126B.	222BB.	222AB.	126.	126B.	222BB.	126.	126B.	126.	21.	45.	59.	126.	126B.	222BB.
<i>Hordeum leporinum</i>	95	2		1	28	24	18	11				1	1	9			1	40	25	18	11
<i>H. marinum</i>	2				1	1												1	1		
<i>H. bulbosum</i>	2				2														2		
<i>Agropyron scabrum</i>	32	2	1		8	5	4	4	2	1	3			2			1	14	6	7	4
<i>A. epicatum</i>	1									1									1		
<i>A. velutinum</i>	1			1						1							1				
<i>A. pectinatum</i>	1				1														1		
<i>Amphibromus Neesii</i>	1				1														1		
<i>Elymus</i> sp.	2				2														2		
<i>Aegilops ovata</i>	1													1					1		
<i>Deoxyia quadrisetata</i>	1				1														1		
Totals	139	4	1	1	42	32	22	15	2	2	3	1	1	12	1	1	1	61	35	25	15

In all but two of the years, rust was found on rye. From it four races were isolated. In one case, races 33 and 126 were present together in the one field collection. Race 126 was found in almost 90% of the isolates.

Barley was a host of wheat rust in each of the years. In all, seven races were found on it. On six occasions, races 126 and 126B were found together, once races 14 and 126B, and once races 33 and 126. The commonest race was 126, which occurred to the extent of 70% of the total.

TABLE 3.
Frequency of Occurrence and Distribution of Races of P. graminis tritici on Rye.

Year.	Race.	Number of Isolates.	Distribution in Space.					
			N.S.W.	Qld.	Vic.	S.A.	W.A.	N.Z.
1939	33	1		1				
	126	6	5	1				
1940	126	4	3					
1941	126	6	5				1	
1942	126	6	6					
1943	126	3	3					1
1944	126	3	3					
1945	126	4	4					
	126B	1	1					
1946	126	1	1					
	126B	2	1		1			
1947	126	1				1		
	126B	1	1					
1948	126	1	1					
1949		—						
1950	126	1	1					
	126B	1	1					
	222BB	1	1					
1951		—						
Totals		43	37	2	1	1	1	1

TABLE 4.
Frequency of Occurrence and Distribution of Races of P. graminis tritici on Barley.

Year.	Race.	Number of Isolates.	Distribution in Space.					
			N.S.W.	Qld.	Vic.	S.A.	W.A.	Tas.
1939	33	1		1				
	126	8	4	4				
1940	126	5	4	1				
1941	126	7	7					
1942	45	1	1					
	126	11	8				2	1
1943	126	4	3	1				
1944	126	11	5		1		5	
1945	126	1	1					
	126B	1	1					
1946	126	2	2					
	126B	3	3					
1947	126	3	2		1			
	126B	4	3			1		
1948	126	5	2	1			1	1
	126B	8	5	2		1		
	14	1	1					
1949	126	1	1					
	126B	1	1					
	222AA	1	1					
1950	126	2	2					
	126B	2	2					
1951	222BB	3	3					
	222AB	1	1					
Totals		87	63	10	1	3	8	2

Specialization.

In the determination of physiologic races, the set of differential wheat varieties selected by Stakman and Levine (1922) has been used in order that further comparisons with recorded races might be made. The varieties "Reliance C.I. 7370" and "Kanred C.I. 5146" were found to be interchangeable in the work, using the selection of the latter described in a previous paper (Waterhouse, 1929). The typical reactions shown by important races referred to herein are set out in Table 5.

TABLE 5.
Typical Reactions of Certain Physiologic Races of P. graminis tritici on Selected Differential Varieties of Triticum spp.

Race Number.	Little Club C.I.4066.	Marquis C.I.3641.	Reliance C.I.7370.	Kofa C.I.5878.	Armatka C.I.1493.	Mindum C.I.5296.	Spekhar C.I.6236.	Kubanka C.I.2094.	Ampa C.I.5284.	Biborn C.I.2436.	Vernal C.I.3686.	Khapli C.I.4013.	Eureka.	Valtu.
11	4	4	3	3	4	4	4	3	3	3	1	1		
14	4	2	1	1	3	3	3	3	3	3	1	0		
21	4	4	0	3	4	4	4	4	3	1	0	1		
33	4	2	4	1	1	1	1	3	3	3	1	1		
34	4	4	4	4	4	4	4	3	3	1	0	1		
43	4	3	0	0	0	0	0	x	1	3	1	0		
44	4	3	0	0	0	0	0	3	3	3	1	0		
45	4	2	0	2	4	4	4	x	x	3	3	1		
46	4	3	0	2	4	4	4	1	1	3	3	1		
54	4	3	0	0	0	0	0	1	3	3	1	0		
55	4	4	0	2	4	4	4	x	x	3	3	1		
56	4	3	3	3	1	1	1	3	3	1	1	1		
59	4	2	0	0	1	1	1	x	3	3	1	0		
126	4	4	3	3	x	x	x	x	x	1	1	1	0	0
126B	4	4	3	3	x	x	x	x	x	1	1	1	4	0
222 ¹	4	3	3	3	3	3	3	1	1	0	0	0		
222AA	4	3	3	3	3	3	3	1	1	0	0	0	0	0
222AB	4	3	3	3	3	3	3	1	1	0	0	0	0	4
222BB	4	3	3	3	3	3	3	1	1	0	0	0	3	4

¹ Grateful acknowledgement is made to Dr. E. C. Stakman of Minnesota, U.S.A., for supplying the designation of this race.

During the period under consideration the occurrences of the races in time and space are given in Tables 6 and 7.

TABLE 6.
Summary of the Number of Isolations of Physiologic Races of P. graminis tritici Grouped According to Time of Collection.

Race.	Season of Collection, Ending 31st March of Year Named.													Totals.
	1939.	1940.	1941.	1942.	1943.	1944.	1945.	1946.	1947.	1948.	1949.	1950.	1951.	
126	165	267	93	159	104	114	31	54	88	184	48	65	19	1391
126B				2	27	22	36	155	163	184	68	127	49	833
222BB											3	292	122	417
222AB											2	220	66	288
11	1	3		1										5
14										1				1
21										1				1
33	3													3
45	1	4		1										6
56						1								1
59														1
222AA	1										1			1
Totals	171	274	93	163	131	137	67	209	251	370	122	704	256	2948

TABLE 7.

Summary of the Number of Isolations of Physiologic Races of *P. graminis tritici* Grouped According to Their Source.

Race.	Source of Material.								Totals.
	A.C.T.	N.S.W.	Vic.	Qld.	S.A.	W.A.	Tas.	N.Z.	
126	17	918	115	75	66	143	43	14	1391
126B	2	665	23	68	51	7	11	6	833
222BB		361	10	44			2		417
222AB		246	2	40					288
11		4	1						5
14		1							1
21		1							1
33				3					3
45	1	2		3					6
56		1							1
59		1							1
222AA		1							1
Totals ..	20	2201	151	233	117	150	56	20	2948

The locations from which the collections came year by year are as follows:

DETAILS OF THE OCCURRENCES OF THE RACES OF *P. GRAMINIS TRITICI*.

1939.

r.11.

N.S.W.: H.A. College.

Qld.: Warwick.

r.33.

N.S.W.: Albert.

Qld.: Gatton.

r.126.

N.S.W.: Grafton, Scone, Manilla, Wee Waa, Pilliga, Curlewis, H.A. College, Myall Creek, Bundella, Premer, Tambar Springs, Moree, Warialda, Bingara, Birriwa, Myall Plains, Mendooran, Merrygoen, Narrabri, Pallamallawa, North Star, Inverell, Gum Flat, Cherry Tree Hill, Albert, Gunnedah, Cowra, Cumnock, Rocky Glen, Ulamambie, Purlewaugh, Oberly, Yeoval, Gilgandra, Dubbo, Euchareena, Temora, Cootamundra, Canowindra, Bathurst, Chatswood, Auburn Vale, Tichborne, Nelungaloo, Nundle, Peak Hill, Quandialla, Eugowra, Ballinari, Young, Woodstock, Moulamein, Quirindi, Pine Ridge, Glen Innes, Barry, Newbridge, Millthorpe, Lindfield.

Qld.: Brookstead, Gatton, Roma, Oakey, Dalby, Warwick, Toowoomba.

S.A.: Elbow Hill, Pinkawillinie, Yadnarie, Yeelana, Rudall, Upper Eyre Peninsula, Port Neill.

Tas.: Deloraine, Illawarra, Bishopsbourne, Bish-Long, Erandale, White Hills, Hagley, Longford, Cressy, Brackwell, Oaks, Formosa, North-West Coast, Stoodley, Barrington, Oyster Cove.

A.C.T.: Canberra.

r.45.

N.S.W.: Inverell.

r.59.

N.S.W.: Bathurst.

1940.

r.11.

N.S.W.: Temora, Manilla, Dunedoo.

r.126.

N.S.W.: West Wyalong, Carroll, Narrabri, Condobolin, Parkes, Gunnedah, Grawlin Plains, Ungarie, Biniguy, Trangie, Narrandera, Ivanhoe, Manildra, Temora, Pallamallawa, H.A. College, Black Creek, Wirrinya, Baradine, Wellington, Leeton, Colinroobie, Inverell, Bingara, Culgoora, Werris Creek, Currabubula, Willow Tree, Quirindi, Tamworth, Cobbarah, Leadville, Manilla, Attunga, Boggabri, Mullaly, Oakwood, Dunedoo, Mendooran, Wee Waa, Brobenah, Yerong Creek, Henty, The Rock, Osborne Creek, Loogong, Cudal, Cumnock, Gilgandra, Dubbo, Yeoval, Mathoura, Narromine, Wongarbon, Geurie, Arthur-

ville, Cowra, Bathurst, Bugaldie, Coonabarabran, Binnaway, Euratha, Yanco, Corobimilla, Eursley, Sandigo, Burraja, Ringwood, Daysdale, Jerilderie, Deniliquin, Blighty, Finley, Tocumwal, Berrigan, Cookardinia, Bungowarra, Urana, Cullwel, Rand, Lockhart, Broken Hill, Caragabal, Eugowra, Forbes, Goolagong, Tragene, Uranquinty, Old Junee, Mangoplah, Downside, Coreinbob, Collingullie, Wagga, Balranald, Moulamein, Greenthorpe, Canowindra, Grenfell, Mascot, Lindfield, Muswellbrook, Blayney, Chatswood, Chullora, Glen Innes.

Qld.: Gatton, Pittsworth, Oaken, Cecil Plains, Warwick, Toowoomba.

A.C.T.: Canberra, Yamba, Watangera, Ainslie.

W.A.: Merredin, Salmon Gums, Perth, Northampton, Borden.

Vic.: Werribee, Swan Hill, Donald, Invergordon, Charlton, Longeronong, Swan Vale.

S.A.: Waite, Roseworthy, Saddleworth.

r.45.

Qld.: Gatton, Pittsworth.

A.C.T.: Canberra.

1941.

r.126.

N.S.W.: Taree, Bathurst, Garthowen, H.A. College, Sydney University, Tichborne, Wongalea, Cowra, Glen Innes, Willow Tree, Chullora, Tamworth, Grawlin Plains, Armidale, Inverell, Attunga, Emerald Hill, Bective, Wallabadah, Quirindi, Boggabri, Milvale, Gunnedah, Bungarby, Parkes, Carroll, Guyra, Furracabad, Nelungaloo.

Qld.: Kincora.

Vic.: Dookie, Salisbury, Longeronong, Werribee, Donald.

S.A.: Waite.

A.C.T.: Canberra, Duntroon.

N.Z.: Christchurch, Auckland.

1942.

r.11.

Vic.: Rochester.

r.126.

N.S.W.: Spring Ridge, Duri, Gunnedah, Inverell, Baradine, Narrabri, Kelso, Tichborne, H.A. College, Pallamallawa, Bunaloo, Tambar Springs, Purlawaugh, Forbes, Bingara, Barraba, Yelindenie, Parkville, Goonumbla, Peak Hill, Alectown, Cowra, Bathurst, Binnaway, Mollan, Tamworth, Birriwa, Tooraweenah, Neilrex, Cumnock, Grenfell, Eugowra, Parkes, Jemalong, Ooma, Culcairn, Urangeline, Jindera, Boggabri, Strathfield, Glen Innes.

A.C.T.: Canberra.

W.A.: Merredin, Chapman, Mingenan.

S.A.: Waite.

Vic.: Werribee, Werrimull, Rochester, Rutherglen, Dookie, Donald, Charlton, Longeronong, Salisbury, Walpeup.

Tas.: Wilmot, Cressy, Wesley Vale.

N.Z.: Auckland, Lincoln, Nelson.

r.45.

N.S.W.: H.A. College.

r.126B.

N.S.W.: Gunnedah, Tamworth.

1943.

r.126.

N.S.W.: H.A. College, Narrabri, Curlewis, Gunnedah, Tamworth, Coonabarabran, Somerton, Carroll, Tambar Springs, Purlawaugh, Tichborne, Baradine, Bugaldie, Boggabri, Edgeroi, Cowra, Spring Hill, Borenore, Maryvale, Arthurville, Dubbo, Rawsonville, Parkes, Rocky Dam, Inverell, Attunga, Nemingha, Loomberah, Lane Cove, Balladoran, Wongarbon, Eulomigo, Quirindi, Mungeribah, Glen Innes, Delungra, Bannockburn, Manly, Wallabadah, Goonoo Goonoo, Lindfield, Badgery's Creek.

Qld.: Gatton, Willawa, Winton, Brookstead.

W.A.: Merredin, Salmon Gums.

Vic.: Walpeup, Dookie, Rutherglen, Footscray, Longeronong, Werribee, Maribyrnong.

S.A.: Waite, Paskeville.

r.126B.

N.S.W.: Narrabri, Gunnedah, Tamworth, Somerton, Boggabri, Edgeroi, Cowra, Maryvale, Rocky Dam, Inverell, Attunga, Nemingha, Delungra, Bannockburn.

Qld.: Winton.

1944.

r.126.

N.S.W.: Tichborne, Gunnedah, H.A. College, Binnaway, Temora, Cowra, Wagga, Tambar Springs, Curlewis, Grong Grong, Spring Hill.

Qld.: Brookstead.

W.A.: Merredin, Elabbin, Northampton, Nalkain, Binee, Baandee, Mandiga, Kunonoppin, Ballidee, East Ballidee, Wyalkatchem, Kulja, Bencubbin, South Bencubbin, Naraling, East Salmon Gums, Salmon Gums, Doodlakine, Kollerberrin, Quellington, Grass Valley, Wael, Meenar, Carnamah, Wongan Hills, Highbury, Toompup, Chapman.

S.A.: Waite.

Vic.: Walpeup, Dookie, Salisbury, Longeronong, Werribee.

Tas.: Deloraine.

N.Z.: Winton.

r.56.

N.S.W.: Sydney University.

r.126B.

N.S.W.: Milguy, Gunnedah, H.A. College, Temora, Cowra, Beekom, Wagga, Moombooldool, Ariah Park, Curlewis.

Vic.: Walpeup, Dookie.

Qld.: Brookstead.

S.A.: Waite.

1945.

r.126.

N.S.W.: Curlewis, Wallacia, Gilgandra, Mount George, West Maitland, Rocky Glen, H.A. College, Grafton, Breeza, Gosford, Quirindi, Goonoo Goonoo, Killara.

Vic.: Burnley.

S.A.: Waite.

W.A.: Merredin, Perth.

r.126B.

N.S.W.: Curlewis, Mulgoa, Wallacia, Gunnedah, Gilgandra, H.A. College, Gulargambone, Brindley Park, Baradine, Loomberah, Manilla, Quirindi.

Qld.: Gatton.

1946.

r.126.

N.S.W.: Canowindra, Burdett, Waroo, West Wyalong, Bedgerabong, Cowra, Young, Koorawatha, Ariah Park, Bingara, Narromine, Gunnedah, Curlewis, North Star, Wean, Warialda, Gravesend, Bellata, Edgeroi, Pallamallawa, Tamworth, H.A. College, Warrumbungle, Manilla, Dubbo, Castle Mountain.

Qld.: Lawes.

W.A.: Merredin.

N.Z.: Lincoln.

r.126B.

N.S.W.: Nundle, Curlewis, Nea Siding, Murrurundi, Inverell, Garah, Bingara, New Mexico, Gunnedah, Singleton, Scone, Gravesend, Emerald Hill, North Star, Wallangra, Warialda, Bellata, Pallamallawa, Edgeroi, Tamworth, Manilla, Thorli, Dubbo, H.A. College, Baradine, Somerton, Wee Waa, Balladoran, Berrigal Creek, Coonabarabran, Mullaly, Narrabri, Cookabunna, Castle Mountain, Loomberah, Armatree, Cowra, Eumungerie, Young, Koorawatha, Temora, Moombooldool, Milvale, Ariah Park, Ardlethan, Purlawaugh, Elong Elong, Auburn Vale, Bukkulla, Narromine, Gulargambone, Canowindra, Burdett, Bedgerabong, Waroo, West Wyalong, Maryvale, Culcairn, Gilgandra, Young, Boorowa, Gerogery, Tichborne, Glen Innes, Spring Hill.

Qld.: Lawes, Pittsworth, Brookstead.

Vic.: Werribee.

1947.

r.126.

N.S.W.: Holbrook, Albury, Brocklesby, Walbundrie, Finley, Killara, Orange, Cowra, Leeton, Alfred Town, Corowa, Bungowanah, Kycemba, Gundagai, Gerogery, Jindera, Table Top, Walla, Tichborne, Ladysmith, Burradana, Frogmore, H.A. College.

Qld.: Lawes, Brookstead.

S.A.: Roseworthy, Pinnaroo, Baroota, Waite, Ungarra.

Vic.: Walpeup, Lake Cullullmare.

W.A.: Toompup.

r.126B.

N.S.W.: Holbrook, Grong Grong, Cowra, Killara, Inverell, Glenfield, H.A. College, Clarendon, Windsor, Alfred Town, Albury, Brocklesby, Walbundrie, Bungowanah, Kycemba, Corowa, Gerogery, Ringwood, Table Top, Loomberah, Deniliquin, Finley, Leeton, Howlong, Morven, Pleasant Hills, Orange.

Qld.: Lawes, Bonga, Brookstead.

S.A.: Roseworthy, Pinnaroo, Saddleworth, Waite.

Vic.: Walpeup.

N.Z.: Tai Tapu.

1948.
r.14.
- N.S.W.: Kelso.
- N.S.W.: Kosciusko.
r.121.
r.126.
- N.S.W.: Glen Innes, Kosciusko, Curlewis, Tamworth, Wagga, Moree, Delungra, Crooble, Yanco, Westdale, Wee Waa, Narrabri, Edgeroi, Geurie, Coradgery, Mt. Euroa, Wellington, Wongarbon, Eumungerie, Coonabarabran, Tooraweenah, Boggabri, Trangie, North Star, Grafton, Coolamon, Ganmain, West Wyalong, Orange, H.A. College, Bingara, Young, Wombat, Wyanga, Balldale, Brocklesby, Tichborne, Bergalia, Yarraman, Castle Hill, Kelso.
- Qld.: Horrane, Hermitage, Warwick, Mt. Tyson, Darling Downs, Biloela, Euanslea, Condamine Plains, Wellcamp, Lawes, Archerfield.
- S.A.: Jamestown, Mullewa, Walloway, Roseworthy, Waite, Owen, Mt. Gambier, Penola.
Vic.: Walpeup.
- W.A.: Wongoondy, Mendel, Northampton, Grass Patch, Merredin.
- A.C.T.: Canberra.
- Tas.: Latrobe, Cressy, Deloraine, Pateena, Cambridge, Kindred, Sassafras, Elliott.
- r.126B.
- N.S.W.: Bingara, Temora, Concord, Inverell, Delungra, Scone, Dubbo, Suntop, Binnalong, Mudgee, Calimba Siding, Forbes, Wallen Bullen, Peak Hill, Dandaloo, Middlefield, Curlewis, Willow Tree, Merriwa, St. Elmo, Cowra, Walbundrie, Brocklesby, Tamworth, Barraba, Manilla, Quirindi, Manly, Gaylong, Cunningham, Harden, Gosford, Mangoplah, Culcairn, Gerobery, Howlong, Glen Innes, Bogan Gate, West Wyalong, Curlewis, Moree, H.A. College, Coonabarabran, Crooble, Narrabri, Wee Waa, Geurie, Mt. Euroa, Wongarbon, Wellington, Trangie, North Star, Moree, Boggabri, Condobolin, Orange, Gilgandra, Walmer, Fingerpost, Tumbarumbah, Kelso, Blackheath.
- Qld.: Biloela, Brookstead, Lawes, Hermitage, Dalby, Horrane, Warwick, Mt. Tyson, Darling Downs, Condamine Plains, Archerfield.
- S.A.: Mt. Gambier, Bordertown, Wolseley, Wolloway, Roseworthy.
- Tas.: Launceston, Cressy, Campbell Town.
1949.
r.126.
r.126B.
- N.S.W.: Curlewis, Boggabri, Castle Hill, Bugaldie, Cowra, Trangie, Bathurst, Grenfell, Bribbaree, Marangarell, Temora, Colinroobie, Aria Park, Gundagai, Ganmain, Coolamon, Yanco, Leeton, Gunnedah, Trundle, Gunningbland, Umaralla Mount.
- W.A.: Merredin, Caversham, Ballidee.
- Qld.: Lawes, Hermitage, Scottsdale.
- N.Z.: Waikoikoi, Tairei.
- r.126B.
- N.S.W.: Curlewis, Gilgandra, Cooma, Boggabri, Yanco, Castle Hill, Bellata, Bugaldie, Cowra, Trangie, Bathurst, Grenfell, Bribbaree, Marangarell, Temora, Colinroobie, Aria Park, Gundagai, Yass, Ganmain, Coolamon, Leeton, Gunnedah, Trundle, Gunningbland.
- Tas.: Cressy.
- Qld.: Lawes, Dalby, Hermitage, Nabby.
- N.Z.: West Eyreton.
- r.222AA.
- N.S.W.: Tanja.
- r.222BB.
- Qld.: Lawes, Warwick, Westbrook.
- r.222AB.
- Qld.: Hermitage.
1950.
r.126.
- N.S.W.: Spring Hill, Curlewis, Glen Innes, Gunnedah, Aria Park, Bathurst, Manildra, Forbes, Wyalong, Leeton, Orange, Deniliquin, Coolamon, Ganmain, Matong, Grong Grong, Narrandera, Urana, Oaklands, Berrigan, Balldale, Henty, Walbundrie, Brocklesby, Marina, Wagga, Cootamundra, Cowra, Spring Ridge, Temora.
- Qld.: Allora, Nabby, Toowoomba.
- W.A.: Wongan Hills, Merredin, Gnowangerup, Borden.
- S.A.: Waite, Gladstone, Huddleston, Yandiah, Streaky Bay, Wirrulla, Chandada, Pestubie, Coelie, Mt. Cooper, Collie.
- Vic.: Rutherglen, Dooen, Walpeup.
- Tas.: Moriarty.

r.126B.

V.S.W.: Curlewis, Gunnedah, Berrigan, Deniliquin, Cheeseman's Creek, Bathurst, Parkes, Manildra, Walbundrie, Yiddah, Reefton, Tichborne, Forbes, Marsden, Wyalong, Temora, Leeton, Orange, Coolamon, Ganmain, Matong, Grong Grong, Narrandera, Corobindia, Coonong, Urana, Oaklands, Sangar, Merton, Corowa, Balldale, Henty, Marinna, Illabo, The Rock, Wagga, Junee, Young, Cootamundra, Crowther, Noonbinna, Wallendbeen, Cowra, Blayney, Kingsvale, Tubbet, Gilgandra, Dubbo, Blackheath, Jindera, H.A. College, Spring Terrace.

Fas.: Moriarty, Branxholm.

Qld.: Hermitage.

Vic.: Werribee, Rutherglen, Doon, Walpeup, Dookie.

W.A.: Red Lake, Merredin, Toomup.

S.A.: Waite, Kapunda, Neale's Flat, Gladstone, Huddleston, Laura, Wirrabara, Yandiah, Streaky Bay, Wirrulla, Chandada, Pestubie, Mount Cooper, Collie, Roseworthy, Belvedere.

A.C.T.: Canberra.

N.Z.: Lyalldale, Hook.

r.222BB.

N.S.W.: Gunnedah, Curlewis, Narrabri, Tamworth, Castle Hill, Bellata, Dubbo, H.A. College, Stoney Creek, Boggabri, Wee Waa, Baan Baa, Carroll, Gravesend, West Wyalong, Appleby, Attunga, Grafton, Piallaway, Raleigh, Manilla, Somerton, Bective, Baradine, Gilgandra, Tambar Springs, Coonabarabran, Mendooran, Dunedoo, Leadville, Bogan Gate, Tintinhull, Spring Ridge, Armidale, Binnaway, Beckom, Cudal, Gosford, Barraba, Bingara, Delungra, Inverell, Warialda, Kelvin, Camden, Lucknow, Manildra, Goonumbia, Tichborne, Yiddah, Barmedman, Forbes, Marsden, Temora, Leeton, Rannock, Sebastopol, Berrigan, Merton, Sangar, Brocklesby, Illabo, The Rock, Junee, Young, Crowther, Noonbinna, Lyndhurst, Murrurundi, Deniliquin, Orange, Quandialla, Lockhart, Blackheath, Molonglo, Glen Innes, Spring Terrace, Quirindi, Upperton, Pine Cliff, Wongarbon.

Qld.: Brookstead, Lawes, Wyreema, Biddleston, Westbrook, Mt. Tyson, Hermitage, Bowenville, Toowoomba, Dalby, Oakey.

Fas.: Moriarty.

Vic.: Rutherglen.

r.222AB.

N.S.W.: Narrabri, Gunnedah, Curlewis, Glen Innes, Aria Park, H.A. College, Castle Hill, Bellata, Dubbo, Stoney Creek, Boggabri, Wee Waa, Baan Baa, Carroll, Gravesend, West Wyalong, Appleby, Tamworth, Attunga, Grafton, Piallaway, Raleigh, Somerton, Baradine, Gilgandra, Coonabarabran, Tambar Springs, Mendooran, Manilla, Somerton, Spring Ridge, Armidale, Beckom, Gosford, Cudal, Warialda, Kelvin, Camden, Manildra, Goonumbia, Barmedman, Tichborne, Forbes, Temora, Leeton, Berrigan, Brocklesby, Illabo, The Rock, Junee, Young, Crowther, Noonbinna, Lyndhurst, Murrurundi, Orange, Lockhart, Kelso, Wagga, Pine Cliff, Wongarbon.

Qld.: Westbrook, Lawes, Hermitage, Wyreema, Biddleston, Bowenville, Brookstead, Dalby.

Vic.: Rutherglen.

1951.

r.126.

N.S.W.: Barmedman, Parkes, West Wyalong, Yanco, Tichborne.

r.126B.

N.S.W.: Tichborne, Dubbo, Mogrigny, Alectown, Canowindra, Yanco, Cowra, Grenfell, Quandialla, Bulgandry, Walbundrie, Temora, Nea Siding, Albury, Corowa, Daysdale, Savernake, Ringwood, Gilgandra, Deniliquin, Gunnedah.

S.A.: Port Lincoln, Pygony, Bordertown, Ardrossan, Mangalo.

Vic.: Werribee, Walpeup, Longeronong.

Fas.: Tewkesbury, Sassafras, Cressy.

r.222BB.

N.S.W.: Glen Innes, Tichborne, Curlewis, Kelso, Narrabri, Dubbo, Coradgery, Gilgandra, Mogrigny, Trewilga, Alectown, Wongarbon, North Star, Wellington, Currabubula, Gunnedah, Trangle, H.A. College, Narromine, Leeton, Mendooran, Cowra, Canowindra, Darby's Falls, Yanco, Piallaway, Wee Waa, Mamabri, Boggabri, Quandialla, Woodstock, Binnaway, Baan Baa, Tamworth, Urangeline, Bulgandry, Walbundrie, Armidale, Bribbaree, Manildra, Albury, Corowa, Daysdale, Savernake, Ringwood, Deniliquin.

Qld.: Hermitage, Dalby, Mt. Linster, Pirriuan, Yarrala, Allora, Mt. Tyson, Brookstead.

Vic.: Dookie, Walpeup, Longeronong.

Fas.: Sassafras.

r.222AB.

N.S.W.: Boorowa, Gilgandra, Barmedman, Glen Innes, Curlewis, Tichborne, Parkes, Boggabri, Tamworth, Coolamon, Yanco, Baradine, Piallaway, Gunnedah, H.A. College, Narrabri, Dubbo, Mogrigny, Trewilga, Tomingley, Alectown, Peak Hill, Garah, Wongarbon, Wellington, Trangle, Currabubula, Leeton, Cowra, Wee Waa, Loomberah, Barraba, Mamabri, Walbundrie, Talbragar.

Vic.: Werribee.

Qld.: Hermitage, Warwick, Dalby, Cecil Plains, Mt. Tyson.

A truer perspective of the overall Australian stem rust position is given by a study of the total determinations that have been made since the investigations were commenced. The spread in time and space is shown in Tables 8 and 9.

TABLE 8.

Summary of the Number of Isolations of Physiologic Races of *P. graminis tritici* Grouped According to Time of Collection.

Physiologic Race.	Season of Isolation Ending 31st March of the Year Stated.															
	1922.	1923.	1924.	1925.	1926.	1927.	1928.	1929.	1930.	1931.	1932.	1933.	1934.	1935.	1936.	1937.
11					4	18	152	156	90	181	139	143	93	3	5	2
34					15	14	21							220	189	304
43	20	10	10	55	3	30	6				10	1		4		
44	2	4		1	3	30	6									
45	3			15	5	17	5									
46	14		15	24	1	6	2									
54		1				3	1									
55	2			5		3	2									
59						1									1	
126																
126B																
222BB																
222AB																
14																
21																
33																
56																
222AA																
Totals ..	41	15	25	100	28	89	189	156	90	181	149	144	93	227	199	306

Physiologic Race.	Season of Isolation Ending 31st March of the Year Stated.												Totals.			
	1938.	1939.	1940.	1941.	1942.	1943.	1944.	1945.	1946.	1947.	1948.	1949.		1950.	1951.	
11	7	1	3		1											22
34	236															1925
43																160
44																46
45		1	4		1											55
46																62
54																5
55																10
59		1														2
126		165	267	93	159	104	114	31	54	88	184	48	65	19		1391
126B					2	27	22	36	155	163	184	68	127	49		833
222BB												3	292	122		417
222AB												2	220	66		288
14											1					1
21																1
33			3								1					3
56							1									1
222AA												1				1
Totals ..	243	171	274	93	163	131	137	67	209	251	370	122	704	256		5223

It is seen that during the whole period there have been three major changes in the races present, changes which have had far-reaching consequences to wheat growers.

First major change in races present.

The first occurred in 1926 when r.34 first appeared in Western Australia and quickly spread throughout the wheat-growing areas of Australia and New Zealand. Its rapid supersession by 1929 of the six races previously present was explainable firstly by its wide host range, and secondly by its capacity to produce crops of uredospores in a shorter time than the other races. This has already been discussed (Waterhouse, 1929).

In addition to r.34, it will be seen that five other races were found, but with a relatively low frequency. Studies of competition between associations of races have thrown much light on the failure of certain races to become established (Watson, 1942). Nevertheless, they can be of importance where barberries occur, serving as parents in crosses with other races.

TABLE 9.

Summary of the Number of Isolations of Physiologic Races of P. graminis tritici Grouped According to Their Source.

Physiologic Race.	Source of Material.								Totals.
	A.C.T.	N.S.W.	Vic.	Qld.	S.A.	W.A.	Tas.	N.Z.	
11	2	18	1					1	22
34	68	1387	120	88	105	49	32	76	1925
43		130	7	17	3	2	1		160
44		39		4	2		1		46
45	2	35	3	3	7		2	3	55
46		43	4	3	1		9	2	62
54		4			1				5
55		9		1					10
59		1		1					2
126	17	918	115	75	66	143	43	14	1391
126B	2	665	23	68	51	7	11	6	833
222BB		361	10	44			2		417
222AB		246	2	40					288
14		1							1
21		1							1
33				3					3
56		1							1
222AA		1							1
Totals ..	91	3860	285	347	236	201	101	102	5223

Second major change in races present.

The second major change occurred in 1941 when the variety "Eureka", a popular and fully resistant stem rust wheat bred by Dr. S. L. Macindoe, was found in the north-west of N.S.W. to be heavily attacked by stem rust. Investigation proved that the typical race 34 reactions were not seriously departed from, but that they conformed more closely to those set down for r.126—a race belonging to the r.34 group. At the same time, plant house studies showed that the original stock culture of r.34 now approximated closely to the behaviour of r.126. However, the two cultures could be separated clearly by using the variety "Eureka" or its parent "Kenya W743" as a differential: the old culture gave a resistant reaction whilst the new gave a susceptible one. This distinction is obscured at high temperatures, but it was clear that a new rust had turned up. It has stopped the growing of "Eureka" which has so many other valuable agronomic characters. Details of these happenings have already been given (Watson & Waterhouse, 1949) and the new rust has been styled r.126B.

It will be noted that r.34, which occupies such an important place in the tables setting out the results obtained prior to 1939, is not listed in the subsequent years. The actual differences between r.34 and r.126 are not great according to the register (Stakman, Levine and Loegering, 1944). Both belong to the same race group. The reactions on the durum varieties of the differential set are those which separate them, and it has been shown (Waterhouse, 1929) that temperature fluctuations may cause variations in their rust reactions which are even wider than those shown in the register for the two races on these varieties.

As stated above, the detailed work involved in the study of r.126B in 1941 brought to light the differences in our cultures. Exactly when the change occurred is not known, and for this reason, in the "new" series of results starting with 1939, r.126 and not r.34 is tabulated, although in part the latter may have been present and included in the r.126 numbers given.

The spread of r.126B took place rapidly owing to the well-deserved popularity and wide cultivation of "Eureka" which screened out the other races. Its dispersal as determined by rust collections submitted for examination is clearly shown in the preceding tables.

A collection of single stems taken at random in November, 1946 from crops of fully susceptible varieties by Dr. I. A. Watson to show the relative frequencies of the two biotypes gave the following results, in which the build-up of r.126B is clear:

TABLE 10.

Relative Frequency of Isolation of the Two Biotypes of Race 126 from Susceptible Varieties in Several Localities.

Locality.	Number of Isolations of Biotypes.		
	r.126.	r.126B.	Both.
Alfred Town	9	7	
Albury District	4	18	5
Brocklesby	1	13	2
Walbundrie	10	21	2
Bungowanah	3	10	
Kyeamba	4	3	
Killara	17	17	
Totals	48	89	9

Third major change in races present.

The third major change in the rust flora occurred in 1948. Following upon the establishment of r.126B, five new varieties were liberated in New South Wales, viz., "Celebration", "Charter", "Yalta", "Kendee", and "Gabo". All were resistant to r.126 and r.126B. Early field results indicated that "Yalta" was the least resistant, and on occasion showed a considerable amount of rust on its stems. In all these cases, however, plant-house tests showed that 126B was the rust present and that "Yalta" seedlings gave a resistant reaction: particularly favourable conditions had been responsible for the rust development. Nevertheless, commencing in October, 1947, the precaution was taken to include "Yalta" in the differentials used for testing unknown rusts sent for determination. It was found that rusted "Yalta" specimens continued to give 126B reactions until November, 1948, when heavily rusted "Yalta" sent by S. G. Burns from Lawes, Q., gave full "Yalta" susceptibility in the plant-house tests. It was clearly a new rust.

MORPHOLOGICAL STUDIES.

Comparisons of spore morphology sometimes reveal differences between physiologic races of rust, although there are many exceptions to this (Levine, 1923; Waterhouse, 1930).

To date no aecidiospores of the new rust have been available for measurement, but studies of uredospores and teleutospores have been made. Comparisons with other rusts are set out in Table 11.

TABLE 11.
Comparisons of Measurements of Spore Forms of Certain Australian Races of P. graminis tritici.

Race.	Length in μ .			Width in μ .		
	Mean.	Standard Deviation.	Range.	Mean.	Standard Deviation.	Range.
<i>Uredospores.</i>						
222	30.61	2.57	25-39	17.37	1.62	15-21
Average of 9 Aust. races	31.25	3.68	21-43	18.14	2.01	11-22
34	30.62	2.58	22-37	18.97	1.77	15-22
43	29.39	3.58	21-37	19.44	1.40	17-22
<i>Teleutospores.</i>						
222	44.03	5.08	29-62	13.88	2.06	9-19
Average of 3 Aust. races	44.32	7.40	29-75	15.90	2.27	11-22
34	47.89	8.64	30-74	16.78	2.20	13-22
43	43.64	6.07	34-63	14.53	2.79	11-21

In earlier work details were given of measurements of individual Australian races (Waterhouse, 1930). In the case of the uredospores, the average for nine races is here given, and for the teleutospores, three races. It will be seen that race 222 shows no significant departure from the averages for these spore forms. The uredospore measurements approximate most closely to those of r.34, and those of the teleutospores to those of r.43.

Race Determinations.

Race determinations showed that the new rust bears many similarities to race 126. At the usual temperatures for testing, the reactions on "Kubanka" and "Acme" are consistently lower than those given by rs. 126 and 126B, although at high temperatures these differences, and especially those on "Kubanka", are not so clear. On the other hand, reactions on "Arnautka", "Mindum", and "Spelmar", are higher than those of 126 and 126B. Dr. E. C. Stakman has recently given it the designation of race 222.

Using commercial varieties, tests at a temperature of about 70°F. showed that "Kendee" and "Charter" gave susceptible reactions, whilst "Celebration" and "Gabo" gave resistant reactions: the susceptibility of the last-named increased notably with high temperatures. On "Eureka" the rust is split into two entities at the usual temperatures, one biotype giving susceptible, whilst the other gives resistant reactions: these differences disappear at high temperatures. This behaviour parallels that shown by rs. 126 and 126B, and in the same way makes difficult the separation of the two components on "Eureka". For this reason some isolates giving a susceptible reaction and therefore those classified as 222BB in the survey may really have belonged to 222AB.

The increased frequency of isolates of 222BB and 222AB is mainly due to the widespread cultivation of the five new "resistant" varieties which thus served to screen out 126 and 126B. The latter, however, persist in crops of susceptible varieties like

"Bencubbin", from which these two rusts can commonly be isolated. This is also the case with *Hordeum leporinum* and *Agropyron scabrum*.

The new complex spread rapidly. In April, 1949, isolations were made from the north-west of New South Wales, a month later from Glen Innes, and in the following month from the Central West. As summer approached, its frequency increased throughout Queensland and New South Wales, and in December, 1949, it was found at Rutherglen, Vic. This was followed by isolations from Moriarty, Tas., in February, 1950. To date it has not been found in South Australia or Western Australia, but in the other States it is now well established.

Reports on the field behaviour of the "resistant" varieties during the recent two seasons when rust damage was severe, supplemented by examination of material submitted from the field, show that "Celebration" is highly resistant, although when grown under very favourable conditions, some rust develops on it. "Gabo" shows a higher rust development, and this increases progressively on "Charter", "Kendee", and "Yalta". The last-named is so susceptible that it is no longer recommended for cultivation.

Examination of varieties on hand showed that a number were resistant, and others have since become available. The gene relationships are being studied by Drs. I. A. Watson and E. P. Baker, and already it is clear that a number of useful resistances are available. Back-cross programmes designed to incorporate these in agronomic sorts are now being carried forward.

In addition to strains of *Agropyron* spp. and a number of inbred ryes which show remarkable self-fertility after 20 years of inbreeding, as well as resistance to all the known Australian races, resistant varieties of wheat include the following:

(a) 14-chromosome wheats: Abyssinian, Africano, Akrona, Alberta Red, Beladi (8 strains), Egypt (4 strains), Greece 11, Iumillo, Morocco 34, Nodak, Palestine (2 strains), Pinet, Poona (3 strains), Portugal (7 strains), Russian (3 strains).

(b) 21-chromosome wheats: Bokveld, Egypt, Fedweb, Frondosa, Frontana, Fronteira, Hochzucht, Hofed, Hope, numerous Hope derivatives, Kenya 117A, Kenya 744, La Estanzuela, Malakof, Marquillo, Newthatch, Rhodesian (2 strains), Thatcher, (Triticum \times Agropyron), Sabanero, (Steinwedel \times Khapli), Supreza, Webster.

In addition to this new and very important race complex, it is seen that five other races were found between 1941 and the present time. Just as was the case before that year, no one of the five that turned up became established. This second batch of five occurred with a very low frequency: each of these races was present only once in about 2,300 isolates examined. Presumably they also were unable to compete successfully with the established races.

Mixtures of Races.

Reference has already been made (p. 221) to the side-by-side occurrences of r.126 and r.126B. Much wider mixing occurs, although often a field collection will yield only the one race: the screening action of varieties having differential resistance is all-important in this regard. Where there is complete susceptibility the side-by-side occurrence of different races may be of considerable importance if hyphal anastomoses occur and nuclear migrations do produce new combinations of nuclei.

The race mixtures encountered in the work are set out in Table 12.

ORIGIN OF PHYSIOLOGIC RACES.

Since the investigations commenced, it is seen that 18 races or important biotypes have been determined. Of them, only half have been important in the crops: races 11, 14, 21, 33, 54, 55, 56, 59 and 222AA have been rather of the nature of curiosities, in so far as rust damage is concerned. Nevertheless their occurrence is important as showing that various changes in the fungus take place from time to time. Probably it is a continuing process of mutation. Aecidial formation, with its probability of hybridization, does not enter, and efforts have failed to demonstrate the production of new types of rust from anastomoses of the dicaryotic mycelium and nuclear interchange. In these experiments, dissimilar races (e.g., r.43 and r.34) have been cultured together on fully

susceptible "Federation" wheat for 20 transfer generations: determinations on the differential hosts from time to time yielded only the original races that had been used. It is possible that new combinations of nuclei had occurred, but that these were not discernible in the normal race determinations that were made with the standard differential set. Again, it may be found that particular associations of races show affinities which lead to nuclear interchange. For example, r.11 and r.56 have been found as segregates from barberries inoculated with r.34, and there may be a greater affinity between these races than, say, between rs. 34 and 43.

No evidence of adaptation by the fungus to erstwhile resistant varieties has been obtained. This does not rule out the possibility that a race can adapt itself to the environment imposed by its growth on a partially resistant variety.

TABLE 12.

Frequency of Occurrence of Mixtures of Races of P. graminis tritici on Wheat Collections Examined.

Year of Collection.	Frequency of the Race Mixtures Found.											
	r.33 and 126.	r.59 and 126.	r.11 and 126.	r.45 and 126.	r.126 and 126B.	r.14 and 126B.	222BB and 126B.	222AB and 126B.	222BB and 222AB.	222BB, 222AB and 126B.	222BB, 222AB and 126.	222AB and 126.
1939 ..	4	1	2	1								
1940 ..			3	3								
1942 ..			2	1								
1945 ..					9							
1946 ..					8							
1947 ..					23							
1948 ..					36	1						
1949 ..					39		1	1				
1950 ..					43		12	1	175	11	1	1
1951 ..					4		17		22	5		1
Totals	4	1	7	5	162	1	30	2	197	16	1	2

It has been suggested that the various races and biotypes have been present in Australia all the time, and that only recent detailed work has brought to light their presence. Even so, this simply pushes further back the explanation of how the entities originated. But it is not easy to accept the suggestion that "Eureka", widely grown in the north-west and other areas over the years with complete resistance, should have required such a lapse of time to show the presence of 126B, if indeed this rust was actually present all the time on fully susceptible varieties. Actually "Eureka" had been previously grown—and found resistant—in the particular area where this biotype first occurred. The same applies to "Gabo", as a further example, in respect to both its stem and leaf rust resistance.

There is positive evidence of rust mutation. In the course of the investigations there have been seven occasions on which leaves of seedlings in the plant house have been noted producing a light-coloured uredo pustule amongst the normal-coloured pustules in that particular pot of seedlings. These light pustules have been "Cadmium yellow", Plate iii, or "Light Cadmium", Plate iv, of Ridgway's colour standards. In six of the cases, the race determinations showed that the light-pustuled culture was the same as the parent culture, but in the remaining seventh instance, the light-pustuled culture proved to be race 56. It arose from the stock culture of r.34, and it is not without significance that when teleutospores of r.34 have been used to infect the barberry, it has proved to be heterozygous, and one of the derived races is r.56.

Had it not been for the association of the colour difference with the changed physiology, the presence of r.56 would not have been detected in the culturing on the susceptible variety "Federation" which is used as the host for the rust cultures. The detection of a mutation may be quite fortuitous. If it has the capacity to attack a variety previously resistant or if it gives a resistant reaction on a variety that has been susceptible in previous tests, its presence will be observed. Otherwise it will be carried forward undetected on fully susceptible varieties. It is probable that many mutations, some of large, others of small magnitude, are occurring all the time. It is not easy to work out a method whereby they can be detected with certainty. In the plant-house work the opportunities of determining mutations are few because the quantity of material that can be handled is very limited. In the field, such enormous numbers of spores are produced that the chances of mutation occurring are vastly greater.

To state that the new rust races and biotypes have arisen by mutation is not to explain what happens. Apart from knowing *what* happens, we want to know *why* and *how* the changes take place. It is not known why changes in temperature can alter resistance to susceptibility, or why a variety may be resistant to one race but susceptible to another. The nature of resistance is unknown. It would seem that biochemical work of the highest order is needed, and in this regard, the stimulating work of Humphrey and Dufrenoy (1944) is of outstanding value and should be followed up.

With an understanding of what constitutes resistance, and with a fuller knowledge of the gene relationships in different wheats, the study of physiologic specialization will be placed on a different footing. What constitutes a "physiologic race" and what a "biotype" may well be clarified.

At present, our methods of study reveal all manner of variants in a rust. Using an empirically selected group of differential varieties, entities are sorted out that are termed "physiologic races" on the basis of the series of reactions shown by the particular rust under study. Standardization of the environmental conditions under which the tests are made is all important. Even so, similarity of reactions shown by two isolates does not mean that they are identical. Work with cultures of r.34, one from U.S.A. and one from Australia, has shown clearly that profound differences between them come to light when additional differential varieties are brought into use and when side-by-side comparisons are made under a range of environmental conditions (Waterhouse & Watson, 1941). The use of the present-day set of differentials gives a "rough" sort-up of the rust entities into physiologic races, and to this extent makes possible a comparison of results on a world basis. However, a much more accurate basis will be given when the selection of the differential series is based on a knowledge of the genes for resistance. At the present time it may be far more important for the breeder aiming at developing rust-resistant varieties to use in his country a set of differential varieties that are not recognized as being useful in another country. This has been brought out clearly in our work here.

Of course this raises a considerable difficulty in regard to classification and nomenclature of the rust entities. It is usual to style those which are determined on the accepted set of differential hosts as "physiologic races". Those which are sorted out from races by using additional differentials or which consistently give a minor variation from the reaction on a race differential which is recognized as characteristic for the race, are called "biotypes" of that particular race. Thus we have herein referred to "r.126B": whereas "Eureka", an extra-differential variety, gives a resistant reaction with r.126, it gives a susceptible reaction with r.126B. It might be more satisfactory to call them r.126A and r.126B.

This distinction between a "physiologic race" and a "biotype" is an arbitrary one, and leaves the present system of designating the rust entities in an unsatisfactory position. If, for example, a series of race determinations leads to a particular rust conforming to the reactions for, say, r.34, and the use of an additional variety separates out an isolate of r.34 which gives a susceptible, instead of the expected resistant reaction, it is designated r.34B. Now, suppose that yet another variety outside the differential series splits these biotypes further on the basis of the susceptible and resistant

reactions now shown. These could be designated r.34BA and r.34BB, or as r.34C and r.34D. There is nothing to show which variety is used for the first separation and which for the second. Still further separations may be made involving the use of further letters to designate the biotypes. Confusion is likely unless some clear understanding is reached. Furthermore, a worker in another country using extra-differential varieties may give certain designations to his entities, quite unaware that these have already been used by another investigator. The need for a central institution to control and standardize the results of specialization studies has long been emphasized, and is more than ever evident. Problems caused by possible genetic differences between workers' stocks of the differentials used, as well as those due to environmental effects, would also be eliminated. Accurately determined cultures could be made available for comparative studies in any area where they are required.

LEAF RUST OF WHEAT.

LIFE HISTORY.

In dealing with other cereal rusts it has been emphasized that susceptible grass hosts may play a very important part in carrying over the rust from season to season. To date no common grass host of *P. triticina* has been found, and no infections of *Thalictrum* spp. have been observed, apart from those produced in controlled studies in the plant house. Thus in October 1943, *T. flavum* was inoculated with teleutospores of r.95 from straw which had been exposed to winter conditions at Armidale, N.S.W., and using the aecidial culture, r.95 was recovered from inoculations of "Federation" wheat. Earlier work (Waterhouse, 1932) had shown the derivation of races 96 and 97 from aecidial cultures produced on *Thalictrum* sp. in the plant house.

SPECIALIZATION.

In earlier publications (Waterhouse, 1929, 1932, 1933, 1936, 1938, 1939) the position has been set out in regard to *P. triticina* in Australia, and attention called to the presence of two races which were then styled races 16 and 26. In the Revised Register (Johnston and Rodenhiser, 1951) they are now given the designations 26 and 95.

More recently the leaf rust survey has been carried forward with results in time and space as set out in Tables 13 and 14.

TABLE 13.

Summary of the Number of Isolations of Physiologic Races of *P. triticina* Grouped According to Time of Collection.

Race.	Season of Collection, Ending 31st March of Year Named.														Totals.
	1939.	1940.	1941.	1942.	1943.	1944.	1945.	1946.	1947.	1948.	1949.	1950.	1951.		
95	101	122	42	93	49	38	29	101	78	207	120	37	29	1046	
26	21	38	13	13	8	6	4	9		18	19	16	7	172	
{ 135 and/or 138								6	3	31	93	10		143	
135AB										63	13	105	63	244	
138AB										62	14	149	51	276	
135BB												14		14	
138BB												7	6	13	
53A				3								4		7	
34A				2										2	
98AA										3				3	
Totals	122	160	55	111	57	44	33	116	81	384	259	342	156	1920	

TABLE 14.

Summary of the Number of Isolations of Physiologic Races of P. triticina Grouped According to their Source.

Race.	Source of Material.								Totals.
	A.C.T.	N.S.W.	Vic.	Qld.	S.A.	W.A.	Tas.	N.Z.	
95	2	824	35	102	27	23	8	25	1046
26	1	121	9	20	4		1	16	172
135 and/or 138		119		22	2				143
135AB		171		61	11	1			244
138AB		215	2	52	4	3			276
135BB		8		6					14
138BB		8		5					13
53A								7	7
34A								2	2
98AA								3	3
Totals	3	1466	46	268	48	27	9	53	1920

The sources of the material used are as follows:

DETAILS OF THE OCCURRENCES OF THE RACES OF *P. TRITICINA*.

1939.

r.95.

N.S.W.: H.A. College, Gunnedah, Lindfield, Tottenham, South Gate, Scone, Buriquip, Albert, Tullamore, Alectown, Parkes, Peak Hill; Curlewis, Jumble Springs, Wee Waa, Pilliga, North Parramatta, Dubbo, Myall Creek, Bundella, Premer, Grafton, Nubrex, Narrabri, North Star, Cherry Tree Hill, Binnoway, Coonabarabran, Condobolin, Cowra, Trangie, Chatswood, Taree, Narromine, Oberly, Yeoval, Gilgandra, Trundle, Glen Innes, Goonumbra.

Qld.: Brookstead, Gatton, Roma, Oakey, Toowoomba.

S.A.: Yeelana.

Tas.: North West Coast.

r.26.

N.S.W.: Parkes, Gunnedah, H.A. College, Condobolin, Yeoval, Bathurst, Tichborne, Lindfield, Trangie, Temora.

Qld.: Brookstead, Toowoomba.

S.A.: Pinkawillinie.

1940

r.95.

N.S.W.: Lindfield, Condobolin, Parkes, Tullamore, Cobar, Gunnedah, Narrabri, H.A. College, Coolamon, Chatswood, Narrandera, Hay, Griffith, Junee, Mildura, Renmark, West Wyalong, Trangie, Forbes, Haberfield, Dernasser, Yallabie, Temora, Wyalong, Stockinbingal, Pallamallawa, Black Creek, Wirriya, Inverell, Bingara, Sydney University, Singleton, Birriwa, Cobbarah, Tuchlan, Quirindi, Dunedoo, Wee Waa, Manly, The Rock, Henty, Osborne Creek, Gilgandra, Wellington, Dubbo, Yeoval, Narromine, Wyanga, Coboco, Wongarbron, Eumungerie, Cowra, Bathurst, Yanco, Mangoplah, Downside, Coreinbob, Mascot, Collingullie.

Qld.: Gatton, Pittsworth, Oaken, Cecil Plains.

S.A.: Waite, Waikeri, Roseworthy, Windsor, Port Wakefield, Blanchetown, Smithfield, Booleroo.

Vic.: Werribee, Walpeup, Swan Hill, Donald, Invergordon, Charlton, Salisbury.

W.A.: Salmon Gums.

A.C.T.: Canberra.

r.26.

N.S.W.: Tullamore, Lindfield, Manildra, Yallabie, Forbes, Singleton, H.A. College, Gilgandra, Narromine, Cowra, Coboco, Bathurst, Dubbo, Mangoplah, Coreinbob, Gunnedah, Mascot.

Qld.: Gatton.

Vic.: Werribee, Swan Hill, Donald, Invergordon, Charlton, Salisbury.

S.A.: Waite.

1941.
r.95.
N.S.W.: Bathurst, Lindfield, H.A. College, Garthoven, Cowra, Tamworth, Glen Innes, Inverell,
Attunga, Quirindi, Milvale, Carroll, Tichborne.
Qld.: Kincora.
S.A.: Waite.
Vic.: Dookie, Salisbury, Longeronong, Werribee.
A.C.T.: Canberra.
N.Z.: Auckland.
- r.26.
N.S.W.: Sydney University, H.A. College, Lindfield, Glen Innes, Inverell, Carroll.
Qld.: Kincora.
Vic.: Longeronong.
A.C.T.: Canberra.
N.Z.: Auckland.
1942.
r.95.
N.S.W.: Duri, Gunnedah, Kelso, Tichborne, Spring Ridge, H.A. College, Curlewis, Cowra,
Gilgandra, Wongarbon, Narromine, Griffith, Manly, Campbelltown, Dunedoo, Bunaloo,
Tambar Springs, Purlawaugh, Forbes, Yelindenie, Bathurst, Parkville, Tamworth, Mollyan,
Tooraweenah, Lindfield, Urangeline.
W.A.: Merredin, Chapman.
S.A.: Waite.
Vic.: Walpeup, Rochester, Rutherglen, Dookie, Donald, Charlton.
N.Z.: Lincoln.
- r.34A.
N.Z.: Lincoln.
- r.53A.
N.Z.: Christchurch, Lincoln.
- r.26.
N.S.W.: Gunnedah, H.A. College, Lindfield, Manly.
Vic.: Dookie.
Tas.: Wilmot.
1943.
r.95.
N.S.W.: H.A. College, Narrabri, Curlewis, Gunnedah, Tichborne, Coonabarabran, Somerton,
Tambar Springs, Purlawaugh, Baradine, Bugaldie, Boggabri, Kelvin, Cowra, Spring Hill,
Arthurville, Maryvale, Parkes, Lane Cove, Lindfield, Delungra, Bannockburn, Inverell,
Manly.
Qld.: Gatton, Willawa, Winton.
Vic.: Fern Tree Gully, Walpeup, Werribee, Rutherglen.
- r.26.
N.S.W.: H.A. College, Gunnedah, Inverell.
Qld.: Gatton.
1944.
r.95.
N.S.W.: Gunnedah, H.A. College, Tichborne, Milguy, Boggabri, Curlewis, Manly, Lindfield.
Qld.: Brookstead, Nankin.
W.A.: Merredin, Northampton, Quellington, Wongan Hills.
Tas.: Deloraine.
- r.26.
N.S.W.: H.A. College.
Qld.: Brookstead.
1945.
r.95.
N.S.W.: Badgery's Creek, Mulgoa, Tichborne, H.A. College, Wallacia, Gunnedah, Coolatai,
Curlewis, West Maitland, Grafton, Scone, Gosford.
Qld.: Gatton.
- r.26.
N.S.W.: Mulgoa, H.A. College, Gunnedah.
1946.
r.95.
N.S.W.: H.A. College, Nea Siding, Parkville, Wingen, Inverell, Gunnedah, Curlewis, Garah,
Lenmeal, Parkes, Dubbo, Bingara, Singleton, Scone, Muswellbrook, Gravesend, Emerald Hill,
North Star, Wallangra, Warialda, Pallamallawa, Myall Creek, Bukuila, Cherry Tree Hill,
Bellata, Edgeroi, Boggabri, Cowra, Premer, Tamworth, Moss Vale, Tichborne, Nelungaloo,
Wee Waa, Alectown, Lindfield, Berrigal Creek, Coonabarabran, Narrabri, Castle Mountain,
Young, Koorawatha, Temora, Milvale, Purlawaugh, Elong Elong, Waroo, Culcairn, Holbrook,
Glen Innes.

Qld.: Dalby, Pittsworth, Brookstead.

W.A.: Merredin.

S.A.: Waite.

N.Z.: Lincoln.

r.26.

N.S.W.: Nea Siding, H.A. College.

N.Z.: Lincoln.

r.135 and/or 138.

N.S.W.: Wee Waa, Killara.

Qld.: Brookstead.

1947.

r.95.

N.S.W.: Tichborne, H.A. College, Mildura, Tomingley, Tamworth, Glenfield, Windsor, Penrith, Leeton, Bathurst, King's Plains, Mandurama, Gundagai, Gosford, Bungowanah, Gerogery, Killara, Lindfield, Hurstville, Richmond.

S.A.: Waite, Baroota, Pinnaroo.

Vic.: Walpeup, Lake Cullullmana.

Qld.: Lawes.

N.Z.: Springfield.

r.135 and/or 138.

N.S.W.: H.A. College.

Qld.: Lawes.

1948.

r.95.

N.S.W.: Glen Innes, Killara, Turrumurra, Bathurst, H.A. College, Tichborne, Parkville, Aberdeen, Coonabarabran, Inverell, Bellata, Birriwa, Narrabri, Cowra, Rankin's Springs, Griffith, Tamworth, Crooble, Grafton, Westdale, Winton, Bective, Watermark, Breeza, Pialloway, Wagga, Mt. Euroa, Wellington, Wongarbon, Curlewis, Eumungerie, Toora-weenah, Boggabri, Trangie, Condobolin, Orange, Gilgandra, Gosford, Walmer, Fingerpost, Temora, Scone, Dubbo, Suntop, Mudgee, Binnalong, Calimpa Siding, Forbes, Wallen Bullen, Peak Hill, Dandaloo, Lindfield, St. Elmo, Gerogery, Barraba, Quirindi, Currabubula, Blackheath, Armidale, Castle Hill, Gunnedah, Tambar Springs, Narrandera.

Qld.: Biloela, Mt. Tyson, Euanslea, Condamine Plains, Warwick, Lawes, Dalby, Brookstead, Hermitage.

S.A.: Waite, Roseworthy, Mt. Gambier, Penola.

W.A.: Northampton.

Tas.: Cressy, Campbelltown, Sassafras, Cambridge, Hobart, Latrobe.

N.Z.: Methven.

r.26.

N.S.W.: H.A. College, Curlewis, Trangie, North Star, Boggabri, Orange, Dandaloo, Tichborne.

Qld.: Brookstead, Oakens, Goombungee, Warwick, Dalby, Biloela.

S.A.: Waite.

r.98AA.

N.Z.: Lincoln, Canterbury.

r.135 and/or 138.

N.S.W.: Tichborne, Mt. Euroa, Wellington, Wongarbon, Eumungerie, Coonabarabran, Toora-weenah, Curlewis, Boggabri, Suntop, Binnalong, Forbes, Calimpa Siding, Peak Hill, Lindfield, Dubbo, Gerogery, Barraba, Tamworth, Quirindi, Blackheath, Currabubula.

Qld.: Brookstead, Hermitage.

S.A.: Waite.

r.135AB.

N.S.W.: Killara, H.A. College, Parkville, Tichborne, Gunnedah, Rankin's Springs, Winton, Narrabri, Bective, Curlewis, Pallamallawa, North Star, Moree, Boggabri, Glen Innes, Tamworth, Grafton, Condobolin, Orange, Gilgandra, Gosford, Walmer, Temora, Scone.

Qld.: Brookstead, Oakens, Goombungee, Biloela, Mt. Tyson, Euanslea, Condamine Plains, Warwick, Dalby, Lawes.

S.A.: Roseworthy.

W.A.: Northampton.

r.138AB.

N.S.W.: Killara, H.A. College, Inverell, Tichborne, Crooble, Winton, Narrabri, Bective, Moree, Rankin's Springs, Pallamallawa, Curlewis, North Star, Boggabri, Glen Innes, Tamworth, Grafton, Orange, Condobolin, Gosford, Walmer, Temora, Scone.

Qld.: Brookstead, Biloela, Goombungee, Mt. Tyson, Lawes, Euanslea, Condamine Plains, Warwick, Dalby.

S.A.: Roseworthy.

W.A.: Northampton.

1949.

r.95.

N.S.W.: Tichborne, Dubbo, Coonabarabran, Boggabri, Gunnedah, Curlewis, Castle Hill, Yanco, Westdale, Winton, Parkes, H.A. College, Gerogery, Goonimbla, Gregra, Nelungaloo, Brolgan, Tamworth, Mullally, Gilgandra, Narrabri, Trangie, Birriwa, Dunedoo, Lyndhurst, King's Plains, Grenfell, Bribbaree, Temora, Colimroobie, Ariah Park, Leeton, Wagga, Gundagai, Yass, Narrandera, Gammain, Coolamon, Yanco, Book Book, Trundle, Loomberah, Blackheath, Guyra, Tanja, Bellata, North Star, Bugaldie, Cowra.

Qld.: Toowoomba, Westbrook, Lawes, Jondaryan, Dalby, Mt. Tyson, Willowburn, Brookstead, Warwick, Hermitage, Wyreema.

N.Z.: Lincoln, Hororata, Greendale.

r.26.

N.S.W.: Curlewis, Castle Hill, Pallamallawa, Gulgong, Lindfield, Blayney, Cowra, Grenfell, Gundagai, Coolamon.

Qld.: Hermitage, Lawes.

N.Z.: Lincoln, Hororata, Greendale.

r.135 and/or 138.

N.S.W.: Dubbo, Boggabri, Gunnedah, Curlewis, Castle Hill, Westdale, H.A. College, Gerogery, Goonimbla, Gregra, Nelungaloo, Brolgan, Tamworth, Gilgandra, Coonabarabran, Mullally, Narrabri, Bellata, Boggabri, North Star, Pallamallawa, Gulgong, Bugaldie, Trangie, Lindfield, Dunedoo, Birriwa, Lyndhurst, Cowra, King's Plain, Blayney, Grenfell, Bribbaree, Marangarell, Temora, Colimroobie, Ariah Park, Leeton, Wagga, Yass, Narrandera, Yanco, Gammain, Book Book, Trundle, Loomberah.

Qld.: Toowoomba, Jondaryan, Dalby, Mt. Tyson, Lawes, Willowburn, Brookstead, Warwick, Hermitage.

r.135AB.

N.S.W.: Curlewis, Grafton, H.A. College, Narrabri, Boggabri, North Star.

Qld.: Lawes, Mt. Tyson, Brookstead, Hermitage.

r.138AB.

N.S.W.: Curlewis, Grafton, H.A. College, Narrabri.

Qld.: Lawes, Brookstead, Hermitage.

1950.

r.95.

N.S.W.: Gunnedah, Blackheath, Curlewis, H.A. College, Tichborne, Leeton, Coolamon, Brocklesby, Illabo, Wagga, Junee, Noonbinna, Lyndhurst, Blayney, Bathurst, Spring Terrace.

Qld.: Allora, Hermitage, Lawes, Wyreema.

N.Z.: Lyalldale, Orari, Laghmor, Winchmore.

r.26.

N.S.W.: H.A. College, North Marota, Temora, Deniliquin, Illabo, Junee.

Qld.: Hermitage.

N.Z.: Lyalldale, Orari, Laghmor, Winchmore.

r.53A.

N.Z.: Lyalldale, Orari, Winchmore.

r.135 and/or 138.

N.S.W.: Gunnedah, Curlewis, H.A. College, North Marota.

Qld.: Allora, Hermitage, Lawes, Wyreema.

r.135AB.

N.S.W.: Curlewis, Birriwa, Castle Hill, Grafton, Gunnedah, Bellata, Scone, Narrabri, Stoney Creek, Wee Waa, Boggabri, H.A. College, West Wyalong, Gilgandra, Somerton, Baradine, Lindfield, Coonabarabran, Tambar Springs, Merdooran, Breealong, Leadville, Tintinhull, Attunga, Manilla, Spring Ridge, Armidale, Binnaway, Gosford, Inverell, Warialda, Berrigan, Bathurst, Temora, Henty, Glen Innes, Pine Cliff, Dunedoo.

Qld.: Lawes, Wyreema, Hermitage, Cambooya, Westbrook, Mt. Tyson, Wandoan, Bowenville.

S.A.: Waite.

r.138AB.

N.S.W.: Curlewis, Gunnedah, Ariah Park, Birriwa, Grafton, Narrabri, Castle Hill, Bellata, Scone, Stoney Creek, Boggabri, Wee Waa, West Wyalong, Culgoora, Gilgandra, Piallaway, Raleigh, Manilla, Somerton, Baradine, Lindfield, Coonabarabran, Tambar Springs, Merdooran, Breealong, Leadville, Tintinhull, Attunga, Armidale, Binnaway, Cudal, Gosford, Inverell, Warialda, Berrigan, Dunkeld, Cheeseman's Creek, Manildra, Tichborne, Reefton, Temora, Leeton, Deniliquin, Coolamon, Merton, Corowa, Balldale, Noonbinna, Lyndhurst, Blayney, Bathurst, Daysdale, Sandy Creek, Willow Tree, Spring Terrace, Glen Innes, Dunedoo.

Qld.: Lawes, Dalby, Hermitage, Cambooya, Westbrook, Mt. Tyson, Wandoan, Bowenville, Toowoomba, Nabby.

S.A.: Waite.

r.135BB.

N.S.W.: Attunga, Manilla, Curlewis, Glen Innes, Narrabri, Castle Hill.

Qld.: Westbrook, Hermitage, Lawes, Nabby, Toowoomba.

r.138BB.

N.S.W.: Pine Cliff, Dunedoo, Glen Innes, Curlewis.

Qld.: Hermitage, Lawes.

1951.

r.95.

N.S.W.: Boorowa, Gilgandra, Glen Innes, Tichborne, Wagga, Parkes, H.A. College, Talbragar, Peak Hill, Mogrigny, Alectown, Tomingley, Trewilga, Lindfield, Orange, Castle Hill.

Qld.: Hermitage, Warwick.

S.A.: Port Lincoln.

Vic.: Werribee, Longeronong.

N.Z.: Massey.

r.26.

N.S.W.: Glen Innes, Tichborne, H.A. College.

N.Z.: Massey.

r.135AB.

N.S.W.: Boorowa, Gilgandra, Curlewis, Narrabri, Trangie, Castle Hill, West Wyalong, Gunnedah, Blue Vale, Cowra, Tichborne, Goonumba, Coonabarabran, Parkes, H.A. College, Manildra, Dubbo, Maitland, Temora, Boggabri, Tamworth, Grafton.

Qld.: Hermitage, Warwick, Toowoomba, Gympie, Dalby, Ayr.

S.A.: Waite, Port Lincoln.

r.138AB.

N.S.W.: Gilgandra, Gunnedah, Curlewis, Narrabri, Trangie, Tamworth, Coolamon, Boggabri, Wagga, Ardlithan, Blue Vale, Orange, Parkes, Tichborne, Manildra, Talbragar, Mogrigny, Peak Hill, Dubbo, Alectown, Tomingley, Trewilga, Temora, Grafton.

Qld.: Hermitage, Toowoomba, Dalby, Warwick.

S.A.: Waite, Port Lincoln.

W.A.: Merredin.

Vic.: Longeronong.

r.138BB.

N.S.W.: Gunnedah, Gilgandra.

Qld.: Hermitage, Toowoomba, Dalby.

The complete results since the specialization work started are shown in Tables 15 and 16, and are valuable as giving the overall picture of the position.

The recent work shows that races 26 and 95 were again present—and to the extent of 63% of the isolates—in all the areas except Western Australia, where *r.26* did not occur. Actually its absence has had an appreciable effect upon the plant-breeding programme in that State, where, up to the present, varieties susceptible to this race but resistant to others have given satisfactory resistance to leaf rust. This position must be regarded as precarious, and would, of course, be altered by the appearance in that area of a race like *r.26*.

The New Zealand position is also different from that in Australia. Races 26 and 95 occur there—and with the greatest frequency—but in addition, three other races which have not been recorded for Australia have been found there. *Thalictrum* infections have not been observed, so the origin of these variants remains obscure. No work has been undertaken to find varieties resistant to them that could be used in a breeding programme. Again, in New Zealand, there has so far been no occurrence of races 135 and 138 which now are so important in Australia. This is borne out by the fact that "Gabo" is still valuable for leaf-rust resistance in the Dominion. It is going to be particularly interesting to see whether these races turn up in New Zealand.

In the time distribution it will be seen that until 1946, only races 26 and 95 were recorded in Australia. When the variety "Gabo" was released for cultivation it was completely resistant to leaf rust (races 26 and 95) as well as to stem rust.

In October 1945, Mr. J. A. O'Reilly, of Gunnedah, forwarded from Wee Waa, N.S.W., "Gabo" plants heavily infected with leaf rust. Tests showed that it was a new rust capable of attacking "Gabo". Next month it was present in rusted material from Brookstead, Qld., and was also collected by Dr. I. A. Watson from his experimental plot in Killara, N.S.W. In no one of these localities are *Thalictrum* plants known to be present. To postulate mutation as a cause of the change in the rust flora does not really explain this happening. What really is mutation?

The rust spread rapidly, its wide host range accelerating dissemination. In determining its presence, tests with "Gaza"—the resistant durum parent used in the breeding

TABLE 15.

Summary of the Number of Isolations of the Physiologic Races of *P. triticina* Grouped According to Time of Collection.

Physiologic Races.	Season of Isolation, Ending 31st March of the Year Stated.												
	1927.	1928.	1929.	1930.	1931.	1932.	1933.	1934.	1935.	1936.	1937.	1938.	1939.
95	3	52	60	20	35	63	58	54	107	87	75	48	101
26	3	70	71	20	34	50	56	45	80	63	54	25	21
135 and/or 138													
135AB													
138AB													
135BB													
138BB													
53A													
34A													
98AA													
Totals	6	122	131	40	69	113	114	99	187	150	129	73	122

Physiologic Races.	Season of Isolation, Ending 31st March of the Year Stated.												Totals.
	1940.	1941.	1942.	1943.	1944.	1945.	1946.	1947.	1948.	1949.	1950.	1951.	
95	122	42	93	49	38	29	101	78	207	120	37	29	1708
26	38	13	13	8	6	4	9		13	19	16	7	743
135 and/or 138							6	3	31	93	10		143
135AB									63	13	105	63	244
138AB									62	14	149	51	276
135BB											14		14
138BB											7	6	13
53A			3								4		7
34A			2										2
98AA									3				3
Totals	160	55	111	57	44	33	116	81	384	259	342	156	3153

TABLE 16.

Summary of the Number of Isolations of the Physiologic Races of *P. triticina* Grouped According to their Source.

Physiologic Race.	Source of Material.								Totals.
	A.C.T.	N.S.W.	Vic.	Qld.	S.A.	W.A.	Tas.	N.Z.	
95	24	1337	68	127	64	32	10	46	1708
26	12	582	34	35	42	5	2	31	743
135 and/or 138		119		22	2				143
135AB		171		61	11	1			244
138AB		215	2	52	4	3			276
135BB		8		6					14
138BB		8		5					13
53A								7	7
34A								2	2
98AA								3	3
Totals	36	2440	104	308	123	41	12	89	3153

of "Gabo"—were found to give clearer reactions, and this variety has therefore been used throughout in the plant-house tests.

Recent overseas results are not without interest. In studies at Minnesota, U.S.A., Levine, Aumemus and Stakman (1951) found that "Gabo" was resistant to 21 races of leaf rust that were used in the work. "Gaza" was susceptible to four of the races to which "Gabo" was resistant, and it seems likely that the resistance to the four races is derived from Bobin W39 which is the other parent of "Gabo". These four races, viz., 28, 31, 35 and 52, have not been recorded in Australia so that it is not possible to check on this point.

Investigations of leaf rust present in Uruguay and the Upper Mid-West areas of U.S.A. (Boasso and Levine, 1951) showed that "Gabo" was resistant to the 15 races used in the tests.

Canadian workers (Aitken, Fisher and Anderson, 1951) have recorded "Gabo" as being leaf rust resistant as well as producing high quality grain under their conditions.

At the outset, susceptibility of "Gaza" was taken as sufficient evidence of the presence of the new race. The other variety then involved was "Thew", which is used to differentiate races 26 and 95. It was resistant to the "Gaza"-attacking rust. At a later stage, determinations on the recognized set of leaf rust differentials were made. The occurrence of "4" and "1" reactions on "Webster" was noted, and separations proved that two races were present. The two could be sorted readily at low temperatures, but at higher temperatures the resistant reaction to r.135 changed to near-susceptibility and made differentiation difficult. In the survey, where there was no clear-cut difference, the rust was recorded as r.138.

This variation in reaction caused by alterations in temperature has already been referred to (Waterhouse, 1929), and is a matter of extreme importance in the determination of a particular race. Unless standard conditions are maintained during the rust tests it becomes impossible to make valid comparisons between isolates.

Furthermore, there are cases in which the first seedling leaf gives reactions which are higher than those of the mature leaves. Thus with two isolates of r.135, "Einkorn" gave "4" reactions on a number of plants but only "flecks"—as expected—on the others. These "susceptible" seedling plants, when grown on, showed "flecks" on the older leaves. Again, a wheat like "Chinese White" is completely resistant as a mature plant in the field, but gives fully susceptible reactions on the seedling leaves. "Gabo" shows a very marked gradation with age. Extensive series of plants were used in an experiment in which successive leaves as they developed were inoculated with races 26 and 95. Commencing with a seedling reaction of "X+" there was mounting resistance rising to "flecks" on mature leaves.

In 1949 the first culture giving "Gaza" susceptibility and "Thew" susceptibility was definitely sorted out, although there had been earlier indications that this rust was present. Further studies showed that this dual susceptibility was associated with either susceptibility or resistance in "Webster", and hence the "Gabo"-attacking leaf rust can be one of four entities, viz., races 135AB, 135BB, 138AB, and 138BB. Characteristics of the races dealt with in this paper are set out in Table 17.

IDENTITIES OF RACES.

Cultural studies using the standard set of differential varieties have given the foregoing results under favourable testing conditions, i.e., with a temperature approximating to 70°F.

It will be noted that the variety "Norka" has been retained, and the varieties "Thew" and "Gaza" incorporated in the set. In our work "Norka" has not given the same reactions as "Malakof", although U.S.A. workers have reported that these varieties give similar results. From the Australian plant breeders' point of view, "Thew" and "Gaza" are extremely important in sorting out the races present, and must be included as differentials.

The determination of just what varieties shall be used as differentials in sorting out races or biotypes creates difficulties. It is probably the case that an unlimited

number of these entities could be separated out if sufficiently large numbers of host varieties were used in the testing work. Clearly an arbitrary selection must be made, and this set of differentials is usually accepted as an adequate group. But local conditions will often call for special treatment. Here, for example, it is essential to use "Thew" and "Gaza" as additional varieties. Such a procedure introduces a difficulty in the nomenclature. On the basis of the reactions shown on the accepted set of differentials, a particular number is used to designate the race represented by that rust. With the addition of an extra differential, the components it sorts out may be regarded as biotypes of that race, and designated by the letters "A" for resistance and "B" for susceptibility. Thus we have r.135A and r.135B as entities of r.135, characterized by

TABLE 17.
Typical Reactions of certain Physiologic Races of P. triticina expressed as Means of Rust Infections on selected Differential Varieties.

Physiologic Race.	Norka C.I.4377.	Malakof C.I.4888.	Carina C.I.3756.	Brevil C.I.3778.	Webster C.I.3780.	Lotos C.I.3779.	Mediterranean C.I.3332.	Hussur C.I.4843.	Democrat C.I.3384.	Thew C.I.5002.	Gaza.
1A	0	0	0	0	0	0	1	1	0	0	
1B	0	0	0	0	0	0	1	1	0	4	
10A	4	4	4	4	4	4	1	1	1	0	
10B	4	4	4	4	4	4	1	1	0	4	
12B	0	0	4	4	1	4	4	4	4	4	
15A	0	0	0	1	0	1	4	1	4	0	
15B	0	0	0	1	0	1	4	1	4	4	
20B	4	4	4	4	4	4	0	4	0	4	
26	0	0	4	4	0	4	0	4	0	4	0
34A	0	0	0	0	1	1	4	x	4	0	
53A	0	0	1	2	1	1	0	3	0	0	0
70B	4	x	4	4	4	4	0	x	0	4	
72A	0	0	4	4	x	4	1	x	1	0	
95	0	0	4	4	0	4	0	4	0	0	0
96	4	1	4	4	4	4	1	1	0	4	
97	1	1	4	4	4	4	1	1	0	0	
98AA	0	0	2	4	1	x	x	x	x	0	0
133A	0	0	x	1	1	4	0	4	0	0	
134B	4	1	x	4	4	4	1	1	0	4	
135A	0	0	x	x	x	x	0	x	0	0	
135B	0	0	x	x	x	x	0	x	0	4	
135AB	0	0	x	x	x	x	0	x	0	0	4
135BB	0	0	x	x	x	x	0	x	0	4	4
136A	0	0	1	1	x	x	4	x	4	0	
137B	0	0	x	x	x	x	x	x	0	4	
138AB	0	0	x	x	4	x	0	x	0	0	4
138BB	0	0	x	x	4	x	0	x	0	4	4

their resistance and susceptibility respectively on "Thew". Now with the further addition of "Gaza" separating out still further entities, additional letters "A" and "B" are used to designate them, so that we have, for example, r.135AB and r.138AB, meaning that whilst "Thew" is resistant to each of the two races, "Gaza" is susceptible to both. Instead of this system, the letters "A" and "B" might have been reserved for "Thew" reactions, and "C" and "D" set apart for the "Gaza" reactions, and so on. Each system is somewhat cumbersome, but for the present the use is preferred of the two letters "A" and "B" side by side, one referring to reactions shown by the first variety ("Thew"), and the other to the reactions of the second variety ("Gaza").

SPORE MEASUREMENTS.

Measurements were made under standard conditions of 200 uredospores of r.138AB lightly shaken from fully susceptible pustules on "Gaza". They showed a range of 22-30 μ , a mean of 26.06 μ , and a standard deviation of 2.08 μ for length; and a range of 20-26 μ , a mean of 22.39 μ , and a standard deviation of 1.39 μ for breadth.

Measurements of 200 teleutospores developed on the variety "Gabo" showed a range of 27–52 μ , a mean of 43.6 μ , and a standard deviation of 4.1 μ for length; and a range of 8–17 μ , with a mean of 11.7 μ , and a standard deviation of 1.5 μ for breadth. Details of measurements of other races are not available, but McAlpine (1906) gives for *P. triticina* teleutospores, 39–57 \times 15–18 μ , average 48 \times 16 μ . So far as comparison is possible, this probably means that the race in question has teleutospores that are significantly narrower than those recorded by McAlpine.

FREQUENCY OF OCCURRENCE OF RACES.

For a comparative study of the race frequencies, a truer picture is given if the totals of the r.135 and r.138 components are taken in relation to the totals for races 26 and 95. Over the whole period this gives r.95 1,042 isolations (55%), r.26 169 isolations (9%), and rs.135 and 138, 688 isolations (36%). If the years from 1946 onwards (when the "Gabo"-attacking rust first was determined) are taken, there were 568 isolates of r.95 (43%), 66 of r.26 (5%), and 688 of rs.135 and 138 (52%). The rapid build-up of the "Gabo"-attacking rust is very striking and is accounted for largely by the popularity of this variety and its widespread cultivation, as well as by the wide host range of this rust.

EFFECTS ON BREEDING PROGRAMME.

Naturally the breeding programme was seriously affected by this change in the rust flora. Tests soon brought to light a number of varieties which are resistant to all our Australian races, and these include: "Einkorn", "White Beardless Spelt", "Iumillo", "Norka", "Kawvale", "Salt Wheat", "Hope", "Hofed" and numerous other "Hope" derivatives, "H.44-24", "Argentine", "Klein", "Mentana", "Kleintrou", "Uruguay", and ("Steinwedel" \times "Timopheevi").

Several of these are being used in the back-cross programme, and studies are in progress by Drs. I. A. Watson and E. P. Baker, designed to show what genes for resistance are involved and their relationships. Up to the present, efforts to get teleutospores of the new races to germinate have failed, so that nothing is yet known of their genetics.

LEAF RUST FROM ENGLAND.

In 1948 and 1949 material for determination was sent from Cambridge and Buckinghamshire. In the first case the rust proved to be r.67 and in the second r.72. Both gave resistant reactions on the varieties "Thew" and "Gaza".

LEAF RUST FROM BURMA.

In 1947 rust on wheat was forwarded for determination by the Local Services Officer at Maymyo, Burma. Stem and leaf rusts were sorted out from the uredospore cultures that were developed from inoculations of wheat.

Race Determinations.

As usual, the variety "Federation" was used for the stock culture, but it was noticed that it showed both susceptible and resistant reactions to the leaf rust. Cultures of the former showed that it was r.20, with "Thew" and "Norka" susceptible. The resistant reactions gave trouble at the outset, because the development of 0; and 1 reactions on "Federation" had not previously been seen, and a search had to be made to find a susceptible variety on which to maintain the rust. Finally it was found that "Argentine W1060" and several other varieties which are completely resistant to Australian races were fully susceptible to this Burma leaf rust. This made it possible to build up the culture with safety. Tests with the differential hosts proved that it was r.1. When the variety "Thew" was added, "4" and "1" reactions were produced and separations of these showed that there were the two components of race 1, otherwise not separable on the usual differentials. These are styled r.1A and r.1B.

Numerous varietal tests have been made, and this classification reveals that many wheats which are resistant to the other leaf rust races available retain their resistance to race 1. It is, however, very striking to find a previously resistant wheat like "Argentine W1060" completely susceptible, whilst "Federation", which is regarded as a

most susceptible variety, is so strongly resistant. This accords with earlier reports that in India and Burma this Australian variety was found to be resistant.

Spore Morphology.

Under standard conditions, measurements were made of 200 uredospores lightly shaken from fully susceptible pustules developed on "*Aegilops divaricata*". The range of length was 22-34 μ , with a mean of 27.38 μ and a standard deviation of 2.56 μ ; and the breadth ranged from 20 to 26 μ , with a mean of 22.56 μ and a standard deviation of 1.4 μ .

It is helpful to compare measurements with certain other races, and these are set out in Table 18.

TABLE 18.
Spore Measurements. Constants for Uredospore Measurements of Four Races of P. triticea.

Race.	Length in μ .			Breadth in μ .		
	Mean.	Standard Deviation.	Range.	Mean.	Standard Deviation.	Range.
1	27.38	2.56	22-34	22.56	1.40	20-26
95	24.35	1.97	21-28	20.61	1.37	17-24
26	25.13	1.77	22-30	19.51	1.40	17-22
138AB	26.06	2.08	22-30	22.39	1.39	20-26

In making these measurements, a striking feature was the frequent occurrence of pyriform mesospores. Determinations of the frequency of their occurrence in 1,000 random spores produced on susceptible varieties under similar conditions for all four races gave the following results:

TABLE 19.
Frequency of Occurrence of Mesospores in Four Races of Leaf Rust.

Race.	Percentage of Mesospores.
1	13.3
95	7.4
26	7.0
138AB	4.7

The greatly increased production of mesospores by race 1 could not be ascribed to differences in the environmental conditions. No record has been found of this as a characteristic of any particular race.

MIXTURES OF RACES.

The simultaneous occurrence of different rusts on a host may be a matter of considerable importance. Stem and leaf rusts commonly occur together. Dealing only with leaf rust, frequently a field collection yields only the one rust, especially where a particular variety, e.g., "Gabo", screens out other races to which it is resistant. But the side-by-side occurrence of different races in susceptible varieties commonly takes place, and if anastomoses of the uredo mycelia should take place between different entities, new types may result from nuclear interchange.

Results to date are set out in Table 20, in which the four components which attack "Gabo" are grouped together. It is considered that the newness of the work of sorting them out and the consequent paucity of the numbers involved make this desirable.

The more frequent association of r.95 with r.s.135 and 138 than of r.26 with r.135 and r.138 is accounted for by the happening to which attention has been called in a previous paper (Waterhouse, 1938), viz., that r.26 is very uncommon early in the rust season, but develops later. This is not traceable to any screening action on the part of certain varieties, and at present no adequate explanation of the happening can be given.

TABLE 20.
Frequency of Occurrence of different Mixtures of Races of *P. triticina* in the Various Years.

Year.	Mixtures of Races and Frequency of Occurrence.			
	r.95 with r.26.	r.95 with r.135 and 138.	r.26 with r.135 and 138.	r.26, 95 with r.135 and 138.
1939	18			
1940	35			
1941	11			
1942	8			
1943	6			
1944	2			
1945	4			
1946	4			
1947		2		
1948	4	72	13	1
1949	8	82	6	2
1950	4	21	6	
1951	1	16	1	
Totals	105	193	26	3

OAT STEM RUST.

LIFE HISTORY.

The uredospore stage of *P. graminis avenae* E. & H. is present on self-sown or volunteer oats or susceptible grasses all the year round. To date no barberry infections have been found under natural conditions. However, it is clear that the Australian oat stem rust has not lost its capacity to attack the barberry. In one experiment in 1949, heavily rusted *Avena fatua* at Canberra, A.C.T., was found to be infected by r.1 and/or r.2. Teleutospores developed later, and the straw was exposed there to the full winter conditions. In the spring, viable teleutospores were used to inoculate barberries in the plant house, and this led to the production of abundant spermogonia and aecidia. Spores from the latter were used to inoculate oats, and tests with this uredospore culture showed that the race present was r.1 and/or r.2.

SPECIALIZATION.

In the studies, "Joanette", obtained originally from Dr. E. C. Stakman in 1925, has been used as one of the differentials. Canadian and American workers have latterly used "Sevenothree" in its place. Seed of this variety was kindly supplied by Dr. T. Johnson of Winnipeg in 1944, and the two varieties have since been under study, both being used in the regular differential sowings. Sowings of the original seed of "Sevenothree" gave seedlings of which some were resistant, others susceptible, to a particular culture of stem rust. A number of single plant selections were therefore made, and at the same time similar selections were made of "Joanette". Both series have been carried forward with appropriate rust testing of the single plants taken each season and with morphological comparisons with the "parent" varieties. Many of the selections gave identical results, but others were clearly different. Three of them have been used widely in our testing work.

Typical results given by the three stock races are set out in Table 21.

The results show that although there is morphological similarity between the selections which are typical of the original variety, there are clear physiological differences between them. Thus there are at least two types of "Joanette" and three of "Sevenothree", of which "Joanette 1" and "Sevenothree 3" give the same results, as do also "Joanette 2" and "Sevenothree 5". It is evident that apart altogether from temperature variations making a difference between determinations of r.1 and r.2 and again between r.3 and r.7, the particular selection of the differential host used can make this difference.

This single plant work has also shown the occurrence of biotypes within the recognized races. On individual leaves of "Sevenothree 8" it was noticed that occasionally "3" and "1" reactions developed. Single pustules were taken to build up cultures which were then used to inoculate pots of seedlings. This has shown that sometimes a race determined as either r.1 or 2, r.3 or 7, or r.8 consists of a complex of which one component shows resistance, and another shows susceptibility when tested with "Sevenothree 8". Six isolates from New South Wales and two from Queensland have shown this behaviour, five of the occurrences applying to r.8, two to r.3 or 7, and one to r.1 or 2.

TABLE 21.

Typical Reactions Given by Certain Selections of "Joanette" and "Sevenothree" to Three Races of P. graminis avenae.

Varietal Selection.	Typical Reactions to Races of <i>P. graminis avenae</i> .		
	r.1 or 2.	r.3 or 7.	r.8.
Joanette 1	1	1	3+
Joanette 2	3+	3+	3+
Sevenothree 3	1	1	3+
Sevenothree 5	3+	3+	3+
Sevenothree 8	3+	1	x-

That a race is further separable into other entities (biotypes) is also shown by results in F₃ tests of cross-bred material obtained from a cross between "Fulghum" and "Garry". The former is susceptible and the latter resistant to r.8. In numerous cases particular F₃ plants inoculated with r.8 have shown a mixture of "3+" and "1" pustules. Cultures built up from each type, when used to inoculate the differential set of hosts, have given typical r.8 results and have been inseparable on this basis. The origin of these entities, whether by mutation or otherwise, is quite obscure, but it is quite important to recognize their existence. It may be that tests with other varieties of oats would show some to be resistant to one biotype but susceptible to another, and this could have an important bearing on a breeding programme.

RACE DETERMINATIONS.

Already six races of *P. graminis avenae* have been recorded for Australia (Waterhouse, 1929, 1936, 1938, 1939), and it has been shown that of these races, 1 and 2 can be separated on the differential "Joanette" (or "Sevenothree") only at low temperatures, and that the same applies to races 3 and 7. This fine differentiation has been found so far to be unimportant in the breeding work, and hence in the rust survey the races are recorded as r.2 (not r.1 and/or 2) in the one case, and r.7 (not r.3 and/or 7) in the other. Both could be present instead of only the one.

In the current work, the only other race found has been r.8. The race formerly recorded (Waterhouse, 1929) as r.6 has not been determined during this period.

The typical reactions shown by these races are set out in Table 22.

The distribution of these races in time and space is set out in Tables 23 and 24.

TABLE 22.
Typical Infection Types produced by Physiologic Races of P. graminis avenae on Differential Varieties of Avena spp.

Physiologic Race.	Mean Reaction on Differential Varieties.		
	White Tartar.	Richland.	Joanette.
1	2	1	1
2	2	1	4
3	4	1	1
7	4	1	4
8	2	4	4

TABLE 23.
Summary of the Number of Isolations of the Physiologic Races of P. graminis avenae Grouped According to Time of Collection.

Race.	Season of Isolation Ending on 31st March of the Year Named.												Totals.	
	1939.	1940.	1941.	1942.	1943.	1944.	1945.	1946.	1947.	1948.	1949.	1950.		1951.
1 or 2	58	44	33	47	8	47	16	65	28	67	18	63	34	528
3 or 7	22	50	19	22	16	21	4	29	8	56	15	46	19	327
8	2	12	6		1	1		1	2	10	5	13	23	76
Totals	82	106	58	69	25	69	20	95	38	133	38	122	76	931

TABLE 24.
Summary of Number of Isolations of Physiologic Races of P. graminis avenae Grouped According to their Source.

Race.	Source of Material.								Totals.	Percentage.
	A.C.T.	N.S.W.	Vic.	Qld.	S.A.	W.A.	Tas.	N.Z.		
1 or 2	5	354	15	50	13	32	30	29	528	57
3 or 7	4	272	10	27	2	1	10	1	327	35
8	1	58	3	11			3		76	8
Totals	10	684	28	88	15	33	43	30	931	100

The localities within the States from which the collections actually come are shown for each of the years as follows:

DETAILS OF THE OCCURRENCES OF THE RACES OF *P. GRAMINIS AVENAE*.

1939.

r.1 or 2.

N.S.W.: Tullamore, Curlewis, Glen Innes, Pilliga, H.A. College, Grafton, Gum Flat, Condobolin, Gunnedah, Cowra, Trangie, Uralla, Bathurst, Dubbo, Tichborne, Nelegeloo, Sydney University.

Qld.: Gatton.

Tas.: Cressy.

N.Z.: Winton, St. Romans, Mataura, Kingston Crossing.

r.3 or 7.

N.S.W.: Bemboka, H.A. College, Curlewis, Condobolin, Uralla, Cowra, Bathurst, Dubbo, Tichborne, Guyra, Nelegeloo, Glen Innes, Red Range, Ben Lomond.

A.C.T.: Canberra.

Qld.: Gatton.

Tas.: Cressy.

r.8.

N.S.W.: Glen Innes.

A.C.T.: Canberra.

1940.

r.1 or 2.

N.S.W.: Gunnedah, Junee, Trangie, Temora, Stockinbingal, Werris Creek, Ardglenn, Tamworth, Boggabri, H.A. College, Colinroobie, Cowra, Bathurst, Dubbo, Chullora, Downside, Old Junee.

A.C.T.: Duntroon.

Qld.: Gatton.

S.A.: Port Victoria, Murray Bridge, Booleroo, Waite.

Vic.: Walpeup, Invergordon, Charlton, Werribee.

r.3 or 7.

N.S.W.: Glen Innes, Gunnedah, Junee, Trangie, Temora, Dernasser, Tamworth, Boggabri, Colinroobie, Yerong Creek, Cowra, Bathurst, Dubbo, The Rock, H.A. College, Chullora, Uranquinty, Downside, Wagga, Grafton, Armidale.

Qld.: Gatton.

Vic.: Werribee, Invergordon, Charlton.

r.8.

N.S.W.: Glen Innes, Trangie, Bathurst, Dubbo, The Rock, Uranquinty, Wagga.

Vic.: Werribee.

1941.

r.1 or 2.

N.S.W.: H.A. College, Lindfield, Katoomba, Glen Innes, Guyra, Attunga, Boggabri, Milvale, Bathurst, Tichborne.

Vic.: Werribee.

A.C.T.: Canberra.

N.Z.: Christchurch, West Courtney.

r.3 or 7.

N.S.W.: Lindfield, H.A. College, Glen Innes, Guyra, Gunnedah, Tichborne, Bathurst.

Vic.: Werribee.

r.8.

N.S.W.: Glen Innes, Bungarley.

Vic.: Werribee.

1942.

r.1 or 2.

N.S.W.: Bellalia, Griffith, Gunnedah, Kelso, Tichborne, Cowra, Campbelltown, H.A. College, Manly, Lindfield, Spring Hill, Glen Innes, Forbes, Bathurst.

S.A.: Waite.

W.A.: Merredin.

Vic.: Werribee, Werrimull.

Tas.: Wesley Vale, Staverton, Deloraine, Wilmot, West Pine, Tunnack, Parattah, Mount Seymour, Lilydale.

r.3 or 7.

N.S.W.: Inverell, Gunnedah, Cowra, H.A. College, Spring Hill, Glen Innes.

A.C.T.: Canberra.

Vic.: Werribee.

Tas.: Wesley Vale, Staverton, Wilmot, Mount Seymour.

1943.

r.1 or 2.

N.S.W.: H.A. College, Baradine, Tichborne, Lindfield.

Qld.: Gatton.

Vic.: Footscray.

r.3 or 7.

N.S.W.: H.A. College, Lindfield, Gunnedah, Tichborne, Baradine, Cowra, Inverell.

Qld.: Gatton.

Vic.: Footscray.

r.8.

N.S.W.: Inverell.

1944.

r.1 or 2.

N.S.W.: Beecroft, Lindfield, H.A. College, Bathurst, Cowra.

S.A.: Waite.

Qld.: Burdekin River, Gatton, Brookstead.

W.A.: Merredin, Elabbin, Nalkain, Wael, Wongan Hills, South Borden.

Vic.: Walpeup, Dookie, Werribee.

A.C.T.: Canberra.

N.Z.: Ashburton.

r.3 or 7.

N.S.W.: Hurlstone Park, Yanco, H.A. College, Curlewis, Grong Grong, Spring Hill, Blackheath.

S.A.: Bridgetown.

Qld.: Gatton, Brookstead.

A.C.T.: Canberra.

W.A.: Merredin.

N.Z.: Otautau.

r.8.

N.S.W.: H.A. College.

1945.

r.1 or 2.

N.S.W.: Wallacia, Lindfield, H.A. College, Manly, St. Ives, Glen Innes.

Qld.: Gatton.

r.3 or 7.

N.S.W.: St. Ives, Glen Innes.

Qld.: Gatton.

1946.

r.1 or 2.

N.S.W.: Spring Hill, Lindfield, Epping, Glen Innes, H.A. College, Scone, Curlewis, Wingen, Campbelltown, Lenmeal, Dubbo, Nea Siding, Muswellbrook, Aberdeen, Singleton, Gunnedah, Wean, Gravesend, Baradine, Warrumbungle, Manilla, Tichborne, Cowra, Glenfield, Wee Waa, Narrabri, Armidale, Tomingley West, Gilgandra.

Qld.: Lawes, Brookstead.

r.3 or 7.

N.S.W.: Curlewis, Wingen, H.A. College, Nea Siding, Muswellbrook, Gunnedah, Pallamallawa, Wee Waa, Tamworth, Narrabri, Coonabarabran, Baradine, Warrumbungle, Cowra, Scone, Tomingley West, Spring Hill, Tenterfield, Armidale, Kelso.

Qld.: Brookstead.

r.8.

N.S.W.: Glen Innes.

1947.

r.1 or 2.

N.S.W.: Tichborne, Lindfield, Windsor, Castlereagh, Glenfield, Albury, Finley, Grafton.

Vic.: Lake Cullulleraine.

S.A.: Kingston, Gawler, Mount Gambier, Waite, Narracoorte.

W.A.: Mayanup.

r.3 or 7.

N.S.W.: Windsor, Taree, Finley, Grafton, Lindfield, Glenfield.

r.8.

N.S.W.: Taree.

1948.

r.1 or 2.

N.S.W.: Curlewis, Inverell, Glen Innes, Bogan Gate, Gunnedah, Lindfield, Yanco, Wongarbon, Eumungerie, Tooraweenah, Coonabarabran, Boggabri, Leeton, North Star, Grafton, Nemingha, Gilgandra, Wallen Bullen, Trangie, Willow Tree, Cowra, Manly, Bodalla, Castle Hill, Bemboka, Kelso.

Qld.: Brookstead, Hermitage, Murgon, Biloela, Mt. Tyson, Bongeen, Warwick, Wellcamp, Lawes, Dalby, Condamine Plains.

W.A.: Wongan Hills.

Tas.: Launceston, Cressy, Deloraine, Cambridge, Kindred, Elliott.

r.3 or 7.

N.S.W.: Glen Innes, Inverell, Curlewis, Bowral, Nelungaloo, Parkville, Breeza, Nea Siding, Murrurundi, Gunnedah, Winton, Coonabarabran, Tooraweenah, Boggabri, North Star, Gilgandra, Concord, Wallen Bullen, Grafton, Willow Tree, Manly, Tichborne, Bodalla, Castle Hill, Blackheath, Bemboka, Kelso.

Qld.: Brookstead, Biloela, Bongeen, Warwick, Wellcamp, Cambooya, Hermitage.

Tas.: Launceston.

S.A.: Bordertown.

r.8.

N.S.W.: Glen Innes, Gunnedah, Griffith, Nowra, Tichborne.
Qld.: Brookstead.

1949.

r.1 or 2.

N.S.W.: Curlewis, Castle Hill, Tichborne, H.A. College, Temora, Leeton, Glen Innes, Tanja, Armidale.

Qld.: Lawes, Nabby.

W.A.: Carnavon.

N.Z.: Lincoln.

r.3 or 7.

N.S.W.: Kelso, Castle Hill, Curlewis, Lindfield, Tamworth, Leeton, Armidale.

Tas.: King Island.

Qld.: Jondaryan, Nabby.

r.8.

N.S.W.: Glen Innes.

Qld.: Jondaryan.

1950.

r.1 or 2.

N.S.W.: Lindfield, Spring Hill, Curlewis, Grafton, Yanco, Concord, Bellata, Appleby, Attunga, Dubbo, Gunnedah, Leeton, Carroll, Tamworth, Bective, West Wyalong, Berrigan, Manildra, Narrandera, Urana, Brocklesby, H.A. College, Cootamundra, Barmedman, Spring Terrace, Kelso.

Qld.: Greenmount, Hermitage, Westbrook, Mt. Tyson, Dalby.

Vic.: Rutherglen.

S.A.: Huddleston.

Tas.: Wattle Grove, Sheffield, Ulverstone.

A.C.T.: Canberra.

r.3 or 7.

N.S.W.: Spring Hill, Curlewis, Wee Waa, Nemingha, Castle Hill, Gunnedah, Carroll, Tamworth, Bective, Gilgandra, West Wyalong, Borenore, Manildra, Temora, Leeton, Urana, Walbundrie, Cootamundra, Barmedman, H.A. College, Spring Terrace, Kelso.

Qld.: Hermitage.

Vic.: Rutherglen.

Tas.: Springfield, Ulverstone.

r.8.

N.S.W.: Curlewis, Leeton, Walbundrie, Spring Terrace, Glen Innes.

Qld.: Hermitage, Lawes, Pittsworth.

1951.

r.1 or 2.

N.S.W.: Kelso, Curlewis, Tamworth, Cowra, Tichborne, Trangie, Gilgandra, Kosciusko, Yanco, Leeton, Gunnedah, Narrabri.

Qld.: Hermitage, Warwick.

S.A.: Waite.

Tas.: Cressy, Oaklands, Longford, Ulverstone, Kingston.

N.Z.: Massey College.

r.3 or 7.

N.S.W.: Kelso, Narrabri, Curlewis, Boggabri, Tamworth, Concord, Cowra, Trangie, Tichborne, Gunnedah.

A.C.T.: Canberra.

Tas.: Kingston.

r.8.

N.S.W.: Canowindra, Curlewis, Tichborne, Goonumbla, Badgery's Creek, Wagga, Cowra, Gunnedah.

Qld.: Warwick, Gympie.

Tas.: Cressy, Ulverstone.

It will be seen that the r.1 or 2 isolates have occurred most commonly. This rust does not attack the "Tartarian" or "Richland" types, and its widespread occurrence is due to the wide cultivation of susceptible varieties like "Algerian" and "Fulghum". There is a clear trend in the direction of an increasing frequency of the r.3 or 7 rust, characterized by its ability to attack the "Tartarian" types and of r.8 which attacks the "Richland" types, although both these types of oats are relatively restricted in cultivation.

A comparison of these specialization phenomena is given with the total results to date, which are set out in Tables 25 and 26 in respect of the time and space distributions.

The overall percentage figures show that whereas r.1 or 2 was present in 69%, r.3 or 7 in 25.5%, r.6 in 0.5%, and r.8 in 5% of all the determinations made, these figures for the first period of 14 years are respectively 86%, 12.5%, 1% and 0.5%, and for the second period of 13 years 57% of r.1 and 2, 35% of r.3 or 7 and 8% of r.8.

TABLE 25.

Summary of the Number of Isolations of the Physiologic Races of *P. graminis avenae* Grouped According to Time of Collection.

Physiologic Race.	Season of Isolation, Ending 31st March of the Year Stated.														Totals.	1939.
	1925.	1926.	1927.	1928.	1929.	1930.	1931.	1932.	1933.	1934.	1935.	1936.	1937.	1938.		
1 and/or 2	30	3	21	38	39	38	62	54	48	34	72	66	55	45	605	58
6				2	6								1		9	9
3 and/or 7				7	4	2	13	5	6	5	5	8	9	25	89	22
8														3	3	2
Totals	30	3	21	47	49	40	75	59	54	39	77	74	65	73	706	82

Physiologic Race.	Season of Isolation, Ending 31st March of the Year Stated.											Totals.	Grand Totals.	
	1940.	1941.	1942.	1943.	1944.	1945.	1946.	1947.	1948.	1949.	1950.			1951.
1 and/or 2	44	33	47	8	47	16	65	28	67	18	63	34	528	1133
6														9
3 and/or 7	50	19	22	16	21	4	29	8	56	15	46	19	327	416
8	12	6		1	1		1	2	10	5	13	23	76	79
Totals	106	58	69	25	69	20	95	38	133	38	122	76	931	1637

TABLE 26.

Summary of the Number of Isolations of Physiologic Races of *P. graminis avenae* Grouped According to their Source.

Physiologic Race.	Source of Material.								Totals.	Percentage.
	A.C.T.	N.S.W.	Vic.	Qld.	S.A.	W.A.	Tas.	N.Z.		
1 and/or 2	22	826	40	82	44	40	38	41	1133	69
6		7	2						9	0.5
3 and/or 7	7	345	14	29	2	1	16	2	416	25.5
8	1	61	3	11			3		79	5
Totals	30	1239	59	122	46	41	57	43	1637	100

It is clear that varieties which have been bred for resistance using "Richland" as the "resistant" parent cannot be relied upon: although at present they are limited in their cultivation they may well be contributing to the build up of race 8. Because of the screening action of differential varieties, and the further important effects of competition between races (Watson, 1942), the aim in breeding must be to incorporate resistance to all known races. In our work, the Canadian variety "Garry" has been used as a source of resistance, even though it is susceptible to the serious American disease caused by *Helminthosporium victoriae*, which is not known at present in Australia. It has the added value of being resistant to the races of *P. coronata* that are present in Australia: this resistance is inherited independently of the resistance to stem rust so that types with the combined resistances can readily be obtained from "Garry" crosses. Its resistance to many races of oat smut further enhances its value.

MIXTURES OF RACES.

It has been a common occurrence to find more than one race present in a single collection of rusted material. Obviously a variety like "Richland" has yielded only the one race; with fully susceptible varieties the situation is quite different. During the current investigations, a mixture of r.1 or 2 with r.3 or 7 has been found each year in a single collection: altogether 165 such mixtures have occurred. A mixture of r.3 or 7 with r.8 has shown up 19 times, and r.1 or 2 with r.8 nine times. On three occasions r.1 or 2, r.3 or 7, and r.8 have together been present in the one field collection.

GRASS HOSTS.

Previously it has been pointed out that oat stem rust attacks a number of grasses, native and introduced. In the period under review the occurrences are set out in Tables 27 and 28.

TABLE 27.
Distribution in Time of the Number of Physiologic Races of P. graminis avenae Found on Grasses.

Race.	Season of Isolation Ending 31st March of the Year Named.											Totals.	Per-centage.		
	1939.	1940.	1941.	1942.	1943.	1944.	1945.	1946.	1947.	1948.	1949.			1950.	1951.
1 or 2	6	9	9	15	1	24	6	24	6	20	6	29	11	166	60
3 or 7		11	4	5	4	4	1	5	1	26	7	16	11	95	34
8	1	2	1		1					2		2	8	17	6
Totals	7	22	14	20	6	28	7	29	7	48	13	47	30	278	100

It is not unexpected to find that the "wild oats" have been the commonest hosts. In most cases the rusted material was clearly *A. fatua*, but in collections where no head specimens were included, the designation given by the collector was accepted. Those of *A. sterilis* and *A. barbata* were definitely correct. These species are not as widely dispersed as the first named, but tests have shown that members of all three are susceptible to our races.

The other grasses listed have shown striking variation in resistance within a given species. Thus in cases like that of *Phalaris tuberosa* or *Bromus unioloides*, a single rusted plant gave cultures of r.1 or 2, which when used to inoculate pots of seedlings from commercial seed gave only resistant reactions. On seedlings from grain of the original susceptible plant, a few proved susceptible but most were completely resistant. It is clear that in this, as in many of the other grasses listed, there is marked variability in the inherent resistance of individuals within the species, although no morphological differences are apparent. This has been described in some detail in a recent paper (Waterhouse, 1951).

MIXING OF RACES.

As in the case of the cultivated oats, many cases came to light in which a particular grass collection yielded more than one race of rust. As might be expected, the wild oats showed the greatest frequency. The results are shown in Table 29.

TABLE 29.
Frequency of Occurrence of Mixtures of Races of Oat Stem Rust on Grasses.

Grass Host.	Number of Isolations of Mixtures of Races.		
	r.1 or 2 with r.3 or 7.	r.1 or 2 with r.8.	r.3 or 7 with r.8.
<i>Avena fatua</i>	21		1
<i>A. sterilis</i>	7		
<i>Hordeum leporinum</i>	2		1
<i>Dactylis glomerata</i>	1	2	
<i>Lamarckia aurea</i>	8		1
<i>Arrhenatherum elatius</i>	1		
<i>Amphibromus Neesii</i>	3		

Admixture with other rusts occurs. In *Hordeum leporinum* isolates there were 19 mixtures of *P. graminis avenae* and *P. graminis tritici*; in *Amphibromus Neesii* 1; and *Agropyron scabrum* 1. There have also been more than 100 instances in which *P. graminis lolii* has been mixed with *P. graminis avenae*, as set out in a recent paper (Waterhouse, 1951).

In addition there have been very many cases of leaf rust occurring with stem rust, both in oats and various grasses.

CROWN RUST OF OATS.

Great damage to oat crops may be caused by this rust, *Puccinia coronata avenae* F. & L., especially in coastal areas. In favourable seasons it has completely ruined crops and has many times been found to kill out wild oats.

LIFE HISTORY.

The alternate host, *Rhamnus* spp., is not present in Australia, except perhaps in some of the Botanic Gardens. Nevertheless, it is a potential source of danger. Thus, in the plant house, viable teleutospores of race 6 were used in an inoculation experiment on *R. cathartica* L.: this led to the production of spermogonia and aecidia from which uredospore cultures were obtained on oats.

As a rule, teleutospores exposed to favourable winter conditions on the Tablelands have failed to germinate, and numerous attempts to break the dormancy of the spores by freezing the material in the refrigerator have failed, even with spores formed late in the season under relatively low temperatures. It may be found that different races behave differently in this regard.

In the absence of the alternate host, it seems probable that under Australian conditions new physiologic races arise by mutation or possibly by "hybridization" brought about by nuclear interchange in the dicaryotic phase, or it may be by adaptive response to different hosts.

The carry-over from season to season takes place on self-sown or "volunteer" oats and on wild oats. Collections of *P. coronata* on *Lolium* spp., *Holcus lanatus* L., *Agrostis avenacea* Gmel., and *Polygonum monspeliensis* (L.) Desf. have been found incapable of attacking oats and are therefore to be regarded as different sub-species of *P. coronata*.

IMPORTANCE OF WILD OATS.

Collections on wild oats have given results comparable with those obtained from the cultivated forms. Both have come to hand in between cropping seasons. The race determinations from wild oats have been recorded separately and these results are set out in Tables 30 and 31.

TABLE 30.

Summary of the Number of Isolations of Physiologic Races of *P. coronata* avenae on Wild Oats Grouped According to Time of Collection.

Race.	Season of Collection, Ending 31st March of the Year Named.													Totals.	
	1936.	1937.	1938.	1939.	1941.	1942.	1944.	1945.	1946.	1947.	1948.	1949.	1950.		1951.
1				1			1								2
3		3		1	1	1	1	5	1			1	1	2	17
6	2	4	1	2		1	3	4	11	5	7	1	5	8	54
7			1	1	1	2		1	5		1			2	18
102										3	4	2	3	5	17
103										2			1		3
40	1	2					1								4
57												1			1
Totals	3	9	2	5	2	4	6	10	17	12	12	5	12	17	116

TABLE 31.

Summary of the Number of Isolations of *P. coronata* avenae on Wild Oats Grouped According to their Source.

Host.	Totals.	Source of Material.													
		N.S.W. Races.							Qld. Races.		N.Z. Races.				
		1	3	6	7	102	103	40	102	103	3	6	7	102	103
<i>Avena fatua</i>	96	2	13	42	12	10	2	4	1	1	2	3	2	1	1
<i>A. sterilis</i>	10		2	5	1	2									
<i>A. barbata</i>	10			4	3	3									
Totals	116	2	15	51	16	15	2	4	1	1	2	3	2	1	1

The host material was in many instances determined definitely in so far as the species was concerned by reason of the fact that panicles or grain were included with the specimens. This applies to all collections listed under *A. sterilis* and *A. barbata*. In other instances the label simply stated "*A. fatua*" and the material was accepted as such. In some of these cases one or other of the remaining species was almost certainly involved: plant house tests have shown that they are susceptible to the races recorded, although many occurrences of both resistant and susceptible reactions on the same leaf of a wild oat plant show that different races may behave differently on wild oats.

It is seen that in only two of the years under review were rusted wild oats not recorded. Eight of the 13 races known to occur have been present. Of these, race 6 was by far the commonest, the frequency of this race and of the others being not unlike that of the totals of all the isolations. The remaining five have been found only rarely on cultivated oats, as shown in Tables 33 and 34.

There have been many cases in which a single collection has contained a mixture of races.

In the case of *A. fatua* collections, seven contained a mixture of three races, these comprising four of races 6, 7, and 102, and one each respectively of 1, 3, and 7; 3, 6, and 40; and 3, 6, and 57. Thirty-five of the collections yielded pairs of races, occurring in many different combinations.

A. sterilis gave one mixture of three races, viz., 6, 7, and 102, and two collections in which two races were present.

Collections of *A. barbata* closely paralleled those of *A. sterilis*, giving one mixture of races 6, 7, and 102, and two others in which a pair of races occurred together.

TABLE 32.
Typical Reactions of Certain Physiologic Races of P. coronata avenae Expressed as Means of the Rust Infections.

Physiologic Race No.	Mean of Reactions on Differential Varieties.												
	Ruakura.	Green Russian.	Hawkeye.	Anthony.	Sunrise.	Victoria.	Green Mountain.	White Tartar.	Red Rust Proof.	Steriel.	Belar.	Bond.	Glabrota.
1	4	4	4	4	4	1	4	4	4	4	3	0	0
3	0	4	4	4	0	1	4	4	0	0	0	0	0
6	0	4	4	4	4	1	4	4	4	4	4	0	0
7	4	4	0	0	4	1	0	0	4	4	4	0	0
9	1	2	3	3	2	0	3	3	1	1	2	0	0
40	4	4	0	0	4	1	4	0	4	4	4	0	0
45	4	4	3	3	4	2	3	3	4	4	4	4	0
47	1	4	0	1	4	2	0	1	4	4	4	0	0
57	1	3	4	3	4	2	4	3	4	4	4	4	0
77	3	0	4	4	4	1	4	4	4	4	4	0	0
102	0	0	4	4	4	1	4	4	4	4	4	0	0
103	4	2	0	0	4	1	0	0	4	4	4	0	0
104	4	2	2	4	4	1	4	4	4	4	4	0	0

SPECIALIZATION STUDIES WITH RUSTS FROM OATS.

The first studies were made in 1925 on a collection of heavily rusted "Richland" oats growing at Glen Innes. Its reactions were determined on a number of oat varieties then on hand. In 1932 similar material was received from New Zealand and a comparison made with the reactions already recorded from the Glen Innes collection. No differences were found between them. The former rust has been maintained in culture until the present time, and is our stock culture of race 6.

In 1934, grain of the differential varieties used in U.S.A. was received from Dr. H. B. Humphrey of the U.S.D.A., and a commencement made with detailed specialization studies. From the outset it became evident that environmental effects, and especially temperature fluctuations, produced most marked variations in the rust reactions shown on the differentials: very numerous cases came to light in which sharp resistance given at low temperatures during the winter changed to susceptibility when the summer temperatures prevailed. For this reason the separation of races can only be carried out satisfactorily under relatively low temperature conditions.

IDENTITY OF RACES DEALT WITH.

Recent word from Dr. H. C. Murphy states that a new revised set of differential oat varieties is being used in North American determinations, commencing with the

1951 collections. The revised set is being adopted because the old set does not, in some cases, give the help needed in the breeding programme. Seed of the new set is expected to be available here in the near future, when the effort will be made to co-ordinate results given by the two sets. It is to be hoped that as far as possible the races determined on the new set in North America will be correlated with those already recognized under the existing scheme. This would give a wider overall picture of the specialization behaviour over a long period of time, apart from linking up with investigations being carried forward elsewhere with the older set of differentials.

It will be seen that, using the older set, a number of races have been determined, and of them 102, 103, and 104 are new records. Their typical reactions are set out in Table 32.

The distributions in time and space are shown in Tables 33 and 34.

TABLE 33.

Summary of the Number of Isolations of Physiologic Races of P. coronata avenae Grouped According to Time of Collection.

Race.	Season of Collection, Ending 31st March of the Year Named.															Totals.		
	1935.	1936.	1937.	1938.	1939.	1940.	1941.	1942.	1943.	1944.	1945.	1946.	1947.	1948.	1949.		1950.	1951.
1		3		5	8	1		1		1								24
3		2	15	8	3	2	1	1		5	7	11			4	2	3	64
6	4	17	20	17	11	6	1	6	4	9	21	34	14	22	16	39	40	281
7		3		5	3		2	2	1	4	2	21	4	7	4	9	12	79
40		4	12	9						1	2					2		30
45															1	1		2
47		1		1		1				1								4
77															2	2		4
9														1	1			2
102													6	15	14	10	19	64
103													3		5	1	1	10
57															2	1		3
Totals	4	30	47	45	25	10	4	10	5	21	32	66	27	45	52	69	75	567

TABLE 34.

Summary of the Number of Isolations of Physiologic Races of P. coronata avenae Grouped According to their Source.

Race.	Source of Material.								Totals.
	A.C.T.	N.S.W.	Vic.	Qld.	S.A.	W.A.	Tas.	N.Z.	
1		16		3				5	24
3	1	54		1	1	1		6	64
6		229	1	30	2	1	4	14	281
7		66		5		1		7	79
40		26		1				3	30
45		2							2
47		1			1				4
77		4						2	4
9		1		1					2
102		51		10	2			1	64
103		8		2					10
57		2						1	3
Totals	1	460	1	53	6	3	4	39	567

The actual locations from which the collections came year by year are shown as follows:

DETAILS OF THE OCCURRENCES OF THE RACES OF *P. CORONATA* AVENAE.

	1935.
	r.6.
N.S.W. : Ulmarra, Ryde, H.A. College, Wollongong.	
	1936.
	r.1.
N.S.W. : H.A. College, Campbelltown.	
N.S.W. : Sydney University.	r.3.
	r.6.
N.S.W. : Lindfield, Grong Grong, Taree, H.A. College, Nowra, Chatswood, Campbelltown, Sydney University, Cowra, Concord, Glen Innes, Killara.	
Qld. : Lawes.	
N.Z. : Palmerston North.	
	r.7.
N.S.W. : Taree, H.A. College, Concord.	
	r.40.
N.S.W. : Pennant Hills, Glen Innes, Killara.	
N.Z. : Palmerston North.	
	r.47.
N.Z. : Palmerston North.	
	1937.
	r.3.
N.S.W. : Chatswood, Sydney University, H.A. College, Glen Innes.	
	r.6.
N.S.W. : Roseville, Chatswood, Sydney University, H.A. College, Condobolin, Taree, Glen Innes, Koonadan.	
	r.40.
N.S.W. : Roseville, Chatswood, H.A. College.	
	1938.
	r.1.
N.Z. : Palmerston.	
	r.3.
N.S.W. : Sydney University, H.A. College, Granville, Hammondville.	
N.Z. : Palmerston.	
	r.6.
N.S.W. : Sydney University, Roseville, H.A. College, Granville, Hammondville, Leeton, Glen Innes.	
N.Z. : Palmerston, Amberley, Lincoln, Willoughby.	
	r.7.
N.Z. : Palmerston, Amberley, Willoughby.	
	r.40.
N.S.W. : Roseville, H.A. College, Granville, Hammondville.	
N.Z. : Palmerston, Lincoln.	
	r.47.
N.S.W. : Leeton.	
	1939.
	r.1.
N.S.W. : H.A. College, Robertson, Kyogle, Bemboka, Chatswood.	
Qld. : Lawes.	
	r.3.
N.S.W. : Taree, Sydney University.	
	r.6.
N.S.W. : Bemboka, H.A. College, Chatswood, Robertson, Kyogle, Urbenville, Oakwood.	
Qld. : Lawes.	
	r.7.
N.S.W. : Taree, Sydney University.	
	1940.
	r.1.
N.S.W. : Trangie.	
	r.3.
A.C.T. : Duntroon.	
S.A. : Waite.	

- r.6.
N.S.W.: Taree, Rankin's Springs, Trangie, Temora.
Qld.: Lawes.
Vic.: Werribee.
- r.47.
S.A.: Waite.
1941.
r.3.
N.S.W.: Lindfield.
- r.6.
N.S.W.: Taree.
- r.7.
N.S.W.: Taree, Lindfield.
1942.
r.1.
N.S.W.: Gilgandra.
- r.3.
N.S.W.: Sydney University.
- r.6.
N.S.W.: Gunnedah, Tichborne.
N.Z.: Auckland, Blenheim.
- r.7.
N.S.W.: Sydney University.
N.Z.: Auckland.
1943.
r.6.
N.S.W.: H.A. College.
Qld.: Lawes.
- r.7.
N.S.W.: H.A. College.
1944.
r.1.
N.S.W.: Lindfield.
- r.3.
N.S.W.: Sydney University, Strathfield, H.A. College.
W.A.: Perth.
- r.6.
N.S.W.: Lindfield, Sydney University, H.A. College, Blackheath.
Qld.: Nankin, Wellington Point.
N.Z.: Ashburton.
- r.7.
N.S.W.: H.A. College, Strathfield.
Qld.: Nankin.
W.A.: Perth.
- r.40.
N.S.W.: Blackheath.
- r.47.
N.Z.: Ashburton.
1945.
r.3.
N.S.W.: Sydney University, Murwillumbah, Miller's Forest, Chatswood, Lindfield, Manly.
- r.6.
N.S.W.: Lismore, Alphadale, Murwillumbah, Grafton, Taree, Richmond River, H.A. College.
West Maitland, Flemington, Miller's Forest, Chatswood, Lindfield, Sydney University, Anna Bay.
Qld.: Lawes.
- r.7.
N.S.W.: Murwillumbah, Manly.
- r.40.
N.S.W.: H.A. College, Grafton.
1946.
r.3.
N.S.W.: Taree, Singleton, Wingen, Aberdeen, Muswellbrook, Maitland, Mayfield, Lindfield, H.A. College.
Qld.: Brookstead.

- r.6.
- N.S.W.: Glen Innes, H.A. College, Lindfield, Badgery's Creek, Wingen, Robertson, Campbelltown, Lenmcal, Kurrajong, Singleton, Aberdeen, Muswellbrook, Maitland, Mayfield, Gravesend, Pallamallawa, Cherry Tree Hill, Gunnedah.
Qld.: Lawes, Brookstead.
- r.7.
- N.S.W.: H.A. College, Lindfield, Badgery's Creek, Wingen, Robertson, Taree, Kurrajong, Singleton, Maitland, Aberdeen, Muswellbrook, Mayfield.
Qld.: Brookstead.
- 1947.
- r.6.
- N.S.W.: Glen Innes, Parramatta, Fairfield, Castle Hill, Killara, Bringelly, Luddenham, Windsor, Taree, Castlereagh.
Qld.: Lawes.
- r.7.
- N.S.W.: Fairfield, Parramatta, Castle Hill, Windsor.
- r.102.
- N.S.W.: Parramatta, Castle Hill, Lindfield, Dundas, Sydney University, Killara.
- r.103.
- N.S.W.: Lindfield, Windsor.
- 1948.
- r.6.
- N.S.W.: Lindfield, Turramurra, Glen Innes, Bowral, Dundas, Murrurundi, Killara, Alstonville, Sydney University, H.A. College, Nowra, Grafton, Eumungerie, Curlewis.
Qld.: Biloela, Warwick, Lawes.
S.A.: Penola.
- r.7.
- N.S.W.: Glen Innes, Badgery's Creek, Lindfield, H.A. College, Sydney University.
Qld.: Biloela.
- r.9.
- Qld.: Warwick.
- r.102.
- N.S.W.: Glen Innes, Badgery's Creek, Lindfield, Turramurra, Killara, Nowra, Grafton, Eumungerie, Bowral.
Qld.: Lawes.
S.A.: Penola.
- 1949.
- r.1.
- N.S.W.: Castle Hill, Grafton, H.A. College.
- r.3.
- N.S.W.: Grafton, H.A. College.
N.Z.: Lincoln.
- r.6.
- N.S.W.: Castle Hill, Grafton, H.A. College, Glen Innes.
Qld.: Lawes, Yeerongpilly, Glenore Grove.
Tas.: King Island.
- r.7.
- N.S.W.: Grafton, H.A. College, Castle Hill.
- r.9.
- N.S.W.: Grafton.
- r.45.
- N.S.W.: Castle Hill.
- r.57.
- N.S.W.: H.A. College.
N.Z.: Lincoln.
- r.77.
- N.S.W.: H.A. College, Castle Hill.
- r.102.
- N.S.W.: Castle Hill, Grafton, H.A. College, Lindfield.
Qld.: Glenore Grove.
N.Z.: Lincoln.
- r.103.
- N.S.W.: Grafton, Castle Hill, H.A. College.

- 1950.
- r.1.*
- N.S.W.: Curlewis.
Qld.: Lawes.
- r.3.*
- N.Z.: Winchmore, Laghmor.
- r.6.*
- N.S.W.: Lindfield, Muswellbrook, Singleton, H.A. College, Castle Hill, Glenorie, North Marota, Penrith, Grafton, Kameruka, Aberdeen, Gunnedah, Stroud, Dunedoo, Armidale, Leeton, Bemboka, Glen Innes, Kurrajong, Gilgandra.
Qld.: Toowoomba, Biddeston, Lawes, Westbrook.
W.A.: Boyup Brook.
N.Z.: Winchmore, Laghmor, Orari.
Tas.: Kimberley, Sheffield.
- r.7.*
- N.S.W.: H.A. College, Lindfield, Kurrajong, Castle Hill, Gunnedah.
Qld.: Lawes.
N.Z.: Winchmore.
- r.40.*
- N.S.W.: H.A. College.
Qld.: Westbrook.
- r.45.*
- N.S.W.: Spring Terrace.
- r.57.*
- N.S.W.: Castle Hill.
- r.77.*
- N.S.W.: Singleton, Cootamundra.
- r.102.*
- N.S.W.: Curlewis, H.A. College, Lindfield, Grafton, Stroud.
Qld.: Toowoomba, Biddeston, Lawes, Pittsworth.
- r.103.*
- Qld.: Pittsworth.
- 1951.
- r.3.*
- N.S.W.: Kelso, Castle Hill, Narrabri.
- r.6.*
- N.S.W.: Kelso, Curlewis, Castle Hill, Tamworth, H.A. College, Coolamon, Aria Park, Lindfield, Blue Vale, Gunnedah, Tichborne, Goonumbra, Peak Hill, Grafton, Badgery's Creek, Maitland, Bodalla, Narrabri.
Qld.: Killarney, Ayr, Warwick, Lawes, Lawnton, Gympie.
S.A.: Waite.
Tas.: Elliott.
- r.7.*
- N.S.W.: H.A. College, Castle Hill, Blue Vale, Gunnedah, Curlewis, Tichborne, Lindfield, Peak Hill, Badgery's Creek, Bodalla.
Qld.: Lawnton.
- r.102.*
- N.S.W.: Kelso, Curlewis, Castle Hill, Tamworth, H.A. College, Boggabri, Lindfield, Blue Vale, Gunnedah, Tichborne, Peak Hill.
Qld.: Killarney, Lawnton, Ayr.
S.A.: Waite.
- r.103.*
- Qld.: Killarney.

On the basis of frequency of isolation and wideness of distribution, race 6 is the most important, occurring in 50% of the determinations. It is the only one of the races that has been present in each of the years during which tests have been made, and is also unique in that it has been found in each of the States of the Commonwealth as well as in New Zealand. Races 3 and 7 come next in importance in both time and space distributions. Only within the past five years have the last six races listed shown up. It has been striking to find so many cases in which the differential variety "Green Russian" has given the mixed susceptible and resistant reactions from which the particular two races have been sorted out. Although many of the races have been found infrequently, their occurrence is important: probably they show that mutation is going on all the time.

MIXTURES OF RACES.

It has been quite usual to find that a single collection of crown rust has yielded more than one race. To date there have been three instances in which four races were sorted out, these being respectively 1, 6, 7, and 57; 3, 6, 7, and 102; and 3, 7, 9, and 103. In 37 cases there was a mixture of three races: 11 of them comprised races 3, 6, and 40, the remainder being various combinations of 3. There were 144 collections in which two races were present: these occurred in varied combinations of which that of races 6 and 7 was the commonest. Details of the groupings are set out in Table 35.

TABLE 35.

*Frequency of Occurrence of Mixtures of Races
of P. coronata avenae on Oats.*

Frequency of Isolates.	Grouping of Races.
13	1 and 6
2	1 and 7
1	1 and 45
19	3 and 6
16	3 and 7
3	3 and 40
1	3 and 102
36	6 and 7
14	6 and 40
2	6 and 47
1	6 and 77
31	6 and 102
1	6 and 103
1	7 and 102
1	77 and 103
2	102 and 103
1	1, 3 and 7
1	1, 6 and 102
8	3, 6 and 7
11	3, 6 and 40
1	3, 6 and 57
1	3, 6 and 102
4	6, 7 and 102
9	6, 102 and 103
1	77, 102 and 103
1	1, 6, 7 and 57
1	3, 6, 7 and 102
1	3, 7, 9 and 103

There has been no significant correlation between the size of the collection (i.e., quantity of rusted material used) and the amount of mixing present. Throughout the groupings, the frequency of occurrence of race 6 is outstanding, but there is no evidence of its particular association with any other particular race or races.

At present nothing is known of the genetic constitution of any of the races. A considerable amount of work with the aecidial stage was planned but was held up by the paucity of germination of the teleutospores.

BREEDING RESULTS.

It will be noticed that the variety "Victoria" is resistant to all the recorded races and it has therefore been used as a parent in the crossing work. It is, of course, susceptible to the races of stem rust that are present in Australia. This has made it a valuable variety to use where stem rust has to be separated from crown rust in a collection. The extreme susceptibility of this variety to *Helminthosporium victoriae* in U.S.A. gives it a doubtful value as a parent here.

"Bond" was similarly used, but the discovery of races 45 and 57 in 1949 alters the situation. To date these races have turned up infrequently, but they must be regarded as potential sources of danger to "Bond" material. Apart from "Victoria" and "Bond" there are several other resistant 14- and 21-chromosome varieties available for use in the breeding programme. "Garry" from Canada is being used with promising results.

This variety has the greatly added value of being resistant to all the races of oat stem rust known here, and genetical studies show clearly the independent inheritance of resistance to the two types of rust. From back-cross material in which the commercial variety "Fulghum" has been used, selections combining resistances are available and are under study for agronomic characters.

LEAF RUST OF BARLEY.

Crops of barley in coastal areas commonly show attack by leaf rust, and this sometimes causes heavy damage. The occurrence of stem rust is referred to elsewhere in this paper where it is shown that it comprises various races of *P. graminis tritici*.

LIFE HISTORY.

Over many years, straw carrying teleutospores has been exposed to winter conditions in Tableland areas and has also been frozen in the refrigerator in order to break the dormancy of the spores. In no case have germinations been obtained. There is no record of the occurrence of the aecidial stage on *Ornithogalum* spp., although plants of *O. umbellatum* L. have been grown under observation. No common grass host of the rust has been found, and it would appear that it carries over from season to season on "volunteer" barley plants growing in favourable areas.

SPECIALIZATION.

Previous reference has been made to the occurrence of this rust in Australia (Waterhouse, 1927, 1929, 1933, 1936, 1938, 1939, and 1947). Comparisons with physiologic races described elsewhere were not given, but in 1936 (Waterhouse, 1936) it was indicated that the rust was different from that described by Mains (Mains, 1930).

Seed of the differential varieties used by d'Oliveira was made available in 1944 and has been used in recent tests. Isolates studied came from the following areas between 1944 and 1950:

New South Wales	9 localities
Queensland	2 ..
Western Australia	1 ..
New Zealand	1 ..

In all cases they conformed to the reactions recorded for race 3 (d'Oliveira, 1939). There were minor departures from the recorded reactions in some instances, but these did not alter the race designation. Temperature variations were probably responsible for the differences. Relatively low temperatures are essential for race determinations of *P. hordei* Otth.

Varietal resistance has been determined in a large number of barley varieties. Detailed work is now being carried forward by Drs. I. A. Watson and E. P. Baker, but it is not without interest to record that crosses already studied have shown simple inheritance of the factor for leaf rust resistance.

An unusual happening was found in a cross between "Kinver" and "Portuguese". The F1 plants were normal, but in the F2 there were two grass clump plants in a population of 157 individuals derived from a single F1 plant (Plate ix).

The occurrence of grass clumps has been extensively studied in wheat (McMillan, 1937), and is well known in rye and oats. In several other barley crosses, plants appeared in the F2 resembling grass clumps at an early stage, but later these were found to be smutted plants which were dwarfed by the disease. Genetical studies to determine the mode of inheritance of the grass clump character were not possible at the time, and nothing is known of the genic relationships.

Other unusual findings in the work have been the occurrence of albinos and chlorophyll-deficient plants, together with plants showing longitudinal striping of the leaves, in parent material carried forward as single plant progenies as well as in segregating generations of crossbred material. Whilst the albinos could not be tested further, the chlorophyll-deficient selections from parent material bred true for their particular character and were therefore classed as mutations, but the striped plants produced normal green progeny.

LEAF RUST OF RYE.

Rye is not extensively cultivated, but crops in very widely dispersed areas commonly show leaf rust infection. It is heaviest in coastal areas. Unless care is exercised, this rust on the sheaths and sometimes on the nodal areas of the stems can be mistaken for stem rust. The latter, as set out elsewhere in this paper, is not *P. graminis secalis*, but is one or other of the races of *P. graminis tritici* that occur in Australia.

LIFE HISTORY.

Numerous efforts to get teleutospores of *P. dispersa* E. & H. to germinate have failed, and there are no records of the occurrence of the aecidial stage on *Lycopsis* spp., although thanks to the help of Mr. W. Hartley of the C.S.I.R.O. at Canberra, plants of *L. arvensis* have been grown and kept under observation.

In no case have common grasses been found to serve as hosts of the rust, and it would appear that it persists in the uredospore stage on self-sown or "volunteer" rye in between cropping seasons. A culture of *Secale montanum* Guss. with a perennial habit obtained from U.S.A. has been completely resistant.

SPECIALIZATION.

It is by no means uncommon to find on the same leaf of a rye plant both resistant and susceptible pustules: the former vary from "flecks" to the reaction styled "2". Sometimes one plant in a varietal row shows resistance whilst the others are susceptible. From resistant reactions, cultures have been sorted out and built up on rye seedlings for further study. Frequently selfed grain of the "mother" plant has been obtained by early bagging of ears, but in no case has it been possible to maintain satisfactory self-fertile families as leaf rust differentials. Open-pollinated material has been of no use.

One of these leaf rust resistant families was maintained for 10 generations of selfing during which the few seedlings obtained consistently gave the expected resistant "fleck" reaction with a stock culture after the G4, but in no generation was the grain supply sufficient for the testing of unknown isolates, and the family finally petered out.

It was possible, however, to use this family in crossing, and the genetical studies using the stock culture showed that there was simple inheritance of a dominant factor for leaf rust resistance.

A number of other characters of a morphological nature also came up for study, including chlorophyll-deficiencies and grass clumps.

Use was made of an extensive series of selfed ryes which have been inbred for 20 generations with continuous testing for their behaviour to races of *P. graminis tritici*. Many are still highly self-fertile, and their reactions to the rusts have been consistent. When tested with isolates of *P. dispersa*, however, all showed complete susceptibility.

Numerous named varieties of rye were similarly tested. Most gave susceptible reactions, but in others there was a mixture of resistance and susceptibility. Attempts to derive supplies of fertile selfed material from this source have also failed.

All that can be said at present, therefore, is that there is clear evidence that physiologic races of the rust do occur, but that their identity has not yet been determined.

CONCLUSION.

From the foregoing it is clear that there are still a number of outstanding problems which require attention. The following are some of the main ones.

Life history studies should include, in the uredospore stage, such questions as that of latent infection. The factors which influence spore germination in the teleutospore stage are not fully understood. At present germination is sporadic, and control of germinability is essential in much of the work.

The survey of rust flora should be continued and expanded. A much more complete knowledge of the specialization of the pathogen in regard to time and space is needed for success in carrying out breeding programmes, as well as for giving fundamental information on the biology of the organisms.

Studies of the genetics of the races and biotypes that have been sorted out are also needed for the two purposes just mentioned. This work will involve control of teleuto-

spore germination and further determinations of variations in susceptibility of species of *Berberis*. Apart from these studies which deal with the aecidial stage, more work is needed on the behaviour of the uredo mycelium where somatic variation may occur.

The origin and production of mutations deserve the fullest study. Experiments with ultraviolet light and various radiations on germinating uredospores would seem to offer prospects of success, but all stages in the development of the pathogen should be studied.

Most outstanding is the basic problem of what constitutes resistance in the host-parasite relationship. Some of the facets of this problem have been referred to, but there are many others. Those which have been clearly delimited already and which call for the highest quality biochemical work should be tackled immediately. Many of the other problems will be solved when we have a full knowledge of what really constitutes resistance.

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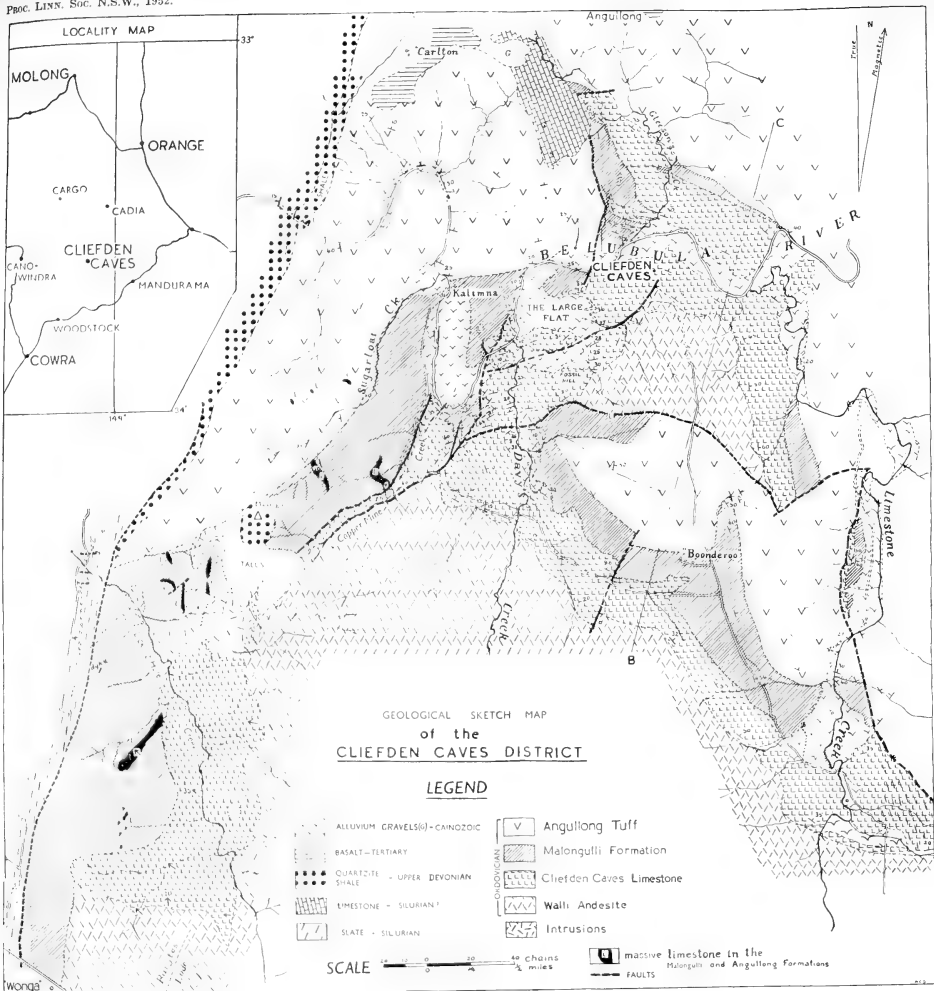
EXPLANATION OF PLATE IX.

Typical barley grass clump in F2 rows of (Kinver × Portuguese).
(The card alongside the plant measures 5 × 3 inches.)

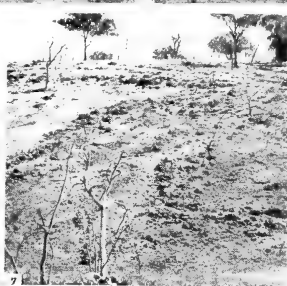
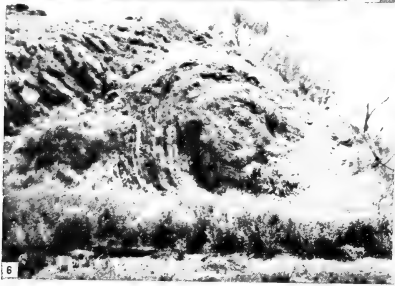
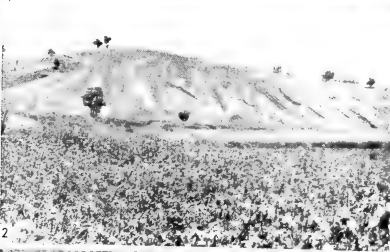
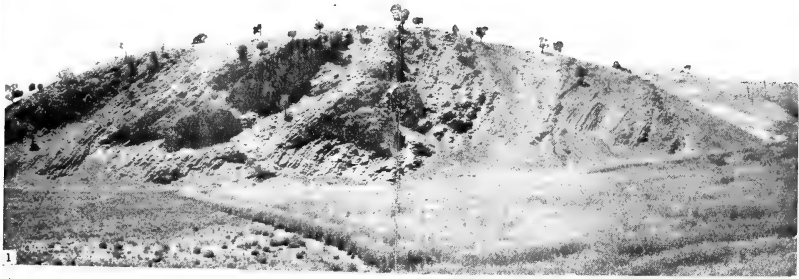


Ernest Clayton Andrews.

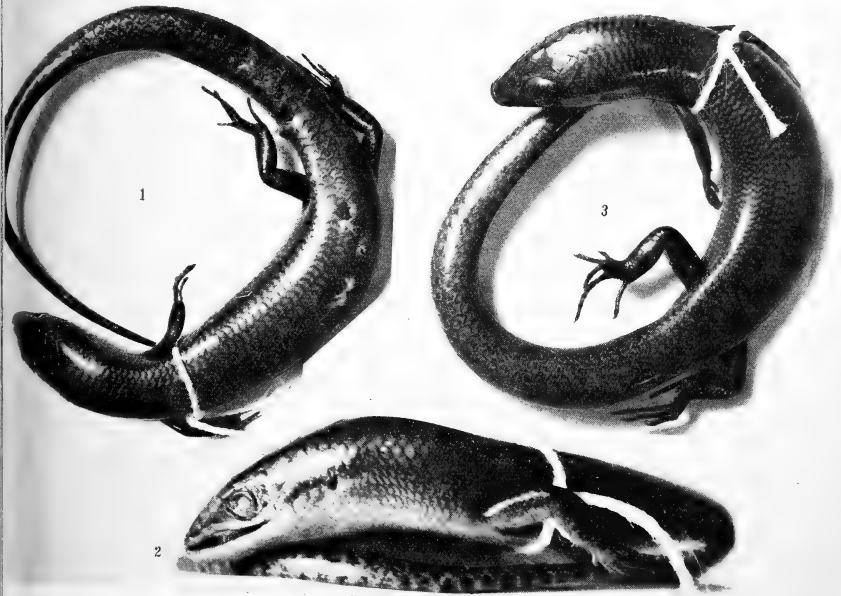






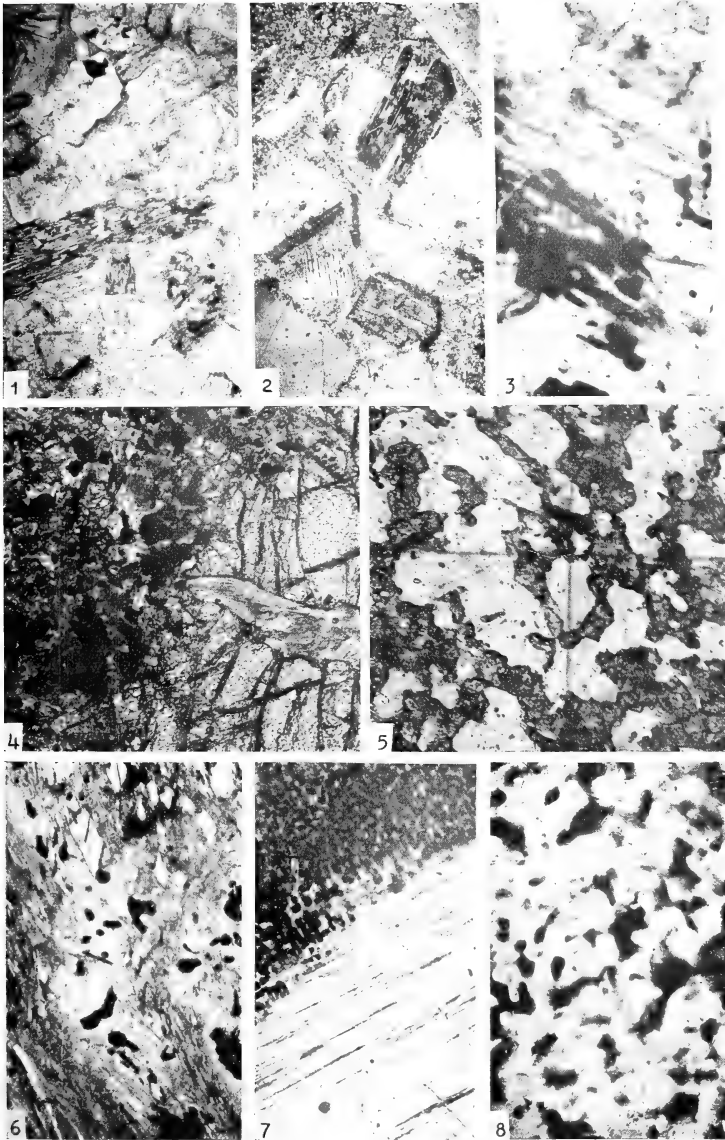


Ordovician stratigraphy at Cliefden Caves.

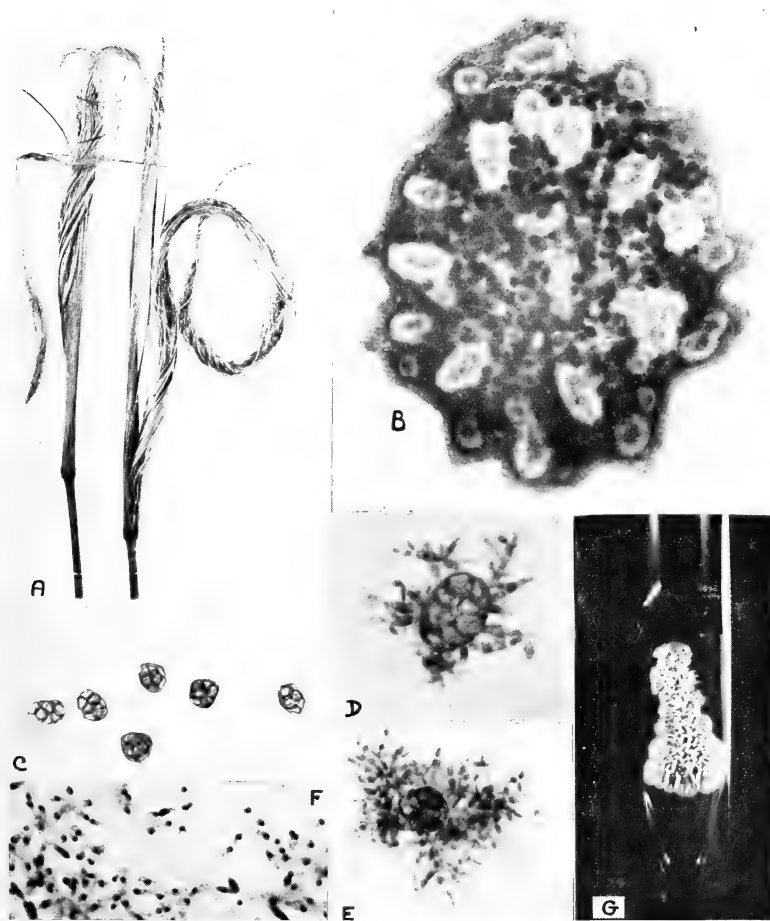


Ablepharus davisi, n. sp.

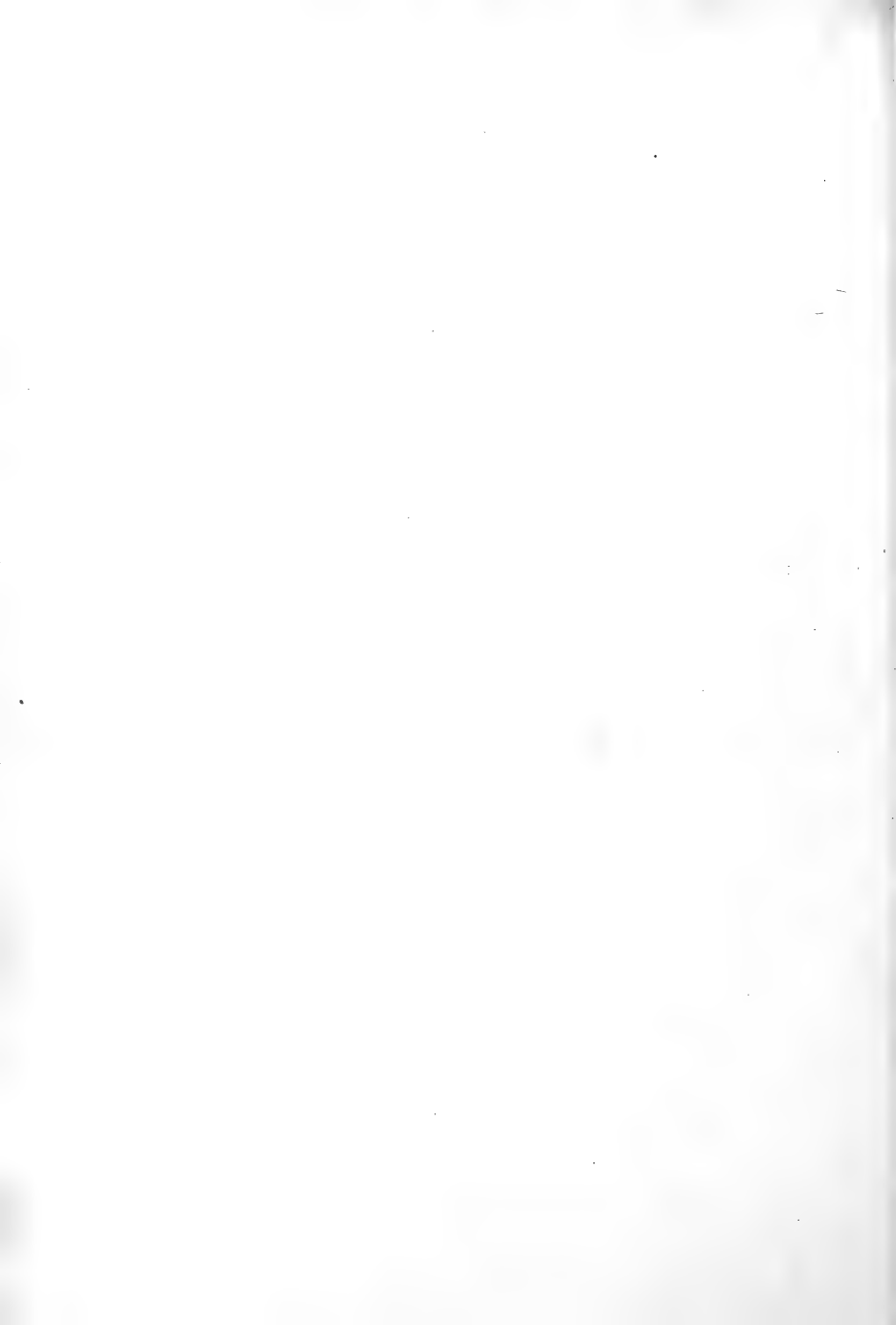




Rocks from Cowra Intrusion and Associated Xenoliths.



Ropy Smut of Liverpool Plains Grass.





Barley Grass Clump in F2 Rows of (Kinver \times Portuguese).

A CORALLANID ISOPOD PARASITIC ON FRESHWATER PRAWNS IN
QUEENSLAND.

By E. F. RIEK.

(Seven Text-figures.)

[Read 24th September, 1952.]

Synopsis.

A new genus and species of Corallanid isopod, *Austroargathona caridophaga*, parasitic on freshwater prawns of the families Palaemonidae and Atyidae in Queensland, is described.

The species described in this paper was collected from a number of localities in Queensland and from several species of prawns, mostly belonging to the family Palaemonidae, but in one case to the family Atyidae. Only the one species of isopod has been recognized with a range from south-east Queensland to the Burdekin River of north Queensland. The parasites are clearly visible externally on the cephalothorax of the host and can be collected readily, for they remain attached to the host until it is removed from the water. The main difficulty is to catch the observed prawn bearing a parasite. Even when the prawn is greatly disturbed the parasite remains attached.

The species is described in a new genus of the family Corallanidae.

Family CORALLANIDAE.

Like other members of the family, the new species described here is able to leave its host and live a free existence for some period.

Genus AUSTROARGATHONA NOV.

Genotype, *Austroargathona caridophaga*, sp. nov.

Peraeon and pleon compact, not relaxed; anterior margin of the cephalon with a small, median process which does not separate the basal segments of the first antennae; flagellum of the first antenna composed of numerous segments and the basal two-segmented peduncle expanded; frontal lamina moderately large; maxilliped with only a three-segmented palp; first maxilla with outer plate slender and styliform, apex furnished only with a single, stout unguis, inner plate short and rounded; second maxilla short and broad, with a single, unarmed apical lobe; mandible without a greatly expanded cutting edge; mandibular palp well developed, basal segment elongated, about half the length of the second; anterior three pairs of legs with the propodus simple, not expanded, dactylus strongly curved, apex pointed.

In external appearance the genus resembles many species of *Aega*, particularly as it has a very broadly expanded peduncle to the first antenna, but the mouthparts are quite distinctive. It shows marked sexual dimorphism in the maxilliped and in female specimens the marsupial plates cover the mouthparts.

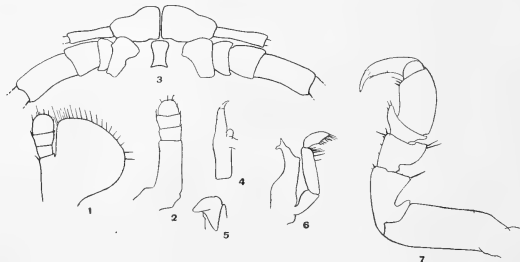
The genus approaches most closely to *Argathona* and *Alcirona* but differs most in the structure of the first maxilla and of the maxilliped. It differs from *Exocorallana* in the structure of the maxilliped and of the second maxilla. The apex of the outer lobe of the first maxilla is similar to that in *Exocorallana* and *Lanocira*.

AUSTROARGATHONA CARIDOPHAGA, sp. NOV.

(Figures 1-7.)

Female.—Form narrowly oval, almost three times longer than greatest width; surface with scattered punctures, rather difficult to see because of the colour-pattern; cephalon about two times wider than medial length, with a slight median triangular process which is not bent downwards to meet the frontal lamina; eyes rather small, rounded, widely separated; peduncle of the first antenna as long as the first three articles of the peduncle of the second antenna, peduncle only two-segmented, first article

large, subquadrate, flattened from above anteriorly and with the anterior border strongly upturned, inner margins of the first article touching, together forming the rounded anterior margin of the head, second article long and thin, as long as the first article, slightly expanded towards the apex; first antenna short, not reaching to the end of the peduncle of the second antenna, flagellum as long as peduncle, with seven or eight segments but the apical one minute, segments decreasing regularly in size; second antenna reaching slightly beyond the posterior margin of the fourth peraeon segment, first two articles of the peduncle short, third subquadrate, fourth and fifth long, twice third, with the fifth slightly the longer, flagellum considerably longer than peduncle, composed of seventeen to twenty-one articles and a terminal style; frontal lamina in ventral view twice as long as greatest width, postero-lateral margins converging, anterior and posterior margins truncate; first article of the mandibular palp about half second and somewhat longer than third, setae on outer margin of apical segment and apex of second; mandible without a well developed cutting edge, apex produced into an acute, stout spine; first maxilla with outer lobe tapering to the acute, slightly curved, terminal unguis, inner lobe small and with rounded apex; second maxilla small, with a



Figures 1-7. *Austroargathona caridophaga*, gen. et sp. nov.

1, Maxilliped of holotype female; 2, Maxilliped of allotype male; 3, Ventral view of bases of first and second antennae; 4, First maxilla; 5, Second maxilla; 6, Mandible; 7, First peripod. (Figures 3-7 from a paratype non-ovigerous female.) All figures $\times 30$.

single, laterally expanded, apical lobe; basipodite of the maxilliped with a greatly expanded, fan-shaped, basal lobe, extending almost as far distally as the palp, its outer margin rounded, inner margin adjoining the palp almost straight, apex bordered with a row of long setae, palp with three distinct segments, subquadrate, the second a little wider than long, third with apex rounded and with a few scattered setae, mesial apical margin of basipodite, first and second segments of palp and lateral apical margin of second segment with a short seta; first peraeon segment embracing sides of cephalon, a little longer than succeeding segments, which are subequal except for the slightly smaller seventh; coxal plates each with an oblique carina in addition to the lateral carina, particularly strong on the sixth and seventh segments, plates of second and third segments obtusely rounded posteriorly, not reaching beyond the posterior margins of their segments, in succeeding segments posterior margin increasingly acute and extending beyond posterior margins of their segments, those of last segment reaching slightly beyond postero-lateral angle of the third pleon segment; pleon not abruptly much narrower than peraeon, first segment almost wholly concealed beneath the last peraeon segment, only a small median area being visible or wholly concealed depending on the state of preservation, at least lateral portion of second segment concealed, third and fourth subequal in length, median length of fifth slightly greater than that of fourth, lateral parts of third and fourth segments large, particularly fourth, each produced into an acute postero-lateral spine; telsonic segment slightly wider than long, lateral margins almost straight, a little convex, converging to the rounded, though subtruncate, apex which is crenulated and furnished with seven or eight short spines

and short hairs; inner process of protopod of uropods reaching to two-thirds the length of the endopod; endopod extends slightly beyond the end of the telson, twice as wide as exopod, with apex subtruncate, outer margin with three or four, apex with six or seven short spines and plumose hairs; exopod with apex entire, rounded, outer margin with six or seven, inner margin with two to four longer, sharp spines and plumose hairs; periopods rather slender, bases of seventh pair not greatly expanded; first pair with curved, tapering dactylus ending in an acute unguis, propodus not expanded, with three stout and one longer finer apical spines on the inner margin, carpus short, produced somewhat on the mesial side almost to the middle of the propodus and with four spines at the apex of the projection, merus expanded somewhat over the outer distal margin, with a spine at the outer apex and four or five on the mesial margin, ischium expanding to the apex, with a spine on both the mesial and lateral apices; spines somewhat variable, more pronounced on the similarly constructed second and third periopods; outer surfaces of the first three pairs of periopods almost smooth; seventh periopods with spines on the distal margins of the ischium, merus, carpus and propodus and a few on the inner margins, merus equal to ischium and about two-thirds the carpus.

Male.—Differs from the female mainly in the structure of the maxilliped and in this respect is similar to non-ovigerous females. Basipodite of maxilliped without an expanded lobe at the base, elongate, longer than the palp, palp three-segmented, first and second segments wider than long, third almost as long as wide, apex rounded and bearing a few scattered, simple spines, a single spine at the outer apex of the basipodite, first and second segments and the inner apex of the second. The spines at the apex may show a slight hooking. Male appendage of the second pleopod long, hair-like, considerably longer than the endopod.

Colour.—Mottled brown-black with the peraeon bearing five irregular longitudinal bands, the median band being much the widest and dividing at the posterior border; pleon with dark median longitudinal band and dark lateral margins but area between mostly light, with only slight mottlings; telson with four darkened bands and, so, light at the meson and with a light area on each side laterad; head nearly all dark, light mesially to eye.

Length up to 19 mm., but generally between 10 and 12 mm.

Types.—Holotype ovigerous ♀, allotype ♂ and a long series of paratypes in the Australian Museum Collection.

Type Locality.—Enoggera Creek, Brisbane.

Distribution.—Coastal Queensland: Enoggera Creek, Brisbane (18 Apr. 1943 and 9 Oct. 1943, E. F. Riek); Enoggera Reservoir (29 May 1943, E. F. Riek); Mary River, Conondale (26 Apr. 1943, E. F. Riek); Burdekin River at Macrossan (June 1943 and Oct. 1943, E. F. Riek); Waraba Creek, Caboolture (6 June 1943, E. F. Riek); 20 miles S.W. of Ayr (5 Oct. 1950, E. F. Riek).

Hosts.—The specimens were collected as ectoparasites of freshwater prawns of the genera *Macrobrachium* and *Paratya*. Only at Caboolture were specimens taken from *Paratya*. In all other cases they were found on species of *Macrobrachium*.

Specimens of this species normally attach themselves to the cephalothorax of the host prawn and only when strongly disturbed do they detach themselves. Almost invariably they returned to a host rather than settle on rocks and other material on the stream bed. The only ovigerous female was collected crawling over a decaying, submerged log near the water's edge and not from a host.

Both the host and the freshwater habitat are abnormal for this family of Isopods. The particular species of host prawns do not migrate to salt water but are entirely restricted to fresh water and breed there.

A NOTE ON THE UNUSUAL LONGEVITY OF *CIBORIA AESTIVALIS* (WINT.) REHM.

By W. L. WATERHOUSE, The University of Sydney.

(Plate x, fig. 1.)

[Read 24th September, 1952.]

Harrison (1935)* recorded the occurrence in Australia of a fungus associated with *Sclerotinia fructicola* (Wint.) Rehm. to which the name *Ciboria aestivalis* (Pollock) Whetzel was given. He called attention to the capacity of the fungus to produce successive crops of apothecia over a lengthy period.

Mummified quinces and peaches collected in late 1921 and early 1922 were almost completely buried in rich garden soil contained in a 12-inch earthenware saucer 2 inches deep, and maintained on the laboratory bench at the University of Sydney under a glass cover. From time to time (usually about three times each year) the saucer was thoroughly wetted and the cover then replaced. After an interval of three to four weeks, apothecia developed and were used for class work to demonstrate dispersal of clouds of ascospores when the cover was lifted. The saucer of material was then allowed to dry out and the cover replaced. In no case were apothecia of *S. fructicola* formed, although it is known that this was originally present in the mummified fruit.

Throughout the years the apothecial development decreased and finally ceased. The last formation was of a solitary apothecium (Plate x, fig. 1) produced in November, 1942. From it a typical culture was obtained by inverting a dish of potato dextrose agar over its spore discharge.

The capacity to produce continuous crops of apothecia over a period of 20 years shows that this fungus may remain viable in the soil under some conditions for a much longer period than is generally supposed, and is worthy of record.

For carrying on the class work it has been found that a very satisfactory procedure is to inoculate pieces of sterile young maize cob on wet cotton wool in test tubes, and after two to three months, during which the maize became a blackened mycelial mass, to place these in rich garden soil in saucers as was done with the original material.

The culture originally isolated in 1922 has since been maintained on potato dextrose agar by mycelial transfers.

PLATE X, fig. 1.

The last formed of the apothecia of *Ciboria aestivalis* growing amongst a mass of moss in the saucer. $\times 3.2$.

* HARRISON, T. H., 1935.—Brown rot of fruits and associated diseases in Australia. *Mycologia*, xxvii: 302-313.

A NOTE ON AN UNUSUAL SPORE FORM IN *Puccinia Malvacearum* BERT.

By W. L. WATERHOUSE, The University of Sydney.

(Plate x, fig. 2.)

[Read 24th September, 1952.]

Puccinia malvacearum Bert., the cause of rust on hollyhocks and numerous plants in the family Malvaceae, is world-wide in its distribution.

Much work has been done on the rust in Europe and U.S.A. It is described as producing teleutospores only in its life history. Arthur (1934)* states, "Pycina unknown, probably not formed."

In class work the rust has been constantly used, both for studies of living and fixed material. In the latter, stained microtome sections of a rusted leaf of *Malva rotundifolia* L. which had been collected in the University grounds in 1937 showed the formation of a spermogonium on the upper surface of a teleutosorus (Plate x, fig. 2). At once a search was made for other occurrences, but without success. Much material has been examined in more recent times, but teleutosori only have been found.

In the case in point, which was shown to the late Professor F. T. Brooks, F.R.S., during his visit in 1939, the same mycelium can be seen to be producing the two spore forms. The fact that it was fixed made it impossible to carry out any cultural studies to determine the significance of the spermogonial formation.

PLATE X, fig. 2.

Section through leaf of *Malva rotundifolia* showing formation of spermogonium above a teleutosorus. $\times 200$.

* ARTHUR, J. C., 1934.—Manual of the rusts in the United States and Canada. Purdue Research Foundation, Lafayette, Ind., 438 pp.

A NOTE ON THE OCCURRENCE OF AN UNDESCRIBED RUST ON
CRYPTOSTEMMA CALENDULACEUM (L.) R. BR.

By W. L. WATERHOUSE, The University of Sydney.

(Plate x, figs. 3, 4.)

[Read 24th September, 1952.]

On each of three occasions, viz., in July, 1937, April, 1939, and August, 1941, a plant of *Cryptostemma calendulaceum* (L.) R. Br. was found in waste land in the Sydney metropolitan area showing rust on the leaves. In each case, careful search revealed that they were the only individuals showing infection amongst some hundreds of plants. An examination of various other species of plants in the neighbourhood failed to reveal the presence of any other rust in any stage of development. In other years no rusted plants have been found although searches have been made.

The first two collections showed only aecidia, but in the third, spermogonia were also present, intermingled with aecidia.

Detailed examinations gave the following results:

Spermogonia epiphyllous, usually occurring singly but sometimes in swollen areas, pale yellow, 1 to 3 mm. in diameter. Spermogonia subspherical, about 100μ in diameter (Plate x, fig. 3).

Aecidia amphigenous but mainly epiphyllous, solitary or grouped in swollen yellowish areas up to 6 mm. in diameter. Peridium pale with a recurved margin. Peridial cells, somewhat rhomboidal in section, 12 to 20μ across (Plate x, fig. 4). Aecidiospores globoid or ellipsoidal with a thin colourless wall about 1μ thick and finely verrucose. Measurements of 100 spores taken at random gave a mean length of $16.8 \pm 0.2\mu$ with a range of 11–21 μ , and a breadth of $14.4 \pm 0.1\mu$ with a range of 10–17 μ .

Viable aecidiospores were used to inoculate leaves of the infected plants, which had been transplanted to pots, as well as a series of seedlings taken at random, but in no instance were infections obtained. Cineraria seedling inoculations also gave negative results.

Inquiries made at the Commonwealth Mycological Institute revealed that no rust on *Cryptostemma calendulaceum* had been recorded there. Similar inquiries sent direct to South Africa, where the plant is indigenous, brought the same reply.

The name *Aecidium cryptostemmatis* is proposed for the rust. Further investigations may reveal its full life history.

PLATE x, figs. 3, 4.

Sections of leaf of *Cryptostemma calendulaceum* showing a typical spermogonium and aecidium. $\times 200$.

STUDY OF SOIL ALGAE.

I. FLUORESCENCE MICROSCOPY FOR THE STUDY OF SOIL ALGAE.

By Y. T. TCHAN,

Macleay Bacteriologist to the Society.

[Read 24th September, 1952.]

Synopsis.

A new fluorescence microscopy technique for the estimation of soil algal population is proposed. A critical examination of the technique shows the advantages of the method over the classical dilution culture technique, and the limits of its possibilities are discussed.

Although the existence of an abundant soil algae flora has been recognized for many years, very few quantitative data on soil algae populations are available, even for soils in which the algal flora is known to be of great economic importance. This paucity of data is ascribed to the lack of an accurate and rapid technique for measuring algal populations.

In the account that follows, a new and rapid technique for the quantitative estimation of algae in the soil, based on the fluorescence of chlorophyll is described. The writer considers that the technique outlined below will provide a valuable tool for the study of algal floras, not only from the academic standpoint, but also from the economic, e.g., in rice fields and irrigated areas^{(1) (4) (6) (8) (17)} which are becoming an increasingly important section in agriculture.

The application of fluorescence microscopy to biology is not new. J. Levaditi⁽¹⁰⁾ gave a good idea of its importance in his review and in 1948 Struger⁽²⁰⁾ described the Orange-acridin to render bacteria visible under fluorescence microscopy. His technique, however, cannot be applied to soil algae because soil particles absorb the dye and can be confused with algae.

The technique described below uses the natural fluorescence of the chlorophylls to detect the soil algae. No dye is needed. The fluorescent algal cells are readily visible as red or orange-red images, according to the presence of associated pigments, against the dark background.

EQUIPMENT.

Light Source: An intense light source is required, and for critical work a special fluorescence lamp or arc lamp is necessary. For ordinary work, however, a low voltage lamp (6-12 volts) slightly overrun is satisfactory. A high aperture condenser lens is used to form a parallel beam. The frosted type of condenser must be rejected. The light is passed through a liquid filter made with CuSO_4 in aqueous ammonia according to the formula given by Augier.⁽²⁾ To prevent the blue light entering the observer's eye, a yellow filter is used. (Ilford delta, Wratten, Zeiss stop filter, or Augier's liquid filter⁽³⁾ are very satisfactory.)

Ordinary microscopes can be used if the condenser has an aperture of at least N.A.-1.2. Aperture of N.A.-1.4 is more desirable. An objective lens of 10 times magnification is used for routine work. Higher power lenses, including immersion lenses, can be used. The eyepiece should be of low magnification. For most routine work a 5 \times eyepiece is satisfactory. The high absorption of light in the prism system makes the binocular microscope unsuitable.

The Counting Chamber used is of hemacytometer type and can be made easily by sticking 2 cover slips (No. 0) with balsam on the surface of an ordinary microscope slide

about 1 cm. apart, but the thickness of the slide should not exceed 2 mm. (Since the cover slips are not uniform in thickness, it is necessary to select two of the same thickness, about 0.1 mm. or slightly less.) Once the balsam is dried the depth of the chamber is determined by a micrometer and verified with a suspension of blood cells or yeasts against a hemacytometer. It is necessary to know the depth of the counting chamber so the volume can be calculated.

PREPARATION OF SOIL SUSPENSION.

Winogradsky⁽⁴⁷⁾ used fractional centrifugation for his direct microscopy. As the counting chamber has a depth of only 0.1 mm., it is better to avoid sand grains in the suspension. Twenty gr. of soil is washed with 50 c.c. lots of water. After each washing, the sand deposit is examined under the fluorescence microscope. Three or four washings are necessary to obtain a sand practically free of algal cells. The water from different washings is collected in a measuring cylinder. The volume is made up to 200 c.c. After 20 minutes of shaking the cylinder is allowed to stand for five minutes. From different levels of the cylinder samples are taken and examined. Most of the algal cells are sedimented with the soil particles. Only a few still remain in suspension. Hand centrifugation for one minute brings all algal cells to the bottom. The algae can be concentrated in a soil suspension in this way. This is quite useful for soils of low algal population and for water samples. The suitable suspension for most soils examined by us is one part of soil for 5 to 10 parts of water. At higher concentrations the soil particles are too dense.

METHOD.

Focus the condenser of the lamp to produce a parallel beam and place the blue filter between the light and the microscope. Adjust the mirror of the substage condenser, then introduce a drop of soil suspension into the counting chamber. A drop of liquid paraffin is used to connect the slide with the condenser of the microscope so that the maximum aperture of the optical system is fully used. The light intensity is cut down by a neutral filter or by reducing the lamp voltage. Focus the microscope on the soil particles. Remove the eyepiece and the neutral filters. Increase the lamp voltage to produce the maximum light intensity. Adjust the mirror of the microscope carefully until a maximum intensity of light can be seen through the objective lens. Replace the eyepiece with the yellow filter. Focus the microscope on the red fluorescent spot and carefully adjust the mirror until the maximum fluorescent light is obtained. The microscope is then ready for use. Algal cells appear as red spots or lines.

Using a 10 \times objective lens and a 5 \times eyepiece count algal cells in 50 fields. If the soil suspension has a very low number of algae, count the total surface of the counting chamber, which has a definite area determined by direct measurement.

As we know the depth of the counting chamber we can calculate the number of algae per gr. of soil.

Effect of Fixatives.

The aim in studying fixatives is to preserve samples for future studies. The fixative also kills the algal cells and motile forms can be more easily counted. The classical fixatives with or without Cu_2SO_4 are not suitable as the fluorescence disappears quickly. Zinc fixatives preserve the fluorescence to some degree but it still fades significantly.⁽⁴⁸⁾ The fluorescence is preserved after heating.⁽⁴⁹⁾ Satisfactory results can be obtained by subjecting the samples to low temperature, which allows the cells to remain apparently unchanged but prevents them dividing. The value of hot and cold treatments in preventing changes in the number of algae is shown by the following experiments.

A suspension of soil containing algae was divided into three portions. Direct counting gave 180 cells per 20 fields. The first portion was kept at room temperature; the second in the refrigerator, and the third heated in boiling water. Counting at regular intervals showed that the number in the first portion had diminished slightly,

the second had a constant number of algae, and the third showed a significant loss of fluorescent cells, as seen in the table below:

	Room Temperature.	Refrigerator.	Heated at 100°.
0 hours	180	180	180
1 hour	182	178	179
3 hours	169	184	—
24 hours	152	172	87
48 hours	140	176	50
7 days	172	180	10

After seven days the first sample nearly regained the initial number. This could be due to the possible multiplication of algal cells at room temperature, especially since it was not kept in the dark. For routine work, we can use the refrigerator for storing samples.

Interference due to Other Plants and Resting Forms of Algae.

Few other types of plant are likely to be confused with algae. Moss protonemata are the main difficulty; these cannot be distinguished from filamentous algae under the fluorescence microscope. However, it can be converted into a light microscope in a few seconds, when careful examination can then distinguish the two types of filament. Confusion from the gemmae of liverworts can be similarly excluded.

The resting stages of algae introduce some difficulties. Certain cells do not fluoresce in the resting form (*Hematococcus*)* while others do. Fluorescence microscopy can only detect cells still containing chlorophyll.

Most works on soil algae deal with the morphology, cytology, taxonomy, and physiology. Very few papers are concerned with algal population in soils. A convenient historical review is given by Petersen.⁽¹²⁾ Real progress was made when the culture technique was introduced, but we still know little about the soil algal populations. Demolon in 1944⁽⁵⁾ stated: "Leur étude encore au stade floristique a permis d'en caractériser plusieurs centaines d'espèces; quant à leur nombre, il est régi par des circonstances inconnues." The culture technique was not the real answer for the study of soil algal population. Smith,⁽¹⁰⁾ when discussing the isolation of single cells by micro-manipulation, referred to the difficulties and wrote: "The problem is not so much a matter of picking out the individual organisms as it is one of finding a suitable nutrient medium once they have been picked out."

The biphasic or soil-water culture described by Pringsheim⁽¹⁴⁾ seems to be the best for the culture of soil algae. Still, according to Pringsheim, some algae refuse to grow on these semi-natural media. Even using a great number of different media, we cannot assume that all species will grow. The data obtained with the artificial media may not represent the real population of soil algae for the following reasons: firstly, the cells living heterotrophically in the soil may develop chlorophyll in the artificial media; secondly, the artificial media may be selective for certain species.

A further disadvantage of the culture technique is the slow growth of algal colonies which involves delays of up to two or three months. Van Overeem⁽²⁰⁾ has reported that some aero-plankton algae took six months to give a visible colony. Filamentous and colonial algae introduce further difficulties. A single filament or colony can give one or many colonies according to the number of viable pieces formed from it during dispersion. This is particularly true with Cyanophyceae.⁽¹²⁾ The tough mucous sheaths of these algae withstand shaking, so that the cells do not separate readily during dispersion. The time of shaking the sample of soil in the water is important in culture techniques; according to Petersen⁽¹²⁾ shaking of twenty minutes gives a maximum number of colonies, prolonged shaking even reduced the number.

Furthermore, in a mixed culture the fast-growing species may crowd out slow-growing species. This can be avoided by high dilution when the number of slow-growing species is higher than or at least equal in number to the fast-growing algae.

* Tisher, J., 1937: Happe-Seyler's Zeitsch. Physiol. Chemie, 250: 147.—According to Tisher a small amount of chlorophyll may still be present in the red form of *Hematococcus*.

On solid media (agar or silicagel) the Chlorophyceae may form zoospores which may spread and form new colonies. It may then be difficult to decide whether a colony is of primary or secondary origin. In addition, the growth of fungi may destroy the culture on solid media, especially when organic matter is added.

It therefore follows that the numbers of soil algae estimated by the dilution technique cannot be regarded as absolutely reliable. If the culture technique has given useful information they may not have an absolute ecological significance. The same problem has been discussed for soil bacteria⁽¹³⁾ and soil fungi.⁽⁶⁾ Only direct microscopy can resolve these difficulties.

Recent direct microscopic techniques introduced by Struger,⁽²⁰⁾ Jones and Mollison,⁽⁹⁾⁽¹³⁾ Manninger and Vamos,⁽¹¹⁾ Vamos,⁽²⁵⁾ and Tchan⁽²¹⁾ deal with bacteria, fungi, and protozoa. No special attention is paid to the soil algae.

Counting algal cells under the microscope does not involve the use of an artificial medium. Therefore, all selection is avoided. If some filamentous or colonial algae are not broken down to single elements during the dispersion of soil in water, direct microscopy would count all the associated cells. Direct microscopy seems very attractive, but has some practical difficulties. The principle of direct microscopy consists in rendering visible the soil microorganisms suspended in water or in agar⁽¹³⁾⁽⁹⁾ by staining on a slide. Since some soils have only a few thousand algae per gramme, many microscopic fields under high power must be counted. For example, using a modified Chalodny's technique Verplanck⁽²⁴⁾ reported 3,700 to 10,000 algal cells per gramme of soil. On the other hand, Petersen⁽¹²⁾ used direct microscopy only for soils showing a macroscopic growth of algae. Their techniques were quite complicated and not suitable for routine work.

Quispel⁽¹⁶⁾ used a plastic film technique, but this is limited to the investigation of the vegetation on the surface of soil, rock, or water. In all existing counting techniques, the low power lens cannot be used because some unicellular algae are too small to be easily detected, especially when intimately associated with soil particles. These difficulties are overcome by the new fluorescence technique proposed here.

The use of fluorescence microscopy for the examination of algal populations in soils has, to the best of my knowledge, not been reported before. The technique proposed is simple, rapid, and easy to use. Although the technique, like the dilution method, does not discriminate between active and certain resting forms of algae, it has the advantage of being rapid and of excluding the non-photosynthetic forms. The long waiting period for the growth of algae is eliminated. It has been established that an inexperienced person can count 8 to 10 samples per day. It is also possible to study the daily variation of algal numbers in the soil. No expensive apparatus is involved because most of the accessories can be made in the laboratory.

The interference by moss protonomena and liverworts can be avoided. Even if we do count them by mistake, functionally they resemble algae. Especially when we compare the soil to a living organism⁽¹³⁾⁽²¹⁾ the anabolic activities are caused by autotrophic organisms.

As chlorophyll alone is visible under the fluorescence microscope, the morphology and taxonomy of the algae cannot be studied. As the fluorescence can be converted into an ordinary light microscope, the morphology and taxonomy can be studied separately.*

SUMMARY.

A fluorescence microscopy technique for the estimation of algal populations in soil is rapid. All soil algae are counted without selection. No large quantity of glassware is needed. It excludes heterotrophic forms without chlorophyll. It can be adopted for the study of water algae. The method cannot be used for taxonomic work, but the microscope is easily convertible to a light microscope for this purpose.

* Certain species of algae cannot be classified by simple morphology. The study of the life cycle is needed. By the introduction of a suitable fluorochrom, the technique may be adopted for the estimation of flagellata and microfauna of the soil. Further research is in progress.

Acknowledgements

The author is indebted to Professor N. A. Burges, Dr. J. McLuckie, Dr. N. C. W. Beadle, of the University of Sydney, Honorary Professor L. Baas-Becking and Dr. H. S. McKee of C.S.I.R.O., and Dr. F. Moewuss and Mrs. L. Moewuss, Timbrol research fellows, for their criticism and help.

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NOTES ON THE MORPHOLOGY AND BIOLOGY OF *ECTENOPSIS VULPECULA* WIED.
VAR. *ANGUSTA* MACQ. (DIPTERA, TABANIDAE, PANGONINAE).

By KATHLEEN M. I. ENGLISH, Department of Zoology, University of Sydney.

(Eleven Text-figures.)

[Read 29th October, 1952.]

Synopsis.

The genus *Ectenopsis* was erected by Macquart for *Chrysops vulpecula* Wied. Specimens described under other names by Macquart and Bigot were recorded as synonyms by Ricardo. Ferguson doubted whether they were really synonymous with *E. vulpecula* Wied. The relevant literature is quoted or listed.

Larvae, pupae and imagos of *E. vulpecula* Wied. var. *angusta* Macq. were found at Woolwich, Sydney, N.S.W. Larva and pupa are described and figured.

Introduction.

The genus *Ectenopsis* was erected by Macquart (1838) for *Chrysops vulpecula* Wied. (1828), a Tabanid, whose country was unknown, in the Berlin Museum. Walker (1848) in his List of the Specimens of Dipterous Insects in the Collection of the British Museum, lists "*Ectenopsis vulpecula* Macq., *Chrysops vulpecula* Wied.", with references, and a question mark for the country of origin. Macquart (1847) described *Pangonia angusta*, from Nouvelle-Hollande, in the collection of M. Bigot. Bigot (1892) described *Corizoneura angusta* and *C. rubiginosa*, from Australia, in his own collection. Ricardo (1915) recorded the synonymy of the above three species with *E. vulpecula* Wied. the type of the genus. Ferguson (1921) agreed that the three species were the same but doubted whether they were really synonymous with *E. vulpecula* Wied. He says: "I have not seen Wiedemann's original description, but apparently the name was applied to a species with black legs. I have taken a species at Sydney which has the legs, except the coxae, deep black, the wings are also smoky, almost deep black in fresh specimens, but fading somewhat with age, the palpi variable in colour, black to testaceous. Compared with this . . . are specimens in which the legs are yellowish (testaceous) and the wings clear, the stigma being inconspicuous in marked contrast to the black stigma of the other form.

"While I recognise that the species may prove sufficiently variable to include the two forms, I think that at any rate varietal names should be given to each. *E. vulpecula* Wied. evidently from all evidence, should be applied to the black legged form. . . . *E. angusta*, Macq. (= *E. angusta*, Bigot and *E. rubiginosa*, Big.) would apply to the paler legged form."

From this it can be seen that, over the years, there has been some confusion about the naming of the species and some doubt whether the specimens described belonged to one variable species or possibly to two distinct species.

The material which forms the subject of this paper includes thirteen imagos collected during one summer in a very small area at Woolwich, Sydney, N.S.W. The adults are the pale-legged form, though even among these few there is some variation in colour, none have wholly black legs, and the stigma of the wing is inconspicuous.

Adults were sent to Dr. I. M. Mackerras, who said: "The Pangonines are undoubtedly *Ectenopsis vulpecula* Wied. var. *angusta* Macq. as identified in the Ferguson collection."

Some were sent also to Mr. H. Oldroyd for comparison with Bigot's types of *rubiginosa* ♂ and *angusta* ♀ which are in the British Museum, where they are all under the one name *Ectenopsis vulpecula* Wied. "as placed by Miss Ricardo".

However, as it appears possible that two species may exist, the varietal name is used for these specimens.

OCCURRENCE.

Larvae and adults were collected at Woolwich, Sydney, N.S.W., in 1949-1950.

A larva was found on 27th November, 1949; it pupated next day, and a female emerged on 17th December. This is the only specimen for which larval and pupal exuviae were obtained. On 4th December a female was found on leaves a few inches from the ground. It had just emerged, and on the soil below it was the pupal exuvia.

In December, 1949, and January, 1950, thirteen adults, nine males and four females, were collected on foliage near where the first larva was found. They were always resting on leaves when taken, so it was not determined what flowers they visited.

In September-October-November, 1950, twenty-seven larvae and one pupa were found in the soil. Two of the larvae pupated, but these and the collected pupa failed to emerge. Of the remaining larvae some were killed and preserved, some died, and eight were still alive in June, 1952, twenty to twenty-two months after being collected.

Larvae, pupae and adults were all collected in a very small area where shrubs, citrus trees and cannas had been planted years before. The soil was a black sandy loam, usually quite moist, as there was some soakage from a sandstone ledge above, but the ground was well drained and was not at all swampy. The larvae were within a few inches of the surface of the soil, some amongst the canna roots and some in the shade of a citrus tree. No eggs were found.

LARVA. (Text-figs. 1-8.)

The larva is white in colour, the skin shining and longitudinally striated; the striations are slightly coarser on the thorax and last abdominal segments than on the abdominal segments 1-7. The living larva is noticeably widest on the metathorax and narrowest on the seventh abdominal segment, a characteristic which tends to be lost in preserved specimens. One larva, alive but contracted, was about 23 mm. long and about 2.5 mm. in breadth across the meta-thorax, tapering to 1.5 mm. across the seventh abdominal segment; another larva, killed and preserved, was 25 mm. in length. The pro-thorax (Text-fig. 2) tapers sharply to the very small head. The abdomen tapers very gradually to the last segment (Text-fig. 3) which is rounded posteriorly, with four small pointed terminal processes surrounding the spiracular area, and one small pointed process above the posterior spiracle; these processes are just visible to the naked eye. The larva is cylindrical in shape, not flattened at all.

Head: The head can be, and frequently is, completely withdrawn; in freshly killed specimens it can be seen through the integument, and the anterior tips of the mandibles lie just forward of the middle of the meso-thorax. The head capsule is very slender, one being 3.5 mm. long, $\frac{1}{2}$ mm. wide and a little less than $\frac{1}{2}$ mm. high; it is composed of pale chitin with dark red-brown mandibles and tentorial rods (Text-fig. 5), and dark brown parts of the epicranium; the pharynx (Text-fig. 4) is also heavily chitinized. Eye spots are not evident.

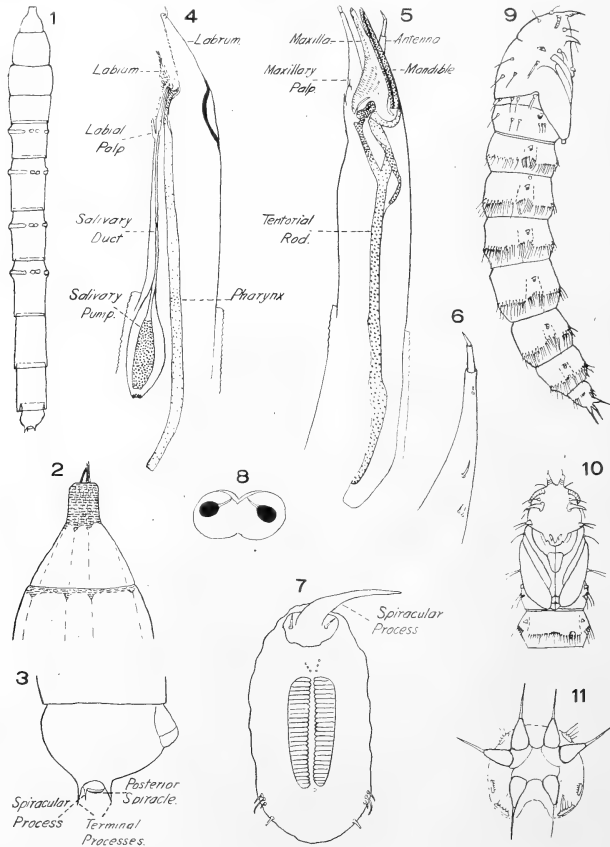
The *antennae* (Text-fig. 6) are three-segmented: the basal segment, broad at the base, long and tapering, is furnished with four very small flexible processes; the second segment is short and slender; the third segment is less than half the length of the second, and tapers to a point on which may be a minute pointed process.

Mouth-parts: The heavily chitinized mandibles (Text-fig. 5) are very long and slender, and have the characteristic longitudinal canal opening on to the anterior dorsal surface, but they lack the serrations on the lower edge that occur in *Tabanus*. The maxillae are longer than the mandibles, and are thickened at the apex and along the lower edge to form a groove into which the mandible fits; they are wide at the base and taper sharply to the slender distal half; they are not heavily chitinized and appear quite transparent, and are apparently very flexible as the distal half frequently folds backwards when being mounted in balsam; on the thickened lower edge are numerous fine hairs and minute teeth, and on the wide basal part are irregular rows of minute teeth.

The *maxillary palp* (Text-fig. 5) is three-segmented. The basal segment is short and broad with a long spine on the ventral distal edge, a smaller spine just behind it, and several minute spines on the lateral surface. The second segment is very long and

tapers gradually to the short third segment which has a rounded end furnished with minute papillae.

The *labrum* (Text-fig. 4) is chitinized but is of a pale colour. It is long and slender with two slender curved spines on the dorsal surface near the apex; the ventral surface is furnished, on the edges, with fine hairs. Other very small structures occur on the



Text-figures 1-11. *Ectenopsis vulpecula* Wied. var. *angusta* Macq.

1. Larva, lateral view, $\times 3$ approx.—2. Larva, anterior end, lateral view, $\times 12$ approx.—3. Larva, posterior end, lateral view, $\times 12$ approx.—4, 5. Mouth parts of larva, longitudinal section, $\times 27$ approx.—6. Antennae of larva, $\times 64$ approx.—7. Spiracular area and posterior spiracle of larva, $\times 12$ approx.—8. Graber's organ of larva, $\times 120$ approx.—9. Pupa, lateral view, $\times 4$ approx.—10. Anterior end of pupa, ventral view, $\times 4$ approx.—11. Posterior end of pupa, end view, $\times 16$ approx.

labrum also. The labium is about half the length of the labrum; it tapers sharply to a point and is covered with rows of fine hairs; there is a pair of labial palps on the ventral posterior portion, and the salivary duct runs back from the labium to the large salivary pump.

Thorax: The pro-thorax (Text-fig. 2) is encircled anteriorly by a wide collar, or annulus, of skin with a network pattern of longitudinal and transverse lines, the latter being armed with minute backwardly-directed spines; this part of the prothorax can be completely retracted. At the anterior edge of both meso- and meta-thorax is a very narrow band of skin similarly marked and armed. Near the posterior edge of the prothorax, one on each side, are the minute unchitinized slit-like openings for the anterior spiracles. On each thoracic segment, on the ventral surface, are two groups of fine hairs, one group on each side of the middle line; the hairs are very small and to be seen a magnification of at least 100 is required.

Abdomen: On segments 2 to 5, towards the anterior border of each, is a circlet of more or less prominent pseudopods: a ventral pair, more or less rounded and fairly prominent, a lateral pair on each side very similar to the ventral ones, and a dorsal pair, very slightly raised, elongated, and meeting on the dorsum. Pseudopodia are present also on segments 6 and 7 but they are very much reduced. The longitudinal striations of the abdomen are broken up on the pseudopodia by transverse lines forming a network pattern; these areas do not appear to have spines or hairs on them. Segment 8 (Text-fig. 3) appears rounded like a ball when the larva is moving. On the ventral surface is the anus bordered by prominent folds of skin; posteriorly the segment is produced into four pointed terminal processes round the spiracular area.

The posterior spiracle (Text-fig. 7), with bars of heavier chitin, is of the typical Tabanid form; it emerges from a vertical slit in the spiracular area and protrudes very slightly. The spiracular area is approximately an oval and the striations on the area more or less follow the same shape. At the dorsal edge of the area, above the spiracle, is a single finger-like process with a very small process on each side at the base. Ventrally, near the outer edge of the area on each side is a group of three small processes and below them and nearer the edge is a single process; these can be seen in mounted specimens with a magnification of about 185. Immediately above the spiracle is a group of small mounds.

Graber's organ (Text-fig. 8) is not visible in the living larva. In mounted specimens of larva that have died or been killed, only two black bodies have been seen. Similarly only two black bodies are to be seen in the slide of the last larval exuvia of the only specimen that was reared from a larva.

PUPA. (Text-figs. 9-11.)

The pupal exuviae obtained are approximately 18 mm. in length; one pupa which failed to emerge, and was preserved in good condition, is about 20 mm. long and 3.5 mm. broad on the thorax. The head and thorax are armed with thorns and slender spines. On the head are two pairs of strong thorns, one pair anterior to the eyes and one pair below the eyes, which are broad at the base and terminate in a fine point; on each of the second pair is a long thin spine placed about midway on its posterior surface. There are two pairs of spines above the anterior thorns and another pair between the two pairs of thorns, each spine set on a prominent small tubercle; posterior to the second pair of thorns, on each side, is a tubercle bearing two spines. On the ventral surface, at each side of the apex of the sheath of the labrum is a short thorn.

The thorax bears three pairs of spines on the dorsal surface, each on a tubercle; and at the base of each wing, on a single tubercle, is a pair of alar spines which are frequently so close together as to appear as one spine. The thoracic spiracle is prominent. The meta-thorax bears, on each side, a pair of lateral spines on one tubercle, and three dorsal spines.

On the first abdominal segment, on each side, are three lateral spines close together just posterior to the prominent spiracle, and three dorsal spines. Abdominal segments 2-7 bear a small spiracle on each side, and a girdle of spines towards the posterior border of each segment. On segment 2 the spines are more or less in a single line, but on each succeeding segment there are more spines in a second line until on segment 7 there are two irregular rows of spines forming the girdle. The last segment bears three

groups of small spines on each side, and it terminates in an aster (Text-fig. 11) of six tubercles, each bearing a long slender spine.

As only females were reared no comparison of the male pupa can be given.

The specimens used in the preparation of this paper, e.g., the adult flies with pupal exuviae, and slide mount of larval exuvia, together with larva and pupa in spirit, slide preparations of larvae, and collected adults, have been deposited in the Macleay Museum at the University of Sydney.

CONCLUSION.

The larva and pupa described run down to Tabanidae in Keys to Families given by Malloch (1917). Insufficient material exists as yet for a key of the immature stages of Australian Tabanidae to be attempted. Fuller (1936) suggested that a distinguishing character of Pangoninae pupae might be the reduced aster on the terminal segment, of two projections only, as this occurs in the Australian *S. auriflua* Don. and the American *G. chrysocoma* Osten-Sacken; but the aster of *Ectenopsis* with six projections shows that, though the two-pronged aster may be a valuable part of a key, it is not a character of the whole group. Characters that may be of use in larval keys, generic or specific, are the small processes on the first antennal segment, and the processes on the spiracular area of the posterior spiracle, and for that reason they have been described and figured in detail.

Acknowledgements.

The writer is indebted to Professor P. D. F. Murray and Dr. A. R. Woodhill, Department of Zoology, University of Sydney, who made available laboratory accommodation at the Department; to Dr. I. M. Mackerras of the Queensland Institute of Medical Research who identified the adult flies; and to Mr. H. Oldroyd of the British Museum, (Natural History), who compared the adults with Bigot's types in the British Museum.

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REVISION OF AUSTRALIAN AND NEW ZEALAND SPECIES OF
THELEPORACEAE AND HYDNACEAE IN THE HERBARIUM
OF THE ROYAL BOTANIC GARDENS, KEW.

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and Industrial Research, Auckland, New Zealand.

(Communicated by Professor N. A. Burges.)

[Read 29th October, 1952.]

Through the courtesy of the Director of the Royal Botanic Gardens, Kew, England, I was enabled to examine in 1951 all collections in the herbarium of species of the families Theleporaceae, Hydnaceae, Clavariaceae and Heterobasidiomycetes. This paper provides a complete list of collections of the Theleporaceae and Hydnaceae from Australia, Tasmania, New Zealand and New Guinea deposited therein, gives correct names and synonyms, and indicates under which species they have been filed when incorrectly identified. A subsequent list covering the Clavariaceae and Heterobasidiomycetes will be prepared at a later date.

I am grateful to Sir Edward Salisbury, F.R.S., Director of the Royal Botanic Gardens, and Dr. R. W. G. Dennis, Deputy Keeper of the herbarium, for permission to examine collections in the herbarium and for facilities kindly provided; and to the Trustees of the Nuffield Foundation for their generous grant to defray travelling expenses.

Valid species are set in small capitals, synonyms in italics, incidental species and misdeterminations in upper and lower case, individual collections in inverted commas. I have added abbreviations of Australian States to locality references since these were seldom inserted on the herbarium sheets at Kew. Literature references in all cases were checked in the library at Kew, so are accurate both for valid species and synonyms.

acerinus, *Aleurodiscus* (Pers.) H. & L. Under this cover at Kew are two collections. "N.Z., Wellington, Travers, No. 376" so named by Cooke is of *Corticium scutellare*; "Tasmania", placed by Berkeley under *Stereum acerinum*, is a *Sebacina*, of the Heterobasidiomycetes.

1. AFFINE, *STEREUM* Lev., *Ann. Sci. Nat.*, Ser. III, 2, 1844: 210.

mellisii, *Stereum* Berk. ex Cke., *Grev.*, 13, 1884: 3, *nomen nudum*.

Two collections from New Guinea are at Kew. "New Guinea, Strickland River, Everell's Expedition" was filed by Cooke under *Stereum mellisii*. Bresadola had noted on the sheet that it was not this species, but to him was unknown. A second, "Kumusi River, New Guinea, Fitzgerald, 1895" Cooke placed under *Stereum pergamenum*.

2. ALBIDUS, *ALEURODISCUS* Mass., *Grev.*, 17, 1889: 55.

The only collection under the cover at Kew is the type, ex "Brisbane, Q., No. 620". *alutacea*, *Odontia* (Fr.) Bourd. & Galz. Collections from the region filed under this cover by Cooke are "Near Melbourne, Vic., June 1884, F. Reader, No. 5", "N.Z., Colenso, b.6" and "Tasmania, W. Archer", the last being the type of *Hydnum flicicolum*. All are specimens of *Odontia arguta*.

amaenum, *Stereum* (Lev.) Mass. = *Stereum percome*.

3. ANOMALA, *SOLENIA* (Pers.) Fcl., *Symb. Myc.*, 1, 1871: 290.

anomala, *Peziza* Pers., *Myc. Eur.*, 1, 1822: 270.

Four collections from the region agree with authentic specimens, namely "Tasmania, Archer", "Tasmania, W. Archer", "Australia, 1882" and "N.Z., Colenso, b. 582".

4. AOTEAROA, STEREUM G. H. Cunn.

On the type sheet of *Stereum contrarium* is a collection ex "Puhī Puhī, N.Z., T. Kirk, No. 221". Bresadola had written on the sheet—"An *St. medicum* Currey sed vix *Stereum*; *Trpez.* Non scytali affine". It is of an endemic species not uncommon in New Zealand which will be described in a forthcoming paper.

arachnoideum, *Corticium* Berk. Three collections from the region are filed under this cover at Kew. "Australia, S.53" so named by Berkeley, is of *C. sphaerosporum*; "Tasmania, W. Archer Esq." and "Tasmania", the latter consisting of three collections, are too fragmentary to name, but are not of this species.

archeri, *Corticium* Berk. = *Odontia archeri*.

archeri (*Veluticeps*), *Hymenochaete* (Berk.) Cke. = *Stereum illudens*.

5. ARCHERI, ODONTIA (Berk.) Wakef., *Trans. Proc. Roy. Soc. S. Aust.*, 1930: 157.

archeri, *Corticium* Berk., *Fl. Tas.*, 2, 1860: 260.

chrysocreas, *Corticium* Berk. & Curt., *Grev.*, 1, 1873: 178.

crociocreas, *Corticium* Mass., *Jour. Linn. Soc.*, 27, 1890: 151.

The species resembles *Grandinia australis* in that in both the context hyphae are coated with brown mucilaginous granules. Collections from the region at Kew are the type of *Corticium archeri* ex "Tasmania", "Sydney, N.S.W., J. B. Cleland, May 1919", "Mt. Lofty, S. Aus., J. B. Cleland, May and June 1928" and "Brown's River, Tasmania, J.B.C., Jan. 1928".

archeri, *Stereum* Berk. = *Stereum illudens*.

6. ARCHERI, THELEPHORA Berk., *Fl. Tas.*, 2, 1860: 258.

The type, labelled "Tasmania", was referred by Bresadola to *Lachnocladium*; but Corner (1950, p. 723) correctly showed it to be a *Thelephora*. A second collection on the type sheet, ex "Delegate Hill, Vic., E. Reader" may be the same, but this could not be ascertained since spores were not found.

7. ARGUTA, ODONTIA (Fr.) Quel., *Enchiridion*, 1886: 196.

argutum, *Hydnum* Fr., *Syst. Myc.*, 1, 1821: 424.

filicolum, *Hydnum* Berk., *Fl. Tas.*, 2, 1860: 256.

Three Australian collections at Kew correctly named by Miss Wakefield are "Pillagra scrub, near Queensland Border in N.S.W., J. B. Cleland, 1918, W", "National Park, Tasmania, J.B.C., Jan. 1928" and "Brown's River, Tasmania, J. B. Cleland, Jan. 1928". Other collections of the species filed under *O. alutacea* are "Near Melbourne, Vic., June 1884, F. Reader, No. 5", "N.Z., Colenso, b.6" and "Tasmania, W. Archer". The last is the type of *Hydnum filicolum*.

8. ARIDA, CONIOPHORA (Fr.) Karst., *Finska Vet.-Soc. Bidrag. Natur och Folk*, 37, 1882: 161.

arida, *Thelephora* Fr., *Elench.*, 1, 1828: 197.

luteocincta, *Thelephora* Berk., *Jour. Linn. Soc.*, 13, 1873: 168.

luteocinctum (*Coniophora*), *Corticium* (Berk.) Cke., *Grev.*, 8, 1880: 89.

luteocincta, *Coniophora* (Berk.) Sacc., *Syll. Fung.*, 6, 1888: 648.

cookei, *Coniophora* Mass., *Jour. Linn. Soc.*, 25, 1889: 136.

Collections at Kew from the region are ex "Bunyip, Vic., No. 376" placed under *Coniophorella olivacea*; "b.507" filed by Cooke under *Corticium sulfureum*; "Wangaretta, Vic.", the type of *Coniophora luteocincta*, which consists of several fragments attached to rotten wood, not growing on the ground as was recorded by Berkeley.

9. ARTOCREAS, HYDNUM Berk. & Curt., ex Cke., *Grev.*, 20, 1891: 1.

New Zealand collections agree with the type ex Venezuela, No. 139.

atrocinerea, *Peniophora* (Kalch.) Mass. = *Duportella schomburgkii*.

atrovirens, *Corticium* Fr. A collection placed by Cooke under this cover, ex "Brisbane, Q., Bailey, No. 526", labelled on the sheet *Coniophora atrovirens* Berk. & Br., is of a species of *Septobasidium*.

atrum, *Stereum* (Weinm.) Cke. Three collections so referred by Cooke, ex "Brisbane, Q., Bailey", "Illawarra, N.S.W., Camara" and "Gippsland, Vic., Murray" are of *Stereum elegans*.

10. ATTENUATA, HYMENOCHAETE Lev., *Ann. Sci. Nat.*, Ser. III, 5, 1846: 152.

attenuatum, *Stereum* Lev., *Ann. Sci. Nat.*, Ser. III, 2, 1844: 212.

Two Australian collections under the cover are "Southport, Q., J. H. Simmonds, Sept. 1914" and "Moruya, N.S.W., W. N. Cheesman, 1914".

auferianum, *Corticium* Mont. Four collections from the region are filed under this cover at Kew. "Clarence River, N.S.W., Dr. Beckler", so named by Berkeley, consists of three specimens of a sterile *Stereum* showing receding growth; "Currey, New Zealand" is a specimen of *Peniophora incarnata*; "N.Z., Colenso, b.662, b.772" are specimens of a white multiple-layered *Peniophora*.

australe, *Stereum* Lloyd = *Stereum lobatum*.

australis, *Cladoderris* Berk., ex Cke. The only collection on the type sheet is of *Cladoderris infundibuliformis*. Berkeley referred it to *Thelephora dendritica*, Lloyd to *Cladoderris spongiosa*.

11. AUSTRALIENSIS, ALEURODISCUS Wakef., *Kew Bull. Misc. Inf.*, 1918: 208.

The type is at Kew, ex "Buderim Mt., Q., C. T. White, No. 4, Apl. 1912".

australiensis, *Cyphella* Cke., *Grev.*, 20, 1891: 9. The type, ex "Melbourne, Vic., Berggren, No. 378" is a specimen of an immature *Aleurodiscus*. A second collection, so named by Masee, ex "Centennial Park, N.S.W., E. Cheel, No. 21" is of *Cyphella villosa*.

12. AUSTRALIS, GRANDINIA Berk., *Fl. Tas.*, 2, 1860: 257.

pevatum, *Hydnum* Mass., *Kew Bull. Misc. Inf.*, 1901: 157.

Collections under the cover at Kew are the type, ex "Tasmania, Archer", "Tasmania, J. B. Cleland, 1928", "National Park, Sydney, N.S.W., W. N. Cheesman, 1914" "N.S.W., J. B. Cleland, 1928" and the type of *Hydnum pevatum* ex "Tasmania, Rodway, No. 340". "N.Z., Colenso, b.831" is a specimen of *Corticium scutellare*. Specimens of *Odontia archeri* filed under the cover are ex "Gippsland, Vic., May 1884" and "Naree Warree, Vic., Martin, Nos. 867, 1111".

baileyianum, *Stereum* Berk., in herb. Kew. A specimen so labelled, now unrecognizable, ex "Russell River, Q., Sayer, No. 49" is filed under *Stereum prolificans*. Cooke (1892, p. 183) recorded it as a synonym of the latter species.

13. BERGGRENI, ALEURODISCUS (Cke.) nov. comb.

berggreni, *Hypocrea* Cke., *Grev.*, 8, 1879: 65.

peziculoides, *Aleurodiscus* Wakef., *Kew Bull. Misc. Inf.*, 1931: 201.

Four collections from New Zealand are at Kew, the type of *Hypocrea berggreni* ex "N.Z., Dr. S. Berggren"; the type of *Aleurodiscus peziculoides* ex "York Bay, Wellington, E. J. Butler-G.H.C., July 1923, No. 1210"; a third labelled *Corticium polygonium* Fr. ex "U.S.A. Curtis", a faulty locality record since the species is endemic; and "N.Z., Colenso, b.252" filed by Cooke under *Stereum frustulosum*.

beyrichii, *Lloydella* (Fr.) Bres., *nom. ined.* Under *Stereum pannosum* Cooke placed a weathered specimen of *S. illudens* ex "N.Z., Colenso, b.906". On the sheet Bresadola had written—"=*Lloydella beyrichii* (Fr.) Bres. meo sensu. Specimen a vetusta hymenio ex acetate collapsio = *S. membranaceum* P. Henn.". Included as part of the type collection of *Duportella schomburgkii* ex "Port Darwin" is a specimen of *S. illudens*. Regarding it Bresadola had noted on the type sheet—"=*Lloydella beyrichii*, meo sempi vix vel parum diversa".

14. BICOLOR, ODONTIA (A. & Sw.) Bres., *Ann. Myc.*, 1, 1903: 87.

bicolor, *Stereum* A. & Sw., ex Fr., *Syst. Myc.*, 1, 1821: 417.

Though the species is common in New Zealand, there are no collections from the region at Kew.

15. BICOLOR, STEREUM (Pers.) Fr., *Epicrisis*, 1838: 549.

bicolor, *Thelephora* Pers., ex Fr., *Syst. Myc.*, 1, 1821: 438.

coffeatum, *Stereum* Berk. & Curt., *Grev.*, 1, 1873: 164.

fusca, *Thelephora* (Schrad.) Pers., ex Quel., *Myc. Fr.*, 1888: 14.

pannosum, *Stereum* Cke. & Mass., *Grev.*, 21, 1892: 38.

Three collections from the region are at Kew ex "New Guinea, Armit" and "Korumburra, Vic., Mrs. Martin, Nos. 1067, 1071". The last is the type of *S. pannosum* Cke. & Mass.

16. BOMBYCINUM CORTICIUM (Somm.) Karst., *Hedw.*, 32, 1893: 120.

One collection from Australia is at Kew, ex "Kuitpo, S. Aus., J. B. Cleland, June 1928", identified by Miss Wakefield.

boryanum, *Stereum* Fr. The five collections from the region filed under this cover, ex "New Guinea, W. E. Armit", "Daintree River, Q., Pentzcke", "North Queensland", "Tweed River, N.S.W., Camara, No. 84" and "Richmond River, N.S.W., Camara" are of *Stereum lobatum*, of which the type is merely a pallid form.

butleri, *Auricularia* Mass. = *Stereum hispidulum*.

17. CACAO, HYMENOCHAETE Berk., *Jour. Linn. Soc.*, 10, 1868: 333.

cacao, *Stereum* Berk., *Hook. Jour. Bot.*, 6, 1854: 169.

The only collection at Kew from Australia, ex "Cooroy, Q., C. T. White, Apl. 1911, No. 8" agrees with the type from India save that the pileus hairs are more strongly developed.

18. CAESIA, PENIOPHORA Bres., in Bourd. & Galz., *Bull. Soc. Myc. Fr.*, 28, 1912: 406.

Two collections are at Kew from New Zealand, filed under *Peniophora cinerea*, namely "New Zealand, 1866, b.268" and "Mamaku, W. N. Cheesman, 1914".

calcareum, *Hydnum* Cke. & Mass. = *Irpex calcareum*.

19. CANDIDA, SOLENIA Pers., *Myc. Eur.*, 1, 1822: 334.

fasciculata, *Solenia* Pers., *l.c.*, p. 335.

Collections at Kew ex "Brisbane, Q., Bailey, No. 735" and "N.Z., Colenso, b.14" agree with European specimens. Judging from the description, no specimens being in the herbarium, *Cyphella schneideri* appears to have been based on a Queensland collection.

20. CAPERATUM, STEREUM (Berk. & Mont.) Mass., *Jour. Linn. Soc.*, 27, 1890: 161.

caperata, *Thelephora* Berk. & Mont., *Ann. Sci. Nat.*, Ser. III, 11, 1849: 241.

lamellata, *Thelephora* Berk. & Curt., *Am. Jour. Sci. and Arts*, Ser. II, 11, 1851: 94.

lamellatum, *Stereum* (Berk. & Curt.) Cke., in herb. Kew.

Collections from the region at Kew are ex "Norfolk Island, June 1855, No. 34, H.M.S. Herald", "New Caledonia, R. H. Compton", "Morton Bay, Q., F. M. Bailey, No. 12", "Clarence River, N.S.W." (labelled *Thelephora dendritica*), "Coomerong Island, Shoalhaven River, N.S.W., No. 866, F. A. Rodway", "Illawarra River, N.S.W., Kirton", "Lord Howe Island", and "Baradi, Papua, C. E. Carr, No. 13471" (the last labelled *Cladoderris infundibuliformis*). Under the cover of *Stereum lamellatum* are filed the type ex "Aru Island, Challenger Expedition", "New Guinea, Armit", "Solomon Islands, 1884, Hart Guppy", "Dunk Island, Q., W. Cottrell Dormer, Aug. 1927" and "Toowoomba, Q., Hartmann". This last Massee treated as a variety of *Stereum caperatum*; and on the type sheet Bresadola had written—"= *Cladoderris infundibuliformis*, juvenilis, hymenio nondum tuberculoso".

21. CAPUTMEDUSAE, HYDNUM (Bull.) Fr., *Syst. Myc.*, 1, 1821: 409.

Massee so named a collection ex "Tasmania, L. Rodway, No. 234".

carnea, *Peniophora* (Berk. & Curt.) Cke. A specimen so labelled by Cooke, ex "Walcha, New England, N.S.W., Crawford" does not resemble the type ex Texas.

castanea, *Hymenochaete* Wakef. = *Duportella tristicula*.

ceriferum, *Stereum* Wakef. = *Stereum hispidulum*.

22. CERVICOLOR, ASTEROSTROMA (Berk. & Curt.) Mass., *Jour. Linn. Soc.*, 25, 1889: 155.
cervicolor, *Corticium* Berk. & Curt., *Grev.*, 1, 1873: 179.
corticola, *Asterostroma* Mass., *Jour. Linn. Soc.*, 25, 1889: 155.
albidocarneum, *Asterostroma* Mass., *l.c.*

New Zealand collections match the type ex Alabama. No specimens from the region are in Kew herbarium.

cervinum, *Hydnum* Berk., *Fl. Tas.*, 2, 1860: 256. The type, ex "Tasmania, Archer", is a sterile fragment on decayed wood. It appears to be portion of a *Grandinia*.

23. CHEESMANII, PENIOPHORA Wakef., *Kew Bull. Misc. Inf.*, 1915: 371.

The type at Kew is ex "Moruya, N.S.W., W. N. Cheesman, 1914".

24. CHLORINUS, TOMENTELLA (Mass.) nov. comb.

chlorinus, *Hypochnus* Mass., *Kew Bull. Misc. Inf.*, 1901: 158.

The type at Kew, ex "Tasmania, Rodway, No. 266" has coloured, globose verruculose spores.

chrysocreas, *Corticium* Berk. & Curt. = *Odontia archeri*.

25. CINERASCENS, PENIOPHORA (Schw.) Sacc., *Syll. Fung.*, 6, 1888: 646.

cinerascens (*Stereum*) *Thelephora* Schw., *Trans. Am. Phil. Soc.*, 4, 1832: 167.

cinerascens, *Hymenochaete* (Schw.) Lev., *Ann. Sci. Nat.*, Ser. III, 5, 1846: 152.

aschistum, *Corticium* Berk. & Curt., *Proc. Am. Acad. Arts and Sci.*, 4, 1858: 123.

moricola, *Stereum* Berk., *Grev.*, 1, 1873: 162.

dissitum, *Stereum* Berk., *l.c.*, p. 164.

ephebrium, *Corticium* Berk. & Curt., *l.c.*, p. 178.

berkeleyi, *Peniophora* Cke., *Grev.*, 8, 1879: 20.

neglectum, *Stereum* Peck, *N.Y. State Mus. Rept.* 33, 1880: 22.

schweinitzii, *Peniophora* Mass., *Jour. Linn. Soc.*, 25, 1889: 145.

cinerascens, *Stereum* (Schw.) Mass., *Jour. Linn. Soc.*, 27, 1890: 179.

occidentalis, *Peniophora* Ell. & Ev., *Bull. Torrey Bot. Club*, 24, 1897: 277.

cinerascens, *Lloydella* (Schw.) Bres., in *Lloyd's Myc. Notes*, No. 5, 1900: 51.

purpurascens, *Stereum* Lloyd, *Letter* 53, 1914: 15.

Collections at Kew from the region are ex "Samoa, C. G. Lloyd", "Port Denison, Q., Shann, f. 15" (placed by Cooke under *Stereum schomburgkii*), "Clarence River, N.S.W., Wilcox", three specimens filed by Cooke under *Stereum rugosum*, and "N.Z., Colenso, No. 619", placed by Cooke under *Stereum ochroleucum*.

26. CINEREA, PENIOPHORA (Pers. ex Fr.) Cke., *Grev.*, 8, 1879: 20.

cinerea, *Thelephora* Pers., ex Fr., *Syst. Myc.*, 1, 1821: 435.

cinereum, *Corticium* (Pers.) Fr., *Epicrisis*, 1838: 563.

Though common in New Zealand there are no collections from the region in Kew herbarium. Those filed under the cover, ex "N.Z., 1866, b.268" and "Mamaku, W. N. Cheesman, 1914" are of *P. caesia*.

27. CAERULEUM, CORTICIUM FR., *Epicrisis*, 1838: 562.

Collections from the region under this cover at Kew are "Port Denison, Q., Shann, f.11", "Condamine River, Q., 1880, F.v.M.", "Clarence River, N.S.W." and "Clarence River, N.S.W., Miss Thornton, No. 1". One filed under the cover by Cooke, ex "Strickland River, New Guinea, Bauerlen, No. 10" is the sterile stroma of a *Hypoxylon*.

cinnabarinum, *Corticium* Mass., *Jour. Linn. Soc.*, 27, 1890: 140.

The type, ex "Clarence River, N.S.W., Wilcox", was by Cooke labelled 'dubium' and filed under the unnamed species. Masee later described the collection as a new species and stated that spores were "subglobose 5-6 μ ". Examination showed the collection to consist of a daub of red barn paint on the bark of a shrub, probably forwarded by the collector by way of a joke. Sections showed the specimen to be without hyphae or spores, and to consist of amorphous pigment granules embedded in a film of dried oil.

28. CIRRHATUM, HYDNUM Pers., ex Fr., *Syst. Myc.*, 1, 1821: 411.

meruloides, *Hydnum* Berk. & Br., *Trans. Linn. Soc.*, Ser. II, 2, 1833: 63.

A collection ex "Gippsland, Vic., 1884, No. 27" appears to be of this species. A deformed specimen ex "Brisbane, Q., Bailey, No. 246" is the type of *H. meruloides*. *clavarioides*, *Hydnum* Berk. & Curt. A collection referred to the species by Cooke, ex "Richmond River, N.S.W., Mrs. Hodgkinson" does not resemble the type from Cuba.

29. CLELANDII, GRANDINIA Wakef., *Trans. Proc. Roy. Soc. S. Aust.*, 1930: 156.

The type is ex "New South Wales, J. B. Cleland, 1928 A".

30. COMEDENS, CORTICIUM (Nees ex Fr.) Fr., *Epicrisis*, 1838: 565.

comedens, *Thelephora* (Nees) Fr., *Syst. Myc.*, 1, 1821: 447.

decorticans, *Thelephora* Pers., *Myc. Eur.*, 1, 1822: 137.

cartylei, *Corticium* Mass., *Jour. Linn. Soc.*, 27, 1890: 148.

Though not uncommon in New Zealand, there are no specimens at Kew from the region.

complicatum, *Stereum* Fr. = *Stereum rameale*.

concolor, *Stereum* Berk., *Fl. Tas.*, 2, 1860: 259. The type, ex "Tasmania, W. Archer, Esq." consists of three fragments too incomplete to identify. Their microstructure suggests the species was based on young specimens of *Stereum lobatum*.

31. CONFLUENS, CORTICIUM Fr., *Epicrisis*, 1838: 564.

confluens, *Thelephora* Fr., *Syst. Myc.*, 1, 1821: 447.

A collection named by Miss Wakefield, ex "State Nursery, Creswick, Vic., W. N. Cheesman, 1914", is under this cover at Kew.

confluens, *Craterellus* Berk. & Curt. = *Craterellus odoratus*.

confusum, *Stereum* Berk. = *Stereum sowerbeii*.

32. CONGESTA, THELEPHORA Berk., *Jour. Linn. Soc.*, 13, 1873: 168.

The type, ex "Yarra Yarra Plains, Vic., Jan. 1864" consists of five plants in good condition. A second collection, ex "Gainsford, Q., E. Bowman" contains plants about twice as large as those of the type yet possessing the same microstructure. Other collections are "Brisbane, Q., Bailey, Nos. 732, 775". One filed under the cover by Cooke, ex "Victoria, Dr. Winter" is of *Stereum elegans*.

contrarium, *Stereum* Berk. On the type sheet is a collection ex "N.Z., Puhī Puhī, T. Kirk, No. 221" of an endemic New Zealand species, *Stereum aotearoae*.

cookei, *Coniophora* Mass. = *Coniophora arida*.

33. CORALLOIDES, HYDNUM Fr., *Syst. Myc.*, 1, 1821: 408.

novae-zealandiae, *Hydnum* Col., *Trans. N.Z. Inst.*, 21, 1888: 79.

Two collections from New Zealand are under the cover at Kew, "N.Z., Dall" and the type of *H. novae-zealandiae*, ex "N.Z., Colenso, b.761" which is merely a large form of this European species.

corrige, *Stereum* Lloyd = *Stereum percome*.

corticola, *Asterostroma* Mass. = *Asterostroma cervicolor*.

crassa, *Hymenochaete* (Lev.) Berk. = *Peniophora vinosa*.

cretaceum, *Corticium* (Pers. ex Fr.) Fr. Two collections from the region are filed under the cover at Kew. "Tasmania" is a fragment that cannot now be identified; "N.Z., Colenso, b.404" so named by Cooke consists of a sheet of resin on bark of *Dacrydium cupressinum*.

34. CRINALE, HYDNUM Fr., *Epicrisis*, 1838: 516.

tabacinum, *Hydnum* Cke., *Grev.*, 14, 1886: 129.

ferruginosa, *Caldesiella* Sacc., *Syll. Fung.*, 6, 1888: 478.

The type of *H. tabacinum* ex "N.Z., Colenso, b.150" matches authentic specimens of *H. crinale* from Europe in Kew herbarium.

crociareas, *Hymenochaete* Berk. & Br. On the sheet of the type of *Hymenochaete innatum* Cke. & Mass. ex "Daintree River, Q." (a species of *Epithete*) Bresadola had

written "— *H. crocicreas* B. & Br. (of Ceylon, but not of N. America)". On the sheet of *H. crocicreas* (Berk. & Curt.) he had noted "This is the true *H. crocicreas* Berk. & Br. of Ceylon". *H. crocicreas* (Berk. & Curt.) is a synonym of *Odontia archeri*.

35. CROCIDENS, HYDNUM Cke., *Grev.*, 19, 1890: 45.

wellingtonii, *Hydnum* Lloyd, *Myc. Notes*, No. 69, 1923: 1200.

The type at Kew, ex "Port Phillip, Vic., French, Aug. 1890" is in good condition. A second collection of the species, ex "Brisbane, Q., F. M. Bailey, No. 757", was filed by Cooke under *Hydnum laevigatum*. The species is also common in New Zealand, where it was named *Hydnum wellingtonii*. Spore measurements given by Cooke are too small, since in the type they are the same as in New Zealand collections, namely 6.5–8 μ , globose, smooth, collapsed.

crustosa, *Odontia* (Pers. ex Fr.) Quel. One collection at Kew, ex "Tasmania", under the cover of *Grandinia crustosa*, labelled *G. australis*, is now merely a fragment of decayed wood. A second, ex "Victoria, Mrs. Martin, No. 494", is a species of *Sebacina*.

36. CRUSTOSA, PENIOPHORA Cke., *Grev.*, 8, 1879: 56.

The type at Kew is ex "N.Z., Waitaki, No. 347". A second collection ex "N.Z., Colenso", is under the cover of *Corticium laeve*.

cupulaeformis, *Cyphella* Berk. & Rav. A collection ex "Buller Valley, N.Z., T. Kirk, No. 236" placed under this cover by Cooke, is of *Cyphella totara*, a species common in New Zealand on *Podocarpus totara*.

curreyi, *Cyphella* Berk. & Br., *Ann. Mag. Nat. Hist.*, Ser. III, 7, 1861: 379. Cooke placed under this cover "N.Z., Murimotu, T. Kirk, No. 241", "N.Z., T. Kirk, on Antirrhinum leaves, No. 36" and "Melbourne, Vic., No. 376". The first was not examined, being fragmentary; the latter are collections of *C. villosa*. *C. curreyi* is a synonym of *C. albo-violascens* (A. & S.) Karst.

cyathiforme, *Stereum* Fr. A collection ex "New Guinea, Armit", placed under this cover by Cooke, is of *Stereum elegans*.

delicatum, *Hydnum* (Kl.) Fr. Cooke so referred a collection of *Veluticeps tabacina* ex "Darling Downs, Q., No. 1095".

delicatum, *Hydnum* (Kl.) Fr. = *Heterochaete delicata*.

37. DENDRITICA, CLADODERRIS Pers., in Freycinet's Voyage 'Uranie', 1826: 22.

spongiosa, *Cladoderris* Fr., in Wahlberg's Fung. Natalensis, 1848: 20.

Two collections at Kew, filed under *C. spongiosa*, ex "New Guinea" and "North Queensland" appear to be of this species. Under the cover of *C. dendritica* are two collections of *Stereum caperatum* ex "Clarence River, N.S.W."

38. DENSA, CYPHELLA Berk., *Fl. N.Z.*, 2, 1855: 184.

The type is at Kew, ex "N.Z., Cape Kidnapper, Colenso, on living bark of *Corynocarpus laevigata*".

discoidea, *Cyphella* Cke., *Grev.* 12, 1884: 85. The type, ex "N.Z., Napier, W. Colenso, b.30", collected on living leaves of *Hypochoeris radicata*, was said to possess "brief basidia, spores globose, smooth, 4 μ ". It consists of several white bodies loosely attached to the leaf hairs, which on examination proved to be empty spider egg-cases composed of woven filaments 0.5 μ diameter.

dispersum, *Hydnum* Berk., *Lond. Jour. Bot.*, 4, 1845: 58. The type ex "Swan River, W. Aus., Drummond, No. 207" now consists of several scattered sterile spines without a subiculum.

dorsale, *Stereum* Kalch. Cooke applied the name to a specimen of *Stereum lobatum* ex "Airey's Inlet, Vic., Miss Berthon" which he placed under the cover of *S. vellereum*. Massee subsequently labelled it *S. vellereum* var. *australiense*.

39. ELEGANS, STEREUM (Meyer) Sacc., *Syll. Fung.*, 6, 1888: 553.

elegans, *Thelephora* Meyer, ex Fr., *Syst. Myc.*, 1, 1821: 430.

Abundant collections from this region are at Kew, dispersed under no less than ten species. Correctly named are "Australia, W. N. Cheesman, 1914", "Gainsford, Q., Bowman", "Goode Island, Q., Powell", "Endeavour River, Q., Persieh", "Wangaretta, Vic.", "Omeo, J. Sterling", "Gippsland, Vic., Webb", "Little Bendigo, Vic., G. Day", "Clarendon, Vic., Tepper, No. 860", "Moe Swamp, Gippsland, Vic.", "Melbourne, Vic., F. Reader, No. 28", and "Tasmania, New Norfolk, Winter, No. 324". Under *Stereum pusillum* Berkeley placed "V.D.L., Gunn". Under *S. nitidulum* Cooke filed "North Queensland" and "Endeavour River, Q., Persieh". Under *S. cyathiforme* he placed "New Guinea, Armit" and under *S. thozetii* "Endeavour River, Q.", "New Guinea, Armit" and "Gippsland, Vic.". A rosetted form, ex "Gippsland, Vic." Cooke filed under *S. petaloides*. One collection from New Zealand, ex "Wairarapa, Dry River, T. Kirk, No. 140" Cooke placed under *S. obliquum*. He also filed "Victoria, Dr. Winter" under *Thelephora congesta*; "Brisbane, Q., Bailey", "Illawarra, N.S.W., Camara" and "Gippsland, Vic., Murray" under *Stereum atrum*; and under *Stereum sprucei* placed "Australia, No. 7".

evolvens, *Corticium* Fr. Under *C. laeve* (a synonym) are several collections at Kew from the region, none being of this species. "Tasmania, W. Archer Esq." and "Tasmania" are sterile, but do not possess the same microstructure; "New Zealand" and "New Zealand, Sinclair" are of *Peniophora incarnata*; "New Zealand, Colenso" consists of three lots, two of *Hymenochaete unicolor*, the third a sterile *Corticium*; "N.Z., Colenso, b.55" is of *Peniophora crustosa*; "Colenso, b.402" is an *Aleurodiscus*; "Colenso, b.288" a sterile *Corticium*; "Colenso, b.386" a specimen of *Corticium scutellare*; and "Strickland River, New Guinea, Bauerlen, 1885" one of the peltate ascomycetes.

exsculpta, *Thelephora* Berk., *Jour. Linn. Soc.*, 13, 1873: 168. The type, ex "Dandeng Ranges, Vic.", is a *Septobasidium* in poor condition.

40. FARINACEA, GRANDINIA (Pers. ex Fr.) Bourd. & Galz., *Bull. Soc. Myc. Fr.*, 30, 1914: 253.

farinaceum, *Hydnum* Pers. ex Fr., *Syst. Myc.*, 1, 1821: 419.

farinacea, *Odontia* (Pers. ex Fr.) Bres., *Ann. Myc.*, 1, 1903: 87.

At Kew are two collections from the region, both identified by Miss Wakefield, "Kuitpo, S. Aus., J. B. Cleland, Aug. 1928" and "Adelaide, S. Aus., J. B. Cleland, Aug. 1928".

fasciculata, *Solenia* Pers. = *Solenia candida*.

41. FILAMENTOSA, PENIOPHORA (Berk. & Curt.) Burt, ex Coker in *Elisha Mitchell Jour. Sci.*, 36, 1921: 162.

filamentosum, *Corticium* Berk. & Curt., *Grev.*, 1, 1873: 178.

Though common in New Zealand, there are only two collections at Kew from the region, "Tasmania" and "Dunedin, N.Z., J. Murray, Feb. 1951", the former placed by Berkeley under *Corticium suffurum*.

filicicola, *Cyphella* Cke., *Grev.*, 14, 1886: 129.

pteridophila, *Cyphella* Cke. in herb.; Sacc., *Syll. Fung.*, 6, 1888: 683.

cookei, *Cyphella* Sacc. & Syd., *Syll. Fung.*, 14, 1899: 231.

Collections at Kew are the type, ex "N.Z., Colenso, b.80", "N.Z., Colenso, b.965, b.1245" and "N.Z., Dr. Th. M. Ralph, ex herb. F.v.M.", the last carelessly recorded by Cooke as from Australia. All were found on living leaves of a species of *Hymenophyllum*. Spores were said to be elliptical, hyaline, $12 \times 4\mu$. Examination showed the 'species' to have been based on empty egg-cases of some butterfly or moth, amorphous bodies without hyphae or spores, loosely attached to the fronds.

filicicola, *Hydnum* Berk. = *Odontia arguta*.

42. FIMBRIATA, ODONTIA (Pers. ex Fr.) Fr., *Epicrisis*, 1838: 529.

fimbriatum, *Hydnum* (Pers.) Fr., *Syst. Myc.*, 1, 1821: 421.
secernibilis, *Odontia* Berk., *Fl. Tas.*, 2, 1860: 257.

On the sheet of the type of *O. secernibilis* at Kew, ex "Tasmania, W. Archer Esq.", H. J. Banker correctly referred the species as a synonym of *O. fimbriata*. This is the only collection from the region at Kew.

flavum, *Hydnum* Swartz. ex Berk. = *Mycobonia flavum* (Swartz) Pat.

Under the cover of *Hydnum flavum* Cooke placed two collections. "Toowoomba, Q., Hartmann" is a specimen of *Epithele glauca*; "Clarence River, N.S.W., Wilcox" cannot be named as the hymenium has been destroyed by insects.

43. FLORIFORME, STEREUM Bresadola, ex Lloyd in *Stipitate Stereums*, 24, 1913; *Annales Mycologici*, 18, 1920: 44.

On the type sheet of *Stereum moselei* are mounted three collections ex "Airey's Inlet, Vic., Miss Berthon" which Bresadola noted were of a different species, and appended a brief description. This Lloyd (*l.c.*) later published. Bresadola in 1920 formally but incompletely (since he did not note gloecystidia) described the species.

frustulosum, *Stereum* (Pers.) Fr. Under this cover Cooke placed two collections from New Zealand. Lars Romell (May, 1906) referred both to *Stereum rufum* on the sheet. They are New Zealand endemic species, "N.Z., Colenso, b.252" being a collection of *Aleurodiscus berggreni*, "N.Z., Colenso, b.297" a related undescribed *Aleurodiscus*.

44. FULIGINOSA, HYMENOCHAETE (Pers.) Lev., *Ann. Sci. Nat.*, Ser. III, 5, 1846: 152.

fuliginosa, *Thelephora* Pers., *Myc. Eur.*, 1, 1822: 145.

Two collections from the region are at Kew. "Moruya, N.S.W., W. N. Cheesman, 1914" was correctly named by Miss Wakefield, "Tasmania" placed by Cooke under *H. rubiginosa*. Both agree with specimens so named by Berkeley, but differ from plants to which the name was applied by Bresadola and certain other European mycologists.

gausapatum, *Stereum* Fr. = *Stereum spadiceum*.

glabrescens, *Hydnum* Berk. & Br. = *Hydnum muelleri*.

45. GLAUCA, EPITHELE (Cke.) Wakef., in Cleland's *Toadstools . . . of S. Aust.*, 1935: 256.

glauca, *Grandinia* Cke., Grev., 17, 1889: 55.

Collections from the region at Kew are the type of *Grandinia glauca* ex "Brisbane, Q., Bailey, No. 627", "Toowoomba, Q., Hartmann" placed by Cooke under *Hydnum flavum*, and "Victoria, J. B. Cleland, 1929".

globosa, *Cyphella* Rodw., *Papers and Proc. Roy. Soc. Tas.*, 1917, 1918: 108. No specimens are in Kew herbarium.

46. GRANULOSA, GRANDINIA (Pers.) Fr., *Epicrisis*, 1838: 527.

granulosa, *Thelephora* Pers. ex Fr., *Syst. Myc.*, 1, 1821: 446.

Of the collections from the region at Kew placed under this cover by Cooke, "N.Z., Colenso, b.133" is an *Odontia*; "N.Z., Colenso, b.389" consists of two lots, one of *Grandinia granulosa*, the other a sterile *Corticium*; "Tasmania" is a sterile *Grandinia*.

47. GRISEO-ZONATA, THELEPHORA Cke., Grev., 19, 1891: 104.

No specimens from the region are at Kew. New Zealand collections resemble the type from Aiken, South Carolina, a form of *T. terrestris* worthy of a specific name.

48. HABGALLAE, PENIOPHORA (Berk. & Br.) Cke., Grev., 8, 1879: 20.

habgallae, *Corticium* Berk. & Br., *Jour. Linn. Soc.*, 14, 1875: 72.

poroniaeforme, *Artocreas* Berk. & Br., *l.c.*, p. 73.

poroniaeformis, *Matula* (Berk. & Br.) Mass., *Jour. Roy. Micr. Soc.*, 1888: 173.

rompeltii, *Michenera* Rick, *Ann. Myc.*, 2, 1904: 243.

rompeltii, *Matula* (Rick) Lloyd, *Myc. Notes*, No. 30, 1908: 391.

cornea, *Cytidia* Lloyd, *Myc. Notes*, No. 47, 1917: 656.

corneus, *Aleurodiscus* Lloyd, *Myc. Notes*, No. 62, 1920: 930.

capensis, *Aleurodiscus* Lloyd, *l.c.*

capensis, *Gloeosoma* Lloyd, *Myc. Notes*, No. 65, 1921: 1088.

habgallae, *Cytidia* (Berk. & Br.) Martin, *Lloydia*, 5, 1942: 160.

Though present in Australia and New Zealand, there are no collections from the region in Kew herbarium.

49. HELVETICA, GRANDINIA (Pers.) Fr., *Hym. Eur.*, 1874: 627.

helveticum, *Hydnum* Pers. *Myc. Eur.*, 2, 1825: 184.

One collection from the region is at Kew, identified by Miss Wakefield, ex "Nambour, Blackall Range, Q., W. N. Cheesman, 1914".

50. HIRSUTUM, STEREUM (Willd.) Fr., *Epicrisis*, 1838: 549.

hirsuta, *Thelephora* Willd., ex Fr., *Syst. Myc.*, 1, 1821: 439.

varicolor, *Stereum* Lloyd, Letter 53, 1914: 10.

Specimens from the region under this cover at Kew are of three species. Correctly named are "Brisbane, Q., Broome, No. 185", "Porongorup, W. Aus.", "Port Jackson, N.S.W., W. Buckingham", "Pennant Hills, N.S.W., Challenger Expedition", "Clarence River, N.S.W., Dr. Beckler", "Upper Yarra River, Vic., F.v.M.", "Near Ballarat, Vic., C. French" and "Domain, Auckland, N.Z., W. N. Cheesman, 1914". The following collections are of *Stereum rameale*: "Mulgrave River, Q., No. 849", "Mt. Lofty Range, S. Aus., F.v.M.", "Sealers' Cove, Vic., F.v.M., No. 142", "New England, N.S.W.", "Melbourne, Vic., Le Fevre, No 208", "V.D.L., herb. Hooker, No. 20" (one collection of *S. rameale*, a second of *S. vellereum*) and "Chatham Islands, N.Z., Travers". One collection ex "Swan River, W. Aus., No. 159" is of *S. vellereum*; and that ex "Tasmania, W. Archer" consist of three species, *S. hirsutum*, *S. rameale* and *S. vellereum*.

51. HISPIDULUM, STEREUM (Berk.) nov. comb.

reflexa, *Phlebia* Berk., *Hook. Jour. Bot.*, 3, 1851: 168.

hispidula, *Phlebia* Berk., *Jour. Linn. Soc.*, 13, 1873: 167.

lugubris, *Stereum* Cke., *Grev.*, 12, 1884: 85.

stereooides, *Thelephora* Cke. & Mass., *Grev.*, 18, 1889: 5.

butleri, *Auricularia* Mass., *Kew Bull. Misc. Inf.*, 1906: 94.

reflexa, *Auricularia* (Berk.) Bres., *Ann. Myc.*, 9, 1911: 551.

ceriferum, *Stereum* Wakef., *Kew Bull. Misc. Inf.*, 1915: 370.

Bresadola referred the species to *Auricularia rugosissima* (Lev.) Bres. (*Ann. Myc.*, 14, 1916: 231) which, though similar in external appearance, differs profoundly in micro-structure. Under the cover of *Phlebia reflexa* at Kew are the following collections from the region, "Moruya, N.S.W., W. N. Cheesman, 1914" and "N.Z., Colenso, b.39, b.338, b.365". Under *Stereum lugubris* is placed the type collection ex "N.Z., Colenso, b.23"; under *Thelephora stereooides* the type ex "Oakleigh, Vic., Mrs. Martin, No. 450"; under *Phlebia hispidula* the type ex "Australia, Dr. Schomburgk, S.13"; under *Stereum ceriferum* the type ex "N.Z., Rotorua, W. N. Cheesman, 1914". One collection ex "Western Australia" Cooke filed under *Stereum illudens*. *Auricularia butleri* was erected on a collection from Dehra Dun, India.

The combination *Stereum reflexum* was applied by Lloyd (*Myc. Notes*, No. 66, 1922: 1128) to a collection from Sumatra. Stevenson & Cash (*Lloyd Library and Mus. Bull.*, 35, 1936: 57) stated that although Lloyd did not describe the species he filed with the collection a brief note which they published. From this, though too incomplete to enable the species to be identified, it is evident the species is not the same as that known as *Phlebia reflexa*, differing in the presence of a colour zone beneath the pileus hairs, among other features. Possibly Lloyd's specimen was of *Stereum lobatum*. The species under consideration is a *Stereum*, and has been named *S. hispidulum* since that name was applied by Berkeley to a collection he labelled *Phlebia hispidula*, the type of which at Kew matches collections of *P. reflexa* and the other synonyms listed.

hollandii, *Stereum* Lloyd = *Stereum prolificans*.

52. ILLUENS, STEREUM Berk., *Lond. Jour. Bot.*, 4, 1845: 59.

archeri, *Stereum* Berk., *Fl. Tas.*, 2, 1860: 259.

pannosum, *Stereum* Cke., *Grev.*, 8, 1879: 56.

archeri (*Veluticeps*) *Hymenochaete* (Berk.) Cke., *Grev.*, 8, 1880: 149.

spiniferum, *Stereum* Lloyd, Letter 51, 1914: 4.

beyrichii, *Lloydella* (Fr.) Bres., in herb. Kew.

Collections at Kew from the region correctly named are the type ex "Swan River, W. Aus., No. 158", "Brisbane, Q., No. 567", "National Park, S. Aus., W. N. Cheesman, 1914", "Sugar Loaf Mts., N.S.W., F.v.M.", "Pennant Hills, N.S.W., Challenger Expedition", "Tift Creek, F.v.M.", "Sealers' Cove, Vic., F.v.M.", "Melbourne, Vic., G. Le Fevre, No. 205", "Narranoom, Vic., E. Stranger", "Moe, Gippsland, Vic., Webb", "Near Ballarat, Vic., C. French", "Airey's Inlet, Vic., Miss Berthon", "Gippsland, Vic., Murray", "Tasmania, Gunn, Nos. 13, 64", "V.D.L., Stuart", "Tasmania, W. Archer, Esq.", "Back River Gully, Tas., 321 H", "N.Z., T. Kirk, Nos. 68, 99" and "N.Z., Colenso, b.176". Filed under *Stereum prolificans* but labelled *S. shraderi* is "Clarence River, N.S.W., F.v.M.". Under *S. spiniferum* are the type ex "Australia, J. T. Paul" and "Gulung, N.S.W., Dr. Barnard". Labelled *Stereum ferrugineum* but filed under *Hymenochaete rubiginosa* is "N.Z., Colenso, b.153". The type of *Stereum archeri* is ex "Tasmania". Under *Stereum pannosum* are placed "Waitaki, N.Z., No. 342", "Dunedin, N.Z., No. 315" (both cited as the type by Cooke), "Papakura, N.Z., T. Kirk, No. 61" and "N.Z., Colenso, b.906". Filed under the cover of *S. illudens* are "West Australia", which is a collection of *Stereum hispidulum*, and "Condamine River, Q., No. 800", which is of a species of *Hymenochaete*.

53. INCARNATA, PENIOPHORA (Pers.) Karst., *Hedw.*, 28, 1889: 27.

incarnata, *Thelephora* Pers., *Myc. Eur.*, 1, 1822: 130.

incarnatum, *Corticium* (Pers.) Fr., *Epicrisis*, 1838: 564.

Collections from the region under this cover at Kew are "Swan River, W. Aus., No. 165", which is not *P. incarnata* but now unidentifiable; "N.Z., Whakarewarewa, E. J. Butler, July 1923", identified by Miss Wakefield; "New Zealand" and "N.Z., Sinclair", the last filed under *Corticium laeve* by Cooke.

54. INFUNDIBULIFORMIS, CLADODERRIS (Kl.) Fr., in Wahlberg's *Fungi Natalensis*, 1848: 21.

infundibuliforme, *Actinostroma* Klotzsch, *Nova Acta Nat. Cur.*, Suppl. 1, 1848: 237.

australica, *Cladoderris* Berk., ex Cke., *Grev.*, 11, 1882: 28, *nomen nudum*.

The only collection from the region at Kew is ex "Gippsland, Vic.". Labelled on the sheet by Berkeley as *Cladoderris dendritica*, Lloyd held it to be a specimen of *C. spongiosa* and Cooke made it the type of *C. australica*.

inmatum, *Hymenochaete* Cke. & Mass., *Grev.*, 15, 1887: 99. The type, ex "Daintree River, Q.", proved on examination to be a species of *Epithele*. Bresadola noted on the sheet that the collection "= *Hymenochaete crocicreas* Berk. & Br."

55. INSGNIS, CRATERELLUS Cke., *Grev.*, 19, 1890: 2.

The type is at Kew, ex "N.Z., Colenso, No. 518".

insularis, *Hymenochaete* Berk. Cooke placed a collection under this cover, ex "Toowoomba, Q., Hartmann" which is of *Duportella tristricula*.

intermedia, *Peniophora* Mass. = *Peniophora vinosa*.

intybacea, *Thelephora* Pers. ex Fr. A collection placed under the cover by Cooke, ex "Sydney, N.S.W., Miss Scott" is of *Thelephora terrestris*.

investiens, *Hydnum* Berk., *Lond. Jour. Bot.*, 4, 1845: 57. The type, ex "Swan River, W. Aus., Drummond, No. 138, on black boys" is a resupinate fragment now unidentifiable.

56. INVOLUCRUM, STEREUM Fr., *Epicrisis*, 1838: 546.

Collections from the region at Kew are ex "New Guinea, Armit", "Strickland River, New Guinea, 1885", "Fly River, New Guinea, W. Bauerlen, No. 49", "Fly River, New Guinea, Everell's Expedition", "North Queensland" and "Daintree River, Q.". The last consists of three lots which were placed by Cooke under *S. molle*.

Fries, Saccardo (1888, p. 560) and Masee (1890, p. 176) cited the author of the species as Klotzsch, *Linnaea*, 7, 1832: 499, but there is no reference to the species in any volume of *Linnaea*.

isidiodes, Hydnum Berk., *Lond. Jour. Bot.*, 4, 1845: 58. The type, ex "Swan River, W. Aus., Drummond, No. 149", consists of two sterile fragments which were said to have grown upon a specimen of *Polyporus gryphaeformis*. A second collection placed under the cover by Cooke, ex "Gippsland, Vic., Miss Campbell" is not of the same species.

kalchbrenneri, *Hymenochaete* Mass. = *Peniophora vinosa*.

Kunzei, *Hymenochaete* (Hook.) Mass. = *Hymenochaete luteobadia*.

laciniata, *Thelephora* (Pers.) Fr. = *Thelephora terrestris*.

lacteum, Corticium Fr. Under this cover Cooke placed a collection ex "Victoria, Miss Campbell". It is the white *Septobasidium*, *S. simmondsii* Couch, which grows upon living species of *Hakea* and *Acacia*.

laeve, *Corticium* (Pers. ex Fr.) Sacc. = *Corticium evolvens*.

57. LAEVIGATUM, HYDNUM (Swartz) Fr., *Syst. Myc.*, 1, 1821: 399.

Of the two collections from the region placed under this cover "Tasmania" agrees with authentic European specimens; "Brisbane, Q., F. M. Bailey, No. 757" is a specimen of *H. crocidens*.

lamellatum, *Stereum* (Berk. & Curt.) Cke. = *Stereum caperatum*.

latissimum, *Stereum* Berk., *Fl. N.Z.*, 2, 1855: 183. No specimens are in Kew herbarium.

latum, *Stereum* Cke. & Mass. = *Stereum percome*.

leichkardtianum, *Stereum* (Lev.) Mass. = *Stereum lobatum*.

58. LIVIDUM, CORTICIUM (Pers.) Fr., *Epicrisis*, 1838: 563.

livida, *Thelephora* Pers., ex Fr., *Syst. Myc.*, 1, 1821: 447.

Two collections are in Kew herbarium, both named by Miss Wakefield, namely, "Lisarow, N.S.W., J. B. Cleland" and "Hawkesbury River, N.S.W., J. B. Cleland, Dec. 1914".

59. LOBATUM, STEREUM (Kunze) Fr., *Epicrisis*, 1838: 547.

lobata, *Thelephora* Kze., in Weigelt's Exsicc. 1827, ex Fr., *Linnaea*, 5, 1830: 527.

boryanum, *Stereum* Fr., *Epicrisis*, 1838: 547.

luteobadium, *Stereum*, Fr., *l.c.*

perlatum, *Stereum* Berk., *Lond. Jour. Bot.*, 1, 1842: 153.

sprucei, *Stereum* Berk. & Curt., *Jour. Linn. Soc.*, 10, 1868: 331.

leichkardtianum, *Stereum* (Lev.) Mass., *Jour. Linn. Soc.*, 27, 1890: 175.

pictum, *Stereum* Berk., ex Mass., *l.c.*, p. 185.

australe, *Stereum* Lloyd, Letter 48, 1913: 10.

Under the cover of *Stereum lobatum* at Kew are the following collections from the region: "Norfolk Island, Robinson, Nos. 5, 90", "Papua, Baridi, C. E. Carr, Nos. 13549, 13884", "Fly River, New Guinea, Bauerlen, No. 60", "Strickland River, New Guinea, Bauerlen", "Astrolabe, New Guinea, Armit", "S.E. New Guinea, Capt. Armit, 1885", "New Guinea, Rev. Chalmers", "Brisbane, Q.", "Endeavour River, Q., No. 207", "Heberon, Q.", "Twofold Bay, Q., Tygrove, White", "Toowoomba, Q., Hartmann, No. 2", "Richmond River, N.S.W., Camara", "Tweed River, N.S.W., Camara, f.80, f.82", "Moonan Brook, N.S.W., Miss H. Carter", "Clarence River, N.S.W., Dr. Beckler", "Berry, N.S.W., F. A. Rodway, No. 14806", "Tarwin, Gippsland, Vic., Mrs. Manton", "Mt. Dromedary, Nos. 29, 38", "Upper Yarra River, Vic., Lucas", "Gippsland, Vic., Webb", "Sealers' Cove, Vic., F.v.M.", "V.D.L., ex Hooker herb.", "V.D.L., Gunn", "V.D.L., Laurence", "Johnny's Creek, Tasmania, No. 172", "V.D.L., Gunn & Laurence", "New Norfolk, Tas.", "N.Z., Nelson, Dr. Sinclair, 1860", "N.Z., Middle Island, Dr. Sinclair", "N.Z., Dr. Lindsay", "N.Z., Colenso, b.11, b.31, b.36, b.260, b.293, b.308" and "N.Z., Wairoa River, Kaipara Harbour, H. Samuel Mossman, 1850, No. 810". Under *Stereum spadiceum* Berkeley placed "Tasmania, W. Archer". Cooke filed under *Stereum perlatum* "New Caledonia, Dr. Sarasin, No. 30" and "Port Denison, Q., Fitzalan, 1882". Under *Stereum boryanum* he

placed "Daintree River, Q., Pentzcke, 1882", "North Queensland", "Tweed River, N.S.W., Camara, f.84" and "Richmond River, N.S.W., Camara". Under *Stereum fasciatum* Cooke placed "Trinity Bay, Q., Sayer, No. 42"; under *Stereum gausapatum* "Russell River, Q., Sayer, No. 48". Miss Wakefield filed "Melbourne Botanic Gardens, Vic., W. N. Cheesman, 1914" under *Stereum leichhardtianum*. Cooke placed "Melbourne, Vic., F.v.M." under *Hymenochaete luteobadia* and labelled the collection *Stereum luteobadium*. Under *Stereum pictum* Berkeley filed the type ex "Back River Gully, Tas., No. 321". One collection ex "Richmond River, N.S.W., Camara, f.92" Cooke placed under *Stereum schomburgkii*. Masseur labelled "Airey's Inlet, Vic., Miss Berthon" as *Stereum vellereum* var. *australiense*. Finally, a collection ex "Wairoa River, Kaipara Harbour, N.Z., Samuel Mossman, No. 814" was found to consist of the three species *S. lobatum*, *S. vellereum* and *Polyporus adustus*.

60. LONGIPES, CYPHELLA Cke. & Mass., *Grev.*, 21, 1892: 38.

The type is at Kew, ex "Queensland, Bailey, No. 938".

lugens, *Hymenochaete* (Kl.) Bres. = *Hymenochaete semilugens*.

lugubris, *Stereum* Cke. = *Stereum hispidulum*.

61. LUTEAURANTIACUM, CORTICIUM Wakef., *Kew Bull. Misc. Inf.*, 1915: 372.

The type is at Kew, ex "Mamaku, N.Z., W. N. Cheesman, 1914".

62. LUTEOBADIA, HYMENOCHAETE (Fr.) Hoehn. & Litsch., *K. Akad. Wiss., Wien, Sitz.*, 116, 1907: 754.

luteobadia, *Thelephora* Fr., *Linnaea*, 5, 1830: 526.

badia, *Thelephora* Kl., in *Hook. Bot. Misc.*, 2, 1831: 163.

kunzei, *Thelephora* Hook., *l.c.*

luteobadium, *Stereum* Fr., *Epicrisis*, 1838: 547.

laetum, *Stereum* Berk., *Jour. Acad. Nat. Sci. Phil.*, 2, 1853: 279.

laeta, *Hymenochaete* Berk., ex Cke., *Grev.*, 8, 1880: 146.

kunzei, *Hymenochaete* (Hook.) Mass., *Jour. Linn. Soc.*, 27, 1890: 100.

Of the collections from the region at Kew "Endeavour River, Q.", agrees with the type of *H. kunzei*; "Blomfield River, Q., Bauer" is the same though placed by Cooke under *H. strigosa*; and "Melbourne, F.v.M.", placed by Cooke under *H. luteobadia*, consists of two collections of *Stereum lobatum*.

luteobadium, *Stereum* Fr. = *Stereum lobatum pro parte* and *Hymenochaete luteobadia*, *p.p.*

luteocincta, *Coniophora* (Berk.) Sacc. The type of *Thelephora luteocincta* Berk., ex "Wangaretta, Vic." consists of several sterile fragments closely adnate on wood. In microstructure they match *Coniophora arida*, consequently the species is best treated as a synonym of the latter.

mellisii, *Stereum* Berk., ex Cke. = *Stereum* affine.

membranaceum, *Hydnum* (Bull.) Fr. A collection placed under this cover by Cooke, ex "N.Z., Colenso, b. 152" is of *Merulius nothofagi*.

meruloides, *Hydnum* Berk. & Br. The type, ex "Brisbane, Q., Bailey, No. 246" is a deformed specimen of *Hydnum cirrhatum* Pers. ex Fr. A second collection under the cover, ex "Australia", Lloyd labelled on the sheet *Irpea meruloides*, and Miss Wakefield correctly referred it to *Irpea brevis*.

miniatum, *Corticium* Cke., *Grev.*, 9, 1880: 2. The type, ex "Condamine River, Q., 1880, F.v.M." is, as Miss Wakefield had noted on the sheet, a specimen of the imperfect stage of a *Hypoxyton*.

molare, *Radulum* Fr. A sterile fragment placed under this cover by Cooke, ex "Brisbane, Q., No. 234, on peach tree", does not agree with authentic specimens. On the sheet it had been labelled *R. subceraceum* Berk. & Br. though published as *R. molare* in *Trans. Linn. Soc.*, Ser. II, 2, 1883: 63.

molle, *Stereum* (Lev.) Sacc. Three collections referred to the species by Cooke, ex "Daintree River, Q." are of *Stereum involucreum*.

moselei, *Stereum* Berk. Under the cover are three collections ex "Airey's Inlet, Vic., Miss Berthon" which Bresadola described under the name of *Stereum floriforme*.

63. MOUGEOTII, HYMENOCHAETE (Fr.) Cke., *Grev.*, 8, 1880: 147.

mougeotii, *Thelephora* Fr., *Elench.*, 1, 1828: 188.

Three collections are at Kew from Australia, ex "New Guinea, Tantawanglo, W. Bauerlen, No. 240", "Brisbane, Q., F. Campbell, No. 499" and "Tasmania, W. Archer, Esq."

micidum, *Hydnum* Pers. ex Fr. A collection placed under this cover by Cooke, ex "N.Z., Colenso, b.1075" is of *Mycocacia subceracea*.

64. MUELLERI, HYDNUM Berk., *Jour. Linn. Soc.*, 13, 1873: 167.

glabrescens, *Hydnum* Berk. & Br., *Jour. Linn. Soc.*, 14, 1875: 59.

The type at Kew was ex "Tweed River, N.S.W. Guilfoyle". A second collection under the cover, ex "Toowoomba, Q., Hartmann" possesses the same microstructure but differs in being imbricate.

muelleri, *Kneiffia* Berk., *Jour. Linn. Soc.*, 13, 1873: 167. The type ex "Adelaide, S. Aus., Dr. Schomburgk" is probably a collection of *Grandinia farinacea*.

65. MULTIPLEX, CRATERELLUS Cke. & Mass., *Grev.*, 18, 1889: 25.

The type at Kew is from "Tasmania, Derwent River, Rodway, No. 658".

murinum, *Corticium* Berk. & Br. Under the cover of the type which is a species of *Coniophora* from Ceylon, are filed two Australian collections, ex "On Eucalyptus, ex Leuchmann, Myc. Univ., No. 1504" and "Berwick, Vic., 1878, F.v.M.". Both are specimens of *Peniophora vinosa*.

66. MUSCICOLUM, ASTEROSTROMA (Berk. & Curt.) Mass., *Jour. Linn. Soc.*, 25, 1889: 155.

musciicola, *Hymenochaete* Berk. & Curt., *Jour. Linn. Soc.*, 10, 1868: 334.

Though present in New Zealand, there are no collections at Kew from this region.

67. NEOCALEDONICUM, STEREUM Pat. & Har., *Jour. de Bot.*, 17, 1903: 6.

Two collections from New Caledonia are at Kew, part of the type ex "Mea, New Caledonia" and "Ignambuti, Sarasin, No. 75". The species has been listed as it will probably be found in Queensland.

nigricans, *Stereum* Lev. = *Hymenochaete villosa*.

68. NIGRUM, HYDNUM Fr., *Syst. Myc.*, 1, 1821: 404.

Two collections from the region placed under this cover at Kew agree with authentic European specimens. They are ex "Pennant Hills, N.S.W., June 1874, Challenger Expedition" and "Upper Yarra River, Vic., C. Walker". *H. sinclairii* is similar, but differs in the caespitose azonate pilei.

nitidulum, *Stereum* Berk. One collection placed under the cover by Cooke, ex "Australia, R. Brown" is of *S. thozetii*. Two others, ex "Endeavour River, Q., Persletz" and "North Queensland", filed here by Cooke, are collections of *S. elegans*.

niveum, *Hydnum* Pers. ex Fr. One collection placed under the cover by Cooke, ex "N.Z., Colenso, b. 740" is of an undescribed *Epithele*.

novae-zealandiae, *Hydnum* Col. = *Hydnum coralloides*.

noxia, *Hymenochaete* Berk., ex Cke., *Grev.*, 8, 1880: 149. The type, ex "Samoa, T. Powell, Jan. 1875" is based on the sterile context of a specimen of *Fomes noxious* Corner.

69. OAKESII, ALEUROIDISCUS (Berk. & Curt.) Cke., *Grev.*, 3, 1875: 172.

oakesii, *Corticium* Berk. & Curt., *Grev.*, 1, 1873: 166.

Three collections from New Zealand, ex "Colenso, b.528, b.590, b.729" agree with the type ex Alabama.

obliquum, *Stereum* Mont. & Berk. One collection filed under the cover by Cooke, ex "N.Z., Wairarapa, Dry River, T. Kirk, No. 140" is a torn and rosetted specimen of *Stereum sowerbeii*.

ochraceoflavus, *Aleurodiscus* Lloyd = *Aleurodiscus zealandicus*.

70. OCHRACEUM, HYDNUM Pers., ex Fr., *Syst. Myc.*, 1, 1821: 414.

radicale, *Corticium* Berk., *Lond. Jour. Bot.*, 4, 1845: 59.

radicale, *Stereum* (Berk.) Mass., *Jour. Linn. Soc.*, 27, 1890: 187.

One collection ex "Victoria, Dandenong Ranges, E. McLennan", filed by Miss Wakefield under this cover, agrees with European specimens. A second, now merely a fragment, ex "Swan River, W. Aus., Drummond, No. 162" is the type of *Corticium radicale*.

ochroleucum, *Stereum* Fr. Six collections from the region were placed under this cover by Cooke. "N.Z., Wellington, T. Kirk, No. 261" and "N.Z., Colenso, b.300, under bark of rimu" are sterile species of *Corticium*; "N.Z., Colenso, b.74" is a specimen of a white *Septobasidium* which grows on living *Pseudopanax arboreum*; "N.Z., Colenso, b.948", named *Corticium spumeum* on the sheet, is also a species of *Septobasidium*; "N.Z., Colenso, b.619" is a collection of *Peniophora cinerascens*; and "N.Z., Crow's Nest, Ngaiu, T. Kirk" is a fragment of an undescribed *Aleurodiscus*.

71. ODORATUS, CRATERELLUS (Schw.) Fr., *Epicrisis*, 1838: 532.

odoratus, *Merulius* Schw., *Nat. Ges., Leipz.*, 1, 1822: 91.

confluens, *Craterellus* Berk. & Curt., *Jour. Linn. Soc.*, 9, 1867: 423.

Under the cover of *C. confluens* are placed four collections, ex "Endeavour River, Q.", "Endeavour River, Q.", "Persieh", "Goode Island, Torres Strait, Q., Powell" and "Lilydale, Vic., Mrs. Martin".

72. OLIVACEA, CONIOPHORA (Fr., ex Pers.) Karst., *Bidr. kann. Finl. Nat. Folk.*, 37, 1882: 162.

Though the species is present in New Zealand, there are no collections from the region at Kew. One so named by Cooke, ex "Bunyip, Vic., No. 376" is of *Coniophora arida*.

olivaceum, *Hymenochaete* Cke. = *Duportella schomburgkii*.

pannosa, *Thelephora* Sow., ex Fr. One collection ex "V.D.L., Mr. Gunn", placed under the cover by Berkeley, was by Cooke correctly referred to *Stereum sowerbeii*.

pannosum, *Stereum* Cke. = *Stereum illudens*.

pannosum, *Stereum* Cke. & Mass. = *Stereum bicolor*.

73. POPYRINA, PENIOPHORA (Mont.) Cke., *Grev.*, 8, 1879: 20.

papyrinum, *Stereum* Mont., in *Hist. Cuba, Pl. Cell.*, 1842: 374.

Three collections from Australia are under the cover of *Stereum papyrinum* at Kew. "Tropical Queensland, Bailey" is of *Peniophora papyrina*; "Wangaretta, Vic." and "V.D.L. Gunn, 382 b" are of *Peniophora vinosa*.

pedicellata, *Thelephora* Schw., ex Fr. = *Septobasidium pedicellatum*.

penetrans, *Corticium* Cke. & Mass. = *Vararia portentosa*.

74. PERCOME, STEREUM Berk. & Br., *Jour. Linn. Soc.*, 14, 1875: 65.

amaena (*Stereum*) *Thelephora* Lev., *Ann. Sci. Nat.*, Ser. III, 5, 1846: 149.

amaenum, *Stereum* (Lev.) Mass., *Jour. Linn. Soc.*, 27, 1890: 193.

latum, *Stereum* Cke., *Grev.*, 20, 1892: 92.

corrige, *Stereum* Lloyd, *Myc. Notes*, No. 57, 1919: 826.

Under *Stereum amaenum* at Kew is filed a collection ex "Stannary Hills, Q., S. L. Bancroft, 1909"; and under *S. percome* are "Dunk Island, Q., W. Cottrell Dormer, Aug. 1927, No. 30" and "Kuranda, Aus., H. F. Dean, No. 21".

Though the earliest specific name for the species is *T. amaena*, the combination *Stereum amaenum* cannot be employed since it was used for an African plant by Kalchbrenner & MacOwan (*Grev.*, 10, 1881: 58).

pergamenum, *Stereum* Berk. & Curt. Of the collections from the region placed under this cover by Cooke, "Kumusi River, New Guinea, Fitzgerald, 1895" is of *Stereum affine*; "Port Jackson, N.S.W., Miss Hopham, No. 2" is too imperfect to identify

perlatum, *Stereum* Berk. = *Stereum lobatum*.

75. PERSIMILE, *ASTEROSTROMA* Wakef., *Kew Bull. Misc. Inf.*, 1915: 372.

Two collections are under the type cover, the type ex "N.Z., Rotorua, W. N. Cheesman, 1914" and "Australia, ex C. G. Lloyd, on *Eucalyptus* bark".

petalodes, *Stereum* Berk. A collection placed under this cover by Cooke, ex "Gippsland, Vic." is a rosetted form of *Stereum elegans*.

pevatum, *Hydnum* Mass. = *Grandinia australis*.

peculoides, *Aleurodiscus* Wakef. = *Aleurodiscus berggreni*.

phaeum, *Stereum* Berk. = *Hymenochaete villosa*.

pictum, *Stereum* Berk., ex Mass. = *Stereum lobatum*.

polygonium, *Corticium* (Pers.) Fr. Of the three collections from the region placed under this cover by Cooke "N.Z., Colenso, b.670" and "N.Z., Colenso, b.2082", are of undescribed species of *Aleurodiscus*; "N.Z., Colenso, 1866, b.447" is of *Peniophora vinosa*.

76. PORTENTOSA, *VARARIA* (Berk. & Curt.) nov. comb.

portentosum, *Corticium* Berk. & Curt., *Grev.*, 2, 1873: 3.

penetrans, *Corticium* Cke. & Mass., *Grev.*, 19, 1891: 90.

Though the species is common in New Zealand there are no collections from this area in Kew herbarium. The only Australian collection is the type of *Corticium penetrans*, ex "Sorrento, Vic., Mrs. Martin, No. 635".

77. PRINCEPS, *STEREUM* (Jungh.) Sacc., *Syll. Fung.*, 6, 1888: 570.

princeps, *Thelephora* Jungh., *Fl. Crypt. Javae*, Fasc. 1, 1818: 38.

A collection ex "Baridi, Papua, C. E. Carr, No. 13565" agrees with other collections under the cover at Kew.

78. PROLIFICANS, *STEREUM* Berk., *Jour. Linn. Soc.*, 16, 1877: 41.

vespilloneum, *Stereum* Berk., *Jour. Linn. Soc.*, 16, 1877: 44.

hollandii, *Stereum* Lloyd, *Syn. Stip. Stereums*, 1913: 30.

Collections from the region at Kew are filed under several covers. Under *S. prolificans* are the type ex "Somerset, Cape York Peninsula, Q., Challenger Expedition", "Russell River, Q., Sayer, No. 49" labelled *S. baileyannum* on the sheet, "Brisbane, Q., F. M. Bailey, No. 314" (a duplicate of the last is under the cover of *S. perlatum* in the British Museum of Natural History). Under *S. vespilloneum* are the type ex "Aru Island, Challenger Expedition" and "Melbourne, Vic., G. Le Fevre" which is an empty peridium of *Scleroderma fluidum*. Under *S. hollandii* are the type ex "Okumi, Cross River Expedition, J. H. Holland, No. 40" and "Loyalty Islands, F. Sarasin". Under *Hymenochaete phaea* are "Daintree River, Q." and "Brisbane, Q., No. 314". One collection placed by Cooke under *Stereum prolificans*, ex "Clarence River, N.S.W., F.v.M." and labelled *S. shraderi* Thuem., is of *S. illudens*.

peridophila, *Cyphella* Cke., ex Sacc. A later name used for *Cyphella filicicola*, which was based upon empty egg-cases of a butterfly or moth.

79. PUBERA, *PENIOPHORA* (Fr.) Sacc., *Syll. Fung.*, 6, 1888: 646.

pubera, *Thelephora* Fr., *Elench.*, 1, 1828: 215.

puberum, *Corticium* Fr., *Epicrisis*, 1838: 562.

pubera, *Hymenochaete* (Fr.) Lev., *Ann. Sci. Nat.*, Ser. III, 5, 1846: 152.

One collection from Australia is in Kew herbarium, named by Miss Wakefield, ex "Katoomba, Blue Mts., N.S.W., W. N. Cheesman, 1914".

pulverulenta, *Coniophora* (Lev.) Mass. A collection from this region filed under this cover by Cooke, ex "Victoria, No. 60, on wall of damp cellar", is of *Merulius lacrymans*.

purpurea, *Hymenochaete* Cke. & Morg. = *Peniophora vinosa*.

80. PURPUREUM, *STEREUM* Pers., ex Fr., *Epicrisis*, 1838: 548.

purpurea, *Thelephora* Pers., ex Fr., *Syst. Myc.*, 1, 1821: 440.

Two collections from the region are at Kew, ex "Wellington, N.Z., A. H. Cockayne, Aug. 1914, on willow" and "Adelaide, S. Aus., D. B. Adam, on *Cytisus scoparius*". Under

the cover Berkeley placed a specimen ex "Tasmania, W. Archer Esq." which is of *Stereum rameale*.

pusillum, *Stereum* Berk. A specimen so named by Berkeley, ex "V.D.L., Gunn" is now placed correctly under *S. elegans*.

radians, *Thelephora* Berk. Both collections placed under the cover by Cooke, ex "Guntawang, N.S.W., Hamilton" and "Mt. Napier, Vic., 1883" are of *Stereum soverbeii*.

81. *RADIATOFISSUM*, *STEREUM* Berk. & Br., *Trans. Linn. Soc.*, Ser. II, 2, 1883: 63.

The type alone is under the cover at Kew, ex "Brisbane, Q., No. 277". On the sheet Bresadola had written "= *Stereum spectabile* Kl. = *Lloydella spectabile* (Kl.) Bres."

radicale, *Corticium* Berk. On the type sheet containing the type collection ex "Swan River, W. Aus., Drummond, No. 162" Berkeley had written: "A very distinct species from any with which I am acquainted." Little wonder, since the type is merely a fragment of *Hydnum ochraceum*.

radicale, *Stereum* (Berk.) Mass. = *Hydnum ochraceum*.

82. *RADICATA*, *PENIOPHORA* (P. Henn.) Hoehn. & Litsch., *K. Akad. Wiss., Wien, Sitz.*, 117, 1908: 1092.

radicatum, *Corticium* P. Henn., in *Engl. Pflanzenwelt Ostaf.*, 1895: 54.

One collection from Australia is at Kew, ex "Ballarat, Vic., W. N. Cheesman, 1914".

83. *RAMEALE*, *STEREUM* (Schw.) Mass., *Jour. Linn. Soc.*, 27, 1890: 187.

rameale, *Thelephora* Schw., *Nat. Ges. Leipz., Schrift.* 1, 1822: 106.

complicatum, *Stereum* Fr., *Epicrisis*, 1838: 548.

ramealis, *Hymenochaete* Berk., *Jour. Linn. Soc.*, 14, 1875: 68.

Collections from the region at Kew correctly named are "South Western Australia, 1881, F.v.M." and "Sugar Loaf Mts., N.S.W., Baron Mueller". Under *Stereum purpureum* Berkeley placed a collection ex "Tasmania, W. Archer Esq.". Under *S. hirsutum* Cooke filed "Mulgrave River, Q., No. 849", "Mt. Lofty, S. Aus., F.v.M.", "Sealers' Cover, Vic., F.v.M., No. 142", "Melbourne, Vic., Le Fevre, No. 208", "New England, N.S.W.", and "Chatham Islands, N.Z., Travers". Under *S. spadiceum* Berkeley placed "Western Point, Vic., F.v.M., June 1853".

84. *REGULARIS*, *THELEPHORA* Schw., *Nat. Ges. Leipz., Schrift.* 1, 1822: 105.

ravenelii, *Thelephora* Berk., *Grev.*, 1, 1873: 148.

hiscens, *Thelephora* Berk., *l.c.*

A collection ex "Strickland River, New Guinea, Bauerlen, 1885, No. 19", though larger, agrees in microstructure with other specimens under the cover at Kew.

reticulatum, *Corticium* Berk. & Br. = *Septobasidium rhabarbarinum*.

retirugum, *Stereum* Cke. A collection so named by Cooke, ex "Australia, Kalchbrenner, No. 7" is of *Duportella schomburgkii*.

85. *RHABARBARINA*, *HYMENOCHAETE* (Berk.) Cke., *Grev.*, 8, 1880: 148.

rhabarbarinum, *Corticium* Berk., *Fl. N.Z.*, 2, 1855: 184.

Only the type collection is at Kew, ex "New Zealand, Colenso". A specimen placed by Cooke under the cover, ex "N.Z., Colenso, b.391" and by Bresadola referred on the sheet to *H. rheicolor*. is of *H. tenuissima*.

86. *RHABARBARINUM*, *STEREUM* (Berk. & Br.) Wakef., *Kew Bull. Misc. Inf.*, 1915: 370.

rhabarbarinum, *Corticium* Berk. & Br., *Jour. Linn. Soc.*, 14, 1875: 69.

The type from Ceylon and "Nowra, N.S.W., W. N. Cheesman, 1914" are the only collections under the cover at Kew.

87. *RHODOSPORA*, *VARARIA* (Wakef.) nov. comb.

rhodospora, *Asterostromella* Wakef., *Kew Bull. Misc. Inf.*, 1915: 372.

The type of *A. rhodospora*, ex "Blackall Range, Q., W. N. Cheesman, 1914" is a *Vararia* with characteristic dichophyses of the genus.

roseum, *Corticium* Pers. ex Fr. Berkeley referred to this species a collection ex "Tasmania, Archer" which, being sterile, cannot now be identified.

rubiginosa, *Hymenochaete* (Dicks) Lev. None of the collections from this region placed under the cover at Kew is of this species. "N.Z., Colenso, b.153", labelled on the sheet *Stereum ferrugineum*, is of *S. illudens*; "Tasmania" is a specimen of *Hymenochaete fuliginosa*; "V.D.L., ex Hooker herb." labelled *Thelephora ferruginea*, "V.D.L., Messrs. Gunn & Laurence" and "V.D.L., ex herb. Hooker, No. 19" are collections of *Hymenochaete villosa*.

88. RUBROPUNCTATUM, CORTICIUM Mass. & Rodw., in Rodway, *Papers and Proc. Roy. Soc. Tas.*, 1898-99, 1900: 98, *nomen nudum*.

The type collection is at Kew, ex "Tasmania, Rodway, No. 561". Although the name was published in a list of Tasmanian fungi compiled by Rodway, the species was not formally described.

89. RUGOSUM, STEREUM Pers. ex Fr., *Epicrisis*, 1838: 552.
rugosa, *Thelephora* Pers. ex Fr., *Syst. Myc.*, 1, 1821: 439.

Under the cover at Kew is a collection ex "Tannuda, S. Aus., W. N. Cheesman, 1914" which agrees with authentic European specimens. It was named by Miss Wakefield. Cooke filed under the cover three specimens of *Peniophora cinerascens*, ex "Clarence River, N.S.W., Wilcox".

9. SAMBUCCI, PENIOPHORA (Pers.) Burt, *Ann. Mo. Bot. Gard.*, 12, 1926: 233.
sera, *Thelephora* Pers., *Myc. Eur.*, 1, 1822: 151.
sambuci, *Thelephora* Pers., *l.c.*, p. 152.
sambuci, *Corticium* (Pers.) Fr., *Epicrisis*, 1838: 565.
serum, *Corticium* (Pers.) Fr., *Hym. Eur.*, 1874: 659.

Though the species is common in New Zealand there are no collections from the region at Kew. Of those filed under the cover (of *Corticium serum*) "N.Z., Waitaki, No. 260" is a specimen of *Polyporus dichrous*; and "N.Z., Wellington, Travers, No. 375" is of a white *Septobasidium* which grows on living branches of *Pseudopanax arboreum*.

91. SANGUINOLENTUM, STEREUM (A. & Sw.) Fr., *Epicrisis*, 1838: 549.
sanguinolenta, *Thelephora* Alb. & Schw., ex Fr., *Syst. Myc.*, 1, 1821: 440.

Four collections from the region are at Kew, namely, "N.Z., Colenso, b.284, b.354", "Domain, Auckland, N.Z., W. N. Cheesman, 1914" and "S. Aus., D. B. Adam".

schneideri, *Cyphella* Berk. & Br., *Trans. Linn. Soc.*, Ser. II, 2, 1887: 220. The type collection was from "Queensland, H. Schneider, comm. Bailey, No. 461". No specimens are at Kew, but the description suggests the species was based on a collection of *Solenia candida*.

92. SCHOMBURGKII, DUPORTELLA (Berk.) nov. comb.
schomburgkii, *Stereum* Berk., *Jour. Linn. Soc.*, 13, 1873: 163.
olivaceum, *Hymenochaete* Cke., *Grev.*, 14, 1885: 11.
atrocinerea, *Peniophora* (Kalch.) Mass., *Jour. Linn. Soc.*, 25, 1889: 141.
atrocinereum, *Corticium* Kalch., in herb. Kew.
schomburgkii, *Hymenochaete* (Berk.) Mass., *Jour. Linn. Soc.*, 27, 1890: 115.

The type collection of *Stereum schomburgkii*, ex "Port Darwin, Aus." consists of two species, one being *Stereum illudens*, as was noted on the sheet by Berkeley. Additional collections from the region under the cover are "Toowoomba, Q., Hartmann", "Port Denison, Q.", "Toowoomba, Q." (type of *Hymenochaete olivaceum*), "Nowra, N.S.W., W. N. Cheesman, 1914", "New England, N.S.W., A. R. Crawford" and "Australia, Kalchbrenner, No. 7". The last Kalchbrenner had labelled *Stereum venapum* and Cooke had filed under *S. retirugum*. Other collections placed under the cover are of three species. "Port Denison, Q., Shann. f.15" is of *Peniophora cinerascens*; "Clarence River, N.S.W., Wilcox", a collection of a sterile *Hymenochaete*; and "Richmond River, N.S.W., Camara, f.92", a specimen of *Stereum lobatum*.

93. SCOPINELLA, ODONTIA (Berk.) Cke., *Grev.*, 20, 1891: 3.

scopinellum, *Hydnum* Berk., *Fl. N.Z.*, 2, 1855: 181.

Three collections from the region are at Kew, the type ex "New Zealand, Colenso", "N.Z., Colenso, b.295" and "Moruya, N.S.W., W. N. Cheesman, 1914".

94. SCUTELLARE, CORTICIUM Berk. & Curt., *Grev.*, 2, 1873: 4.

The following collections from the region agree with the type ex South Carolina: "N.Z., 1866, b.323", "N.Z., Colenso, b.386, b.831, b.895" and "N.Z., Wellington, Travers, No. 376". The second was placed by Cooke under *Corticium taeve*, the third under *Grandinia australis* and the last under *Aleurodiscus acerinus*.

secernibilis, *Odontia* Berk. = *Odontia fimbriata*.

95. SEMILUGENS, HYMENOCHAETE (Kalch.) Bres., *Ann. Myc.*, 9, 1911: 550.

semilugens, *Stereum* Kalch., *Grev.*, 9, 1880: 1.

lugens, *Hymenochaete* Bres., in herb. Kew.

The type at Kew is ex "Rockhampton, Q., F.v.M." though on the sheet the locality was given as New South Wales. Bresadola noted on the type sheet: "Not *Stereum pannosum* (to which the collection had been referred by Cooke) but *Hymenochaete lugens* Kl." Both errors in specific name and author were corrected in *Annales Mycologici*.

sericeum, *Stereum* (Schw.) Morg. Under this cover Berkeley placed an insect-damaged specimen of *Stereum vellereum* ex "East Taieri, Otago, N.Z., Nov. 1861, Dr. Lindsay".

serum, *Corticium* (Pers.) Fr. = *Peniophora sambuci*.

96. SETIGERA, PENIOPHORA (Fr.) Hoehn. & Litsch., *K. Akad. Wiss., Wien., Sitz.* 115, 1906: 1555.

setigera, *Thelephora* Fr., *Elench.*, 1, 1828: 208.

setigera, *Kneiffia* Fr., *Epicrasis*, 1838: 529.

Of the five collections from the region under this cover at Kew, three are correctly named by Miss Wakefield, namely, "Fullarton, Adelaide, S. Aus., J. B. Cleland", "Black-fellow's Creek, S. Aus., J. B. Cleland", and "National Park, Adelaide, S. Aus., W. N. Cheesman, 1914". The others, "Tasmania, W. Archer" and "N.Z., Colenso, b.120", are sterile specimens of *Corticium*.

shraderi, *Stereum.*, Thuem. in herb. Kew. A collection, ex "Clarence River, N.S.W., F.v.M.", so labelled by Thuemen, and placed by Cooke under *S. prolificans*, is of *Stereum illudens*.

97. SIMULANS, THELEPHORA (Berk. & Br.) Corner, *Clavaria*, 1950: 724.

simulans, *Stereum* Berk. & Br., *Trans. Linn. Soc.*, Ser. II, 2, 1883: 64.

simulans, *Lachnocladium* Berk. & Br., *Trans. Linn. Soc.*, Ser. II, 2, 1887: 219.

The type of *Stereum simulans*, ex "Brisbane, Q., F. M. Bailey" is in the herbarium of British Museum of Natural History, part being at Kew. Additional collections under the cover are "Samoa, C. G. Lloyd", "Pennant Hills, Challenger Expedition" and "Q., C. E. Broome".

98. SINCLAIRII, HYDNUM Berk., in *Hook. Hdbk. N.Z. Flora*, 1867: 756.

Endemic to New Zealand, the species is represented at Kew by four collections, the type ex "N.Z., Sinclair, 1860" of five specimens in excellent condition, "Maungaroa, No. 320", "Nelson, Dall" and "York Bay, Wellington, July 1923, E. J. Butler-G.H.C., No. 1217".

99. SOWERBEI, STEREUM Berk., *Fl. N.Z.*, 2, 1855: 182.

sowerbei, *Thelephora* Berk., *Ann. Mag. Nat. Hist.*, Ser. III, 15, 1865: 320.

confusum, *Stereum* Berk., in herb. Kew.

Collections from the region at Kew are "Moonan Brook, N.S.W., Miss Carter", "Daylesford, N.S.W., R. Wallace, 1880", "Gippsland, Vic., Miss Campbell, 1880", "Mt. Ellery, East Gippsland, Vic., E. Merrah", "V.D.L., Mr. Gunn" (labelled by Berkeley *Thelephora pannosa*), "V.D.L., Gunn" (labelled *T. pannosa* by Berkeley but published as

S. sowerbrii), and "New Zealand, Colenso". Two large distorted specimens ex "Guntawang, N.S.W., Hamilton" and "Mt. Napier, Vic., 1883" were filed by Cooke under *Thelephora radians*. Under *Stereum thozetii* Cooke placed "Gippsland, Vic.". Under *S. obliquum* he filed a collection ex "N.Z., Wairarapa, Dry River, T. Kirk, No. 140".

In literature the specific name is often spelled *S. sowerbeyi*.

spadiceum, *Stereum* (Pers.) Fr. Of the two collections under this cover from the region "Tasmania, W. Archer" is of *S. lobatum*, "Western Port, F.v.M., June 1853" is an imperfect specimen of *S. rameale*.

sparsum, *Corticium* Berk. & Br. Under this cover at Kew is a collection ex "N.Z., T. Kirk, No. 318, on dead mahoe bark" which are specimens of the conidial stage of *Nectria otagensis*.

100. SPARSUS, ALEURODISCUS (Berk.) Hoehn. & Litsch., *K. Akad. Wiss., Wien, Sitz.*, 116, 1907: 809.

sparsum, *Stereum* Berk., *Jour. Linn. Soc.*, 13, 1873: 169.

The type collection, ex "Wangaretta, Vic., Aus.", consisting of eight small and irregular colonies, is the only collection at Kew.

101. SPHAEROSPORUM, CORTICIUM (Maire) Bourd. & Galz., *Hym. Fr.*, 1928: 232.

sphaerosporus, *Hypochnus* Maire, *Bull. Soc. Myc. Fr.*, 21, 1905: 164.

One collection, ex "Australia, S.53" was filed by Berkeley under *Corticium arachnoideum*.

spiniferum, *Stereum* Lloyd = *Stereum illudens*.

spongiosa, *Cladoderris* Fr. = *Cladoderris dendritica*.

sprucei, *Stereum* Berk. & Curt. = *Stereum lobatum*.

spumeum, *Corticium* Berk. & Rav. One collection ex "N.Z., Colenso, b.948" so labelled by Cooke but filed by him under *Stereum ochroleucum* is of *Corticium evolvens*.

stereoides, *Thelephora* Cke. & Mass. = *Stereum hispidulum*.

stipitatum, *Hydnum* Fr. Neither collection from the region placed under this cover at Kew is of this species. "Victoria, Dr. Winter, No. 5" possesses gloeocystidia, and "Richmond River, N.S.W." has small obovate spores.

strigosa, *Hymenochaete* Berk. & Br. = *Hymenochaete villosa*.

102. SUBCERACEA, MYCOACIA (Wakef.) nov. comb.

subceracea, *Acia* Wakef., *Trans. Proc. Roy. Soc. S. Aust.*, 1930: 155.

Collections at Kew are the type ex "Mt. Lofty, J. B. Cleland, June 1927", "Mt. Lofty, S. Aus., J. B. Cleland, May 1928", "National Park, S. Aus., J. B. Cleland, Apl. 1924, May 1925" and "N.Z., Colenso, No. 1075" the last filed by Cooke under *Hydnum mucidum*.

103. SUBFASCICULARIA, ODONTIA (Wakef.) nov. comb.

subfascicularia, *Acia* Wakef., *Trans. Proc. Roy. Soc. S. Aust.*, 1930: 155.

The type is at Kew ex "Mt. Lofty, S. Aus., J. B. Cleland, May 1928, W".

subporiferum, *Stereum* Berk. in herb. Kew. The name was given in the herbarium to a specimen ex "Chatham Islands, Travers, No. 7" which on examination was found to be a *Peniophora*.

sulfureum, *Corticium* Fr. Under the cover are two collections from the region, both wrongly named. "Tasmania" is a specimen of *Peniophora filamentosa*, and "b.507" (which is obviously from New Zealand as the label is in Colenso's handwriting) is of *Contiophora arida*.

sulphuratum, *Stereum* Berk. & Rav. Under this cover, which is labelled *S. sulfuratum* Fr., Cooke placed two Australian collections, ex "Clarendon, S. Aus., Tepper, No. 582" and "Port Phillip, Vic., No. 310". Both are of *Stereum vellereum*.

sulphureum, *Stereum* Fr. A collection from Australia so named by Cooke, ex "Toowoomba, Q., Hartmann, 1882" consists of three fragments of an *Aleurodiscus*.

104. SULPHURELLA, CORTICIUM Cke. & Mass., *Grav.*, 20, 1891: 35.

The type at Kew is ex "Oakleigh, Vic., Mrs. Martin, No. 925".

105. SURINAMENSE, STEREUM Lev., *Ann. Sci. Nat.*, Ser. III, 2, 1844: 209.

Though the species is common in New Zealand there are no collections from the region in Kew herbarium.

106. TABACINA, HYMENOCHAETE (Sow.) Lev., *Ann. Sci. Nat.*, Ser. III, 5, 1846: 152.

tabacina, *Thelephora* (Sow.) Fr., *Syst. Myc.*, 1, 1821: 437.

tabacinum, *Stereum* (Sow.) Fr., *Epicrisis*, 1838: 550.

Only one authentic collection from the region is at Kew, ex "Mamaku, N.Z., W. N. Cheesman, 1914", identified by Miss Wakefield. A second filed under the cover by Cooke, ex "Walcha, New England, N.S.W., Crawford" is of *Hymenochaete villosa*.

107. TABACINA, VELUTICEPS (Cke.) Burt, *Ann. Mo. Bot. Gard.*, 6, 1919: 261.

tabacinus, *Aleurodiscus* Cke., *Grev.*, 14, 1885: 11.

The type collection is ex "Moona, Walcha, N.S.W., A. R. Crawford, Feb. 1885". A second collection, filed by Cooke under *Hydnum delicatulum*, is ex "Darling Downs, Q., No. 1095".

tabacinum, *Hydnum* Cke. = *Hydnum crinale*.

108. TASMANICA, HYMENOCHAETE MASS., *Jour. Linn. Soc.*, 27, 1890: 105.

Though in his description Masee stated that the type collection was from New Zealand, on the sheet the type specimen is labelled "Tasmania, herb. Berkeley" in his handwriting. Other collections under the cover are ex "National Park, Adelaide, S. Aus., W. N. Cheesman, 1914" and "Tasmania, L. Rodway, No. 688".

109. TENUISSIMA, HYMENOCHAETE BERK., *Jour. Linn. Soc.*, 14, 1875: 67.

tenuissimum, *Stereum* Berk., *Lond. Jour. Bot.*, 6, 1847: 510.

Under the cover are three collections from the region, ex "Tweed River, N.S.W., Camara", "Toowoomba, Q., Hartmann" and "N.Z., Colenso, b.391". The last was placed by Cooke under *H. rhabarbarina* and on the sheet referred by Bresadola to *H. rheicolor*. *tephra*, *Peniophora* (Berk. & Curt.) Cke. Two collections from the region under the cover at Kew, ex "Australia, S.43, S.48" are not of this species but may be of *P. vinosa*.

110. TERRESTRIS, THELEPHORA (Ehfh.) Fr., *Syst. Myc.*, 1, 1821: 431.

lacinata, *Thelephora* (Pers.) Fr., *Syst. Myc.*, 1, 1821: 431.

Three collections from the region are at Kew, ex "Port Phillip, Vic., 1886", "Sydney, N.S.W., Miss Scott", placed under *Thelephora intybacea* by Cooke, and "Ashburton, N.Z., W. W. Smith, Nov. 1897" which Masee filed under *Thelephora vaga*.

terreum, *Corticium* Berk., *Fl. N.Z.*, 2, 1855: 184. The type collection, ex "N.Z., Ruamahanga, Colenso, on bark of *Knightia excelsa*" is a species of *Septobasidium* commonly on living bark of this host.

111. THOZETII, STEREUM BERK., *Jour. Linn. Soc.*, 18, 1881: 385.

The type, ex "Rockhampton, Q." consists of three specimens in good condition. One other collection, ex "Australia, R. Brown", is filed under *S. nitidulum*. Of the other collections placed under the cover "Endeavour River, Q." and "New Guinea, Armit" are of *Stereum elegans*; "Gippsland, Vic." consists of two species, *S. elegans* and *S. sowerbeii*; and "W. Australia, Thos. Muir" is too imperfect to identify.

112. TOTARA, CYPHELLA G. H. Cunn.

Common on living and dead trunks and branches of *Podocarpus totara* in New Zealand, the species is represented at Kew by one collection ex "Buller Valley, T. Kirk, No. 236" filed under *C. cupulaeformis*. A description is being published elsewhere.

113. TRISTRICULA, DUORTELLA (BERK. & BR.) Reinking, *Philippine Jour. Sci.*, 17, 1920: 364.

tristriculum, *Corticium* Berk. & Br., *Jour. Linn. Soc.*, 14, 1875: 71.

tristiuscula, *Hymenochaete* (Berk. & Br.) Mass., *Jour. Linn. Soc.*, 27, 1890: 111.

castanea, *Hymenochaete* Wakef., *Kew Bull. Misc. Inf.*, 1914: 260.

velutina, *Duportella* Pat., *Philippine Jour. Sci.*, 10, 1915: 87.

velutina, *Hymenochaete* (Pat.) Lloyd, *Myc. Notes*, No. 63, 1920: 966.

Australian collections which match the type from Ceylon are "Cape Direction, Q., D. Thomson" and "Toowoomba, Q., Hartmann". The latter was placed by Cooke under the cover of *Hymenochaete insularis*.

udum, *Hydnum* Fr. One collection placed under the cover by Berkeley, ex "Tasmania, Archer" is not of this species but being sterile cannot be identified.

umbrina, *Hymenochaete* Berk. & Curt. = *Peniophora vinosa*.

114. UMBRINOALUTACEUM, STEREUM Wakef., in Sarasin & Roux, *Nova Caledonia*, B, - 1-L, 2, 1920: 101.

The type was from "Gulf of Prony, New Caledonia, Sarasin, No. 195" and the species listed since it will probably be found in Queensland. It is a species of *Peniophora*, close to *P. papyrina*.

umbrinum, *Stereum* Fr. = *Peniophora vinosa*, possibly.

umbrinum, *Stereum* Berk. & Curt. = *Peniophora vinosa*.

115. UNICOLOR, HYMENOCHAETE Berk. & Curt., *Jour. Linn. Soc.*, 10, 1868: 335.

Two collections from the region are at Kew, ex "N.Z., Colenso", placed by Cooke under the cover of *Corticium laeve*.

varicolor, *Stereum* Lloyd = *Stereum hirsutum*.

vaga, *Thelephora* Berk., *Fl. N.Z.*, 2, 1855: 182. The type ex "N.Z., Sinclair" is not at Kew. A collection placed under this cover by Masee, ex "N.Z., Ashburton, W. W. Smith" is of the common pine mycorrhizal species *Thelephora terrestris*.

116. VELLEREUM, STEREUM Berk., *Fl. N.Z.*, 2, 1855: 183.

Collections from the region at Kew are the type ex "N.Z., Bay of Islands, J. D. Hooker", "N.Z., Colenso", "Middle Island, N.Z., Dr. Sinclair", "York Bay, Wellington, N.Z., E. J. Butler, July, 1923", "Campbell Island, N.Z., J. B. Mayne, March 1908, No. 6", "Mamaku and Wairoa, N.Z., W. N. Cheesman, 1914", "Wairoa River, Kaipara Harbour, Samuel Mossman, No. 813, 1850" (a mixture of *S. vellereum*, *S. lobatum* and *Polyporus adustus*), "N.Z., Colenso, b.49, b.75, b.255, b.290, b.346, b.392", "Waitaki, N.Z.", "East Taieri, Otago, N.Z., Dr. Lindsay, Nov. 1861" (filed by Berkeley under *S. sericeum*), "V.D.L., herb. Hooker, No. 20" (placed by Berkeley under *S. hirsutum*), "Tasmania, W. Archer" (a mixture of three species, one being *S. vellereum*), "Fitzroy Falls, N.S.W., F. A. Rodway, Nov. 1930", "Swan River, W. Aus., No. 159" (placed by Berkeley under *S. hirsutum*), "Near Melbourne, Vic.", "Port Phillip, Vic., No. 310" and "Clarendon, S. Aus., Tepper, No. 582". The last three were placed by Cooke under *S. sulfuratum*.

117. VELUTINA, PENIOPHORA (DC.) Cke., *Grev.*, 8, 1879: 21.

velutina, *Thelephora* DC., ex Fr., *Elench.*, 1, 1828: 203.

velutina, *Hymenochaete* (DC) Lev., *Ann. Sci. Nat.*, Ser. III, 5, 1846: 152.

The only authentic collection from the region at Kew is ex "N.Z., Rotorua, W. N. Cheesman, 1914", so identified by Miss Wakefield. A second placed under the cover, ex "New Zealand", labelled by Berkeley *Thelephora vaga*, is a *Peniophora* I was unable to identify.

118. VERMICULARIS, PENIOPHORA Wakef., *Kew Bull. Misc. Inf.*, 1915: 371.

The type at Kew, ex "N.Z., Rotorua, W. N. Cheesman, 1914" was collected on petioles of a tree fern.

vespilloneum, *Stereum* Berk. = *Stereum prolificans*.

119. VILLOSA, CYPHELLA (Pers.) Karst., *Bidr. kann. Finl. Nat. Folk.*, 25, 1876: 325.

Three collections from the region are at Kew, ex "Centennial Park, N.S.W., E. Cheel, No. 21" placed by Masee under *Cyphella australiensis*, "N.Z., T. Kirk, on Antirrhinum stems" and "Melbourne, Vic., No. 376", both filed by Cooke under *C. curreyi*.

120. VILLOSA, HYMENOCHAETE (Lev.) Bres., *Ann. Myc.*, 8, 1910: 588.*villosum*, *Stereum* Lev., *Ann. Sci. Nat.*, Ser. III, 2, 1844: 212.*nigricans*, *Stereum* Lev., *l.c.**phaeum*, *Stereum* Berk., *Fl. N.Z.*, 2, 1855: 183.*strigosa*, *Hymenochaete* Berk. & Br., *Jour. Linn. Soc.*, 14, 1875: 68.*phaea*, *Hymenochaete* (Berk.) Cke., *Grev.*, 8, 1880: 146.

Collections listed match part of the type of *Stereum villosum* from Java at Kew. Under *H. villosa* is "Moruya, N.S.W., W. N. Cheesman, 1914"; under *H. phaea* are the type of *Stereum phaeum* ex "Bay of Islands, N.Z., J. D. Hooker", "N.Z., Dr. Sinclair", "N.Z., Colenso", "N.Z., Waimea, No. 338", "Condamine River, Q., F.v.M., 1880", "Mt. Dryander, Q., Shann", "Tweed River, N.S.W., Camara, No. 85"; under *H. rubiginosa*, labelled *H. ferruginea* on the sheet, are "V.D.L., ex Hooker herb.", "V.D.L., Messrs. Gunn & Laurence" and "V.D.L., Hooker herb. No. 19"; under *H. strigosa* is "Brisbane, Q., C. E. Broome". Two collections of *Stereum prolificans*, ex "Daintree River, Q." and "Brisbane, Q., No. 314" are filed under the cover. Under *H. tabacina* Cooke placed a collection of the species ex "Walcha, New England, N.S.W., Crawford".

121. VINOSA, PENIOPHORA (Berk.) Mass., *Jour. Linn. Soc.*, 25, 1889: 145.*vinosa*, *Thelephora* Berk., *Hook. Lond. Jour. Bot.*, 4, 1845: 60.*crassa*, *Thelephora* Lev., in *Gaud. Voy. Bonite*, Bot. 1, 1846: 190.*? umbrinum*, *Stereum* Fr., *Pl. Preiss*, 2, 1847: 137.*umbrinum*, *Stereum* Berk. & Curt., *Grev.*, 1, 1873: 164.*murinum*, *Corticium* Berk. & Br., *Jour. Linn. Soc.*, 14, 1875: 70.*vinosa* (*Veluticeps*) *Hymenochaete* Cke., *Grev.*, 8, 1880: 149.*crassa*, *Hymenochaete* (Lev.) Berk., ex Cke., *Grev.*, *l.c.*, p. 148.*umbrina*, *Hymenochaete* Berk. & Curt., ex Cke., *l.c.**multispinulosa*, *Hymenochaete* Peck, *Bot. Gaz.*, 7, 1882: 54.*scabriseta*, *Hymenochaete* Cke., ex Rav., *Fung. Am.*, 1882: 717.*purpurea*, *Hymenochaete* Cke. & Morg., *Grev.*, 11, 1883: 107.*intermedia*, *Peniophora* Mass., *Jour. Linn. Soc.*, 25, 1889: 143.*kalchbrenneri*, *Hymenochaete* Mass., *Jour. Linn. Soc.*, 27, 1890: 116.*murinum*, *Coniophora* (Berk. & Br.) Mass., *l.c.*

The following collections from the region are at Kew. Under *Stereum umbrinum* is "Sydney, N.S.W., P. Bochmer"; under *Hymenochaete umbrina* "N.Z., Wairoa, E. A. Hodgson, No. 40"; under *H. purpurea* are "Brisbane, Q., F. Bailey, Aug. 1912", "Brisbane, Q., W. N. Cheesman, 1914", "Norfolk Island, Robinson", and "Melbourne, Vic., F. Reader, No. 22"; under *H. crassa* is "Clarence River, N.S.W., Wilcox". Types of species and synonyms at Kew are, type of *Thelephora vinosa* ex "Swan River, W. Aus., Nos. 160, 172"; of *Hymenochaete kalchbrenneri* "Australia, Kalchbrenner, No. 8" (under the cover were also placed "N.Z., Colenso, b.521, b.570"); of *Corticium murinum* "Berwick, Vic., 1878, F.v.M." (under the cover was also placed, "Victoria, Leuchmann"). Under *Corticium polygonium* Cooke filed "N.Z., Colenso, 1866, b.447"; and Berkeley placed under *Peniophora papyrina* "V.D.L., Gunn, 382 b" and "Wangaretta, Vic."

122. VIRIDE, CONIOPHORA (Berk.) Sacc., *Syll. Fung.*, 6, 1888: 649.*viride*, *Corticium* Berk., *Fl. N.Z.*, 2, 1855: 184.*viride* (*Coniophora*) *Corticium* (Berk.) Cke., *Grev.*, 8, 1880: 89.

The only collection at Kew is the type ex "New Zealand, Colenso".

viridis, *Thelephora* Berk., *Fl. Tas.*, 2, 1860: 258. The type ex "Tasmania, W. Archer, Esq." is now a resupinate fragment of what is probably a *Tomentella*. On the type sheet had been glued part of the type of *Coniophora viride*.

wellingtonii, *Hydnum* Lloyd = *Hydnum crocidens*.

zealandicum, *Radulum* Berk., in herb. Kew. The type was based on a fragment of *Irpex brevis*, ex "N.Z., Bay of Islands".

123. ZEALANDICUS, ALEURODISCUS (Cke. & Phil.) nov. comb.

zealandica, *Cyphella* Cke. & Phil., *Grev.*, 8, 1879: 57.

ochraceoflavus, *Aleurodiscus* Lloyd, *Myc. Notes*, No. 70, 1923: 1228.

The type, ex "N.Z., Winton, Dr. S. Berggren, No. 230" is a species of *Aleurodiscus* not uncommon on twigs of *Leptospermum* spp. in New Zealand, which was later named *A. ochraceoflavus* by Lloyd. Under the cover of the latter at Kew are part of the type ex "York Bay, N.Z., G.H.C." and "York Bay, N.Z., July 1923, E. J. Butler-G.H.C., Nos. 1214, 1221".

124. ZONATUM, HYDNUM (Batsch.) Fr., *Epicrisis*, 1838: 509.

One collection from Australia is at Kew, ex "Melbourne, Vic., Berggren, No. 366".

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THE EFFECT OF COLCHICINE ON THE SPINDLE OF ROOT TIP CELLS.

By MARY M. HINDMARSH, Linnean Macleay Fellow in Botany.

(Plate xi; one Text-figure.)

[Read 26th November, 1952.]

Synopsis.

In dividing cells of onion root-tips the spindle can be observed after acid fixation. 0.1% colchicine destroys the spindles in all stages of mitosis and prevents spindle formation in cells beginning division during treatment. The spindle appears to be responsible for organizing the cell division process and all the chromosome abnormalities produced by colchicine can be related to the destruction of the spindle.

INTRODUCTION.

Most of the work on cytological effects of colchicine has been carried out using tissue fixed and stained for observing the chromosomes rather than the spindle. The abnormal chromosome arrangements observed in colchicine-treated cells have been explained by postulating an effect on the spindle mechanism, and it is generally agreed that colchicine suppresses spindle formation. Only recently have attempts been made to demonstrate this action of colchicine and in 1951 Gaulden and Carlson, with the phase contrast microscope, examined the effect of colchicine on spindles in living animal cells in culture. They confirmed the earlier deductions that colchicine prevents spindle formation in cells which begin division during treatment, but in addition observed that spindles already formed in metaphase, anaphase and telophase cells were suppressed.

This paper describes the effects of colchicine on the spindle in meristematic plant cells and attempts some discussion of earlier interpretations of the cytological action of colchicine.

Unfortunately the technique employed by Gaulden and Carlson cannot be used for plant cells because of difficulties in obtaining single living plant cells suitable for such experiments. In living animal cells the spindle was identified as a clear area which was not penetrated by mitochondria. After certain types of fixation the spindle can be observed in plant cells and appears to consist of numerous fine fibres. Although these visible fibres are probably the result of acid fixation, they provide a useful indication of the presence of a normal spindle structure. By using plant tissue in which the spindle fibres are clearly visible in untreated cells, as basis of comparison, it should be possible to reconstruct the effects of colchicine on the spindle by examining many cells of a tissue, fixed at known intervals of time after treatment. This was attempted first using paraffin sections of root tips, but this method proved to be slow and tedious and was abandoned. Later it was found that spindles in smears of unstained cells could be observed with the phase contrast microscope after certain types of fixation, and this method was used to study the effect of colchicine on the spindle.

METHODS.

Onion bulb roots about 3 cm. long were treated by immersing in 0.1% (2.5×10^{-4} M) colchicine for periods up to 24 hours at 22°C. Roots were removed and the tips fixed for examination every five minutes during the first hour, then at hourly intervals to 12 hours and at 24 hours. Bulbs were transferred to tap water after various times of treatment up to 24 hours and roots were removed at intervals to determine the cytological changes occurring during recovery. Bulbs with roots in tap water were used as controls.

Roots were fixed in a weak chrom-acetic fixative of: Chromic acid (1%) 25 c.c., acetic acid (1%) 10 c.c., water 65 c.c. After fixing for more than 24 hours, roots were macerated in N.HCl at 60°C. for 10 minutes and squashed in 45% acetic acid. These

unstained smear preparations were examined with a phase contrast microscope. Control and treated roots were photographed under exactly the same conditions.

The rate of penetration of colchicine into the cells is important, as the cells in the outer layers of the root will be exposed to the threshold concentration for spindle inhibition before the cells in the centre. Consequently, variability is encountered between different cells from the same root, and this is especially marked in treatments of one hour or less. The actual concentration of colchicine in any cell at any one time cannot be estimated and, in the absence of data on rates of penetration of colchicine into roots, it is difficult to compare concentration effects with those for single animal cells. Problems of diffusion and penetration are serious difficulties encountered when whole tissues are used for this type of investigation.

RESULTS.

(a) *The spindle in normal roots.*

In all preparations of untreated roots, normal dividing cells with clearly visible spindles at metaphase, anaphase and telophase were observed (Plate xi, A, B).

Small groups of spindle fibres were seen in some late prophase cells, but in most cells earlier than metaphase there was no indication of spindle formation. The spindle first became apparent on either side of the nucleus at the ends of the cell about the time the membrane disappeared.

Cell plates were found in various stages of formation. When the chromosomes began to lose their distinctness, cell plates appeared as a row of dark spots in the centre of the cell. These spots joined together to form a plate which extended towards the sides of the cell, frequently pushing the spindle material to the side walls and leaving a clear area in the centre.

At metaphase, the spindle was a typical double cone which increased in length during anaphase and at telophase was a narrow cylindrical structure separating the two new nuclei, which were then at the ends of the cell. The spindle regained its original cone shape as the cell plate formed across the cell (Darlington, 1937).

At telophase the spindle appeared to be quite separate from the reforming daughter nuclei, and there was a clear area without fibres at each end of the spindle next to each telophase nucleus.

(b) *Treatment with 0.1% colchicine.*

No abnormalities were observed in the cells of roots treated for 5-10 minutes. After 15 minutes' treatment, most of the cells were unaffected and normal cells with well-developed spindles were numerous. In the affected cells, abnormalities occurred in the usual regular arrangement of the chromosomes at anaphase and telophase, though these cells had visible spindles. In some telophase cells, where no spindle could be observed, the two daughter nuclei which normally move to either end of the cell were closer together towards the centre.

After 30 minutes' treatment there were few anaphase and telophase stages. A few of these had spindles, but in most, the spindles had disappeared from the cells. In some abnormal anaphase stages, no spindle was visible but the chromosomes were separated into two groups which were closer together and lacked the regular V-shape and uniform arrangement of normal anaphase chromosomes. Late telophase stages without spindles or cell plates, binucleate cells and dumbbell-shaped interphase nuclei were observed (Plate xi, E-H). No normal metaphase cells were found after 30 minutes' treatment. Metaphase chromosomes were short and thick and scattered at random in the cytoplasm but no spindles were seen in these cells. Prophase was also affected as prophase chromosomes were shorter and thicker than normal.

Blocked metaphases, and prophases with thick chromosomes, were found in the cells of all roots treated longer than 30 minutes, but no spindles (Plate xi, C, D). Binucleate cells, dumbbell-shaped interphase nuclei, abnormal metaphase, telophase without spindles but with chromosome groups close together in the cell were observed up to 60 minutes (Plate xi, G). Division of the centromeres to give a tetraploid chromosome number

was not found in any cell during the first hour of treatment. However, colchicine treatment for longer than one hour produced the well-known sequence of events where polyploid cells are the result of chromosome division without chromosome separation.

This continued succession of prophase, metaphase and then interphase, without any visible spindles, demonstrates that colchicine prevents spindle formation and the result is blocked metaphase with the complete absence of anaphase and telophase.

These results also indicate that the immediate effect of colchicine on dividing cells is on spindles already formed in metaphase, anaphase and telophase. The "untidiness" noticed in anaphase and metaphase after 15 minutes is probably the first indication of a vanishing spindle. This is supported later by the occurrence of anaphase and telophase without spindles but with chromosome groups close together in the cells.

Dumbbell-shaped interphase nuclei probably result from the destruction of anaphase and very early telophase spindles and binucleate cells result from telophase cells where the nuclear membrane is formed or forming when colchicine enters the cell.

The hyaline globule observed by Gaulden and Carlson in animal cells when the spindle disappeared, was not seen in any cells of treated root tips. The fixative used in these experiments was extremely acid and it is possible that the globule could have been formed and either destroyed, or masked by the granulation of the cytoplasm.

(c) *Recovery after treatment for one hour.*

The effects of colchicine persisted for at least 72 hours in cells of roots transferred to water after treatment, but there was a gradual return to the normal cell division process during that time. In the first hour in water, the centromeres of blocked metaphase cells divided forming tetraploid cells with daughter chromosomes lying parallel in the cytoplasm. Some irregular dumbbell-shaped nuclei were seen in early prophase but there were no anaphase or telophase stages and no spindle formation. Ten to fifteen hours later the cells looked very much the same as at one hour, and no cells had passed metaphase which was still "blocked".

After about 19 hours of recovery, however, some cells showed spindles, but most of these were in abnormal cells with multipolar spindles, as described by Levan (1938). These cells would have been unbalanced and would probably have degenerated.

In cells of roots in water for 23 hours, spindles were clearly visible in tetraploid (Pl. xi, M) and diploid cells at metaphase, anaphase and telophase, all of which appeared to be perfectly normal. Cell wall formation was observed in all roots where spindles were formed again. Some prophase cells appeared to be quite normal but prophase with thickened chromosomes persisted to about 19 hours' recovery (Plate xi, J).

These recovery results show that colchicine does no permanent damage to the spindle mechanism which is restored to treated cells when the colchicine is removed, but they do suggest that recovery occurs more slowly than inhibition. The significance of this point will be discussed later.

DISCUSSION.

The results described in this paper confirm the observations of Levan and others that colchicine prevents spindle formation in plant cells. In addition, the results show that colchicine destroys spindles already formed at metaphase, anaphase and telophase. This latter observation has not been reported previously for plant cells, although Gaulden and Carlson (1951) showed a similar result for animal cells.

Cells treated before metaphase, which is the earliest stage obviously organized by the spindle, did not form a normal metaphase plate. The complete absence of a spindle resulted in a blocked metaphase. Centromere division in these cells was followed by the formation of a tetraploid interphase nucleus, as anaphase separation did not occur. These effects indicate the usual sequence of events in colchicine treated material.

When the metaphase spindle was destroyed, the chromosomes clumped together in the cell. These probably form a typical blocked metaphase later, but that would be difficult to ascertain in a multicellular tissue in which blocked metaphase cells produced from suppression of the pre-metaphase spindle are numerous.

The results of spindle suppression in cells at later stages than metaphase are visible abnormalities in the interphase nuclei. When anaphase cells were treated, the two chromosome groups moved towards the centre of the cell and were finally incorporated in one large, irregular, frequently dumbbell-shaped nucleus. Sometimes one or more chromosomes become separated from the chromosome group and form micronuclei. Early telophase stages blocked by colchicine produced the same result as spindle destruction at anaphase. If the membranes of the daughter nuclei were initiated before the spindle disappeared, that is if late telophase was treated, the result was a binucleate cell but the two nuclei usually occupied the centre of the cell.

Effects on pre-metaphase stages were more conspicuous in colchicine treated material than those on later stages, because the absence of a spindle does not prevent new divisions. In colchicine cells continue to come into prophase and pass through blocked metaphase to interphase, but all anaphase and telophase stages soon disappear from treated material and are not replaced. The duration of the cell division stages has been worked out for pea roots at 20°C. (Brown, 1950) where it is about 5 and 13 minutes for anaphase and telophase respectively. Barber (1939) measured the rate of division in *Tradescantia* staminal hairs and found that anaphase took 25 minutes and telophase 4-7 minutes at 25°C. In both plants the total time for anaphase and telophase is half an hour or less. As we have shown, 0.1% colchicine affects the spindles of all dividing cells in a root tip in one hour, so that abnormal cells produced by the destruction of spindles in anaphase and telophase cells would not be found after 1½ hours' treatment. Probably this is why earlier observations on colchicine treated plant cells have not shown that stages later than metaphase could be affected. Abnormal interphase nuclei persist, but these are easily overlooked among the recurring blocked metaphase cells. Levan (1938) examined root tips 7-30 minutes after the beginning of treatment and observed anaphase chromosomes which remained in two groups and were later included in one large nucleus. This can be explained by the removal of an anaphase spindle.

Barber and Callan (1943) have suggested the abnormalities induced in dividing cells of newt can be explained as the inactivation by colchicine of the centromere or the centrosome or both. They postulate inactivation of the centromere only to give "exploded" metaphase, of centrosome only to give "star" metaphase and of both centromere and centrosome to give complete spindle suppression resulting in "prophase"—metaphase and "ball" metaphase. Gaulden and Carlson have shown that "star" metaphase is formed during the destruction of fully formed spindles by high concentrations. Abnormalities grouped as "unorientated" metaphase by Barber and Callan could be the result of lack of spindle formation. This would explain why Barber and Callan found mainly unorientated metaphases in colchicine treated material as "star" metaphases would be produced only as long as anaphase and telophase were being affected and would quickly be replaced by unorientated metaphase as colchicine prevents spindle formation in new cells coming into division. It is possible that centrosomes or centromeres or both are responsible for the organization of the spindle, and it is also possible that colchicine inactivates these cell centres, but it does not seem necessary to postulate degrees of effect on these centres to produce the different abnormalities.

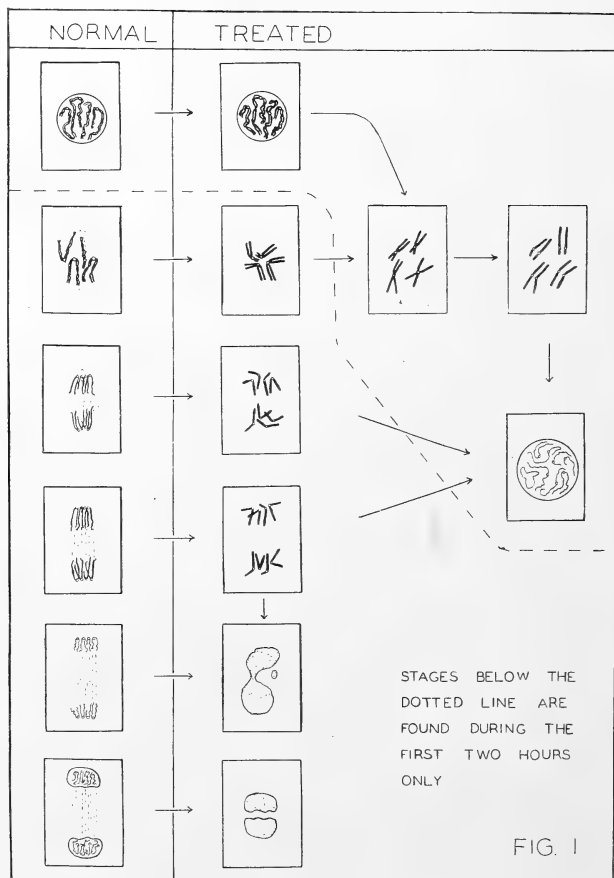
Recovery experiments show clearly that the ability of a cell to form a spindle is not destroyed. After colchicine is removed, spindles reappear and function properly in colchicine induced tetraploids. During colchicine treatment for short periods chromosomes undergo a division cycle without a spindle, so that in recovered cells the spindle lags one division behind the chromosomes.

Spindle suppression is seen in all dividing cells one hour from the beginning of treatment, but spindles are not reformed for about 16 to 20 hours after colchicine is removed. There are a number of possible explanations of this time lag.

(1) Washing in water is not efficient enough and a very low concentration of colchicine might maintain induced abnormalities in the cells.

(2) Colchicine may be adsorbed on to sensitive centres of the cell, perhaps the centromeres, and not readily removed by washing but slowly utilized in the cell.

(3) There is no observable effect on interphase nuclei in colchicine treated material, but neither is there any real evidence about the time of initiation of the spindle, nor about the earliest point at which spindle suppression can occur. Cells treated during a division cycle do not reform a new spindle when colchicine is removed until they have passed through an interphase. Perhaps spindle suppression occurs at late interphase; this could explain why colchicine effects are still visible after 19 hours' recovery time.



Text-fig. 1.—Abnormalities resulting from the destruction of the spindle.

The time of such an action on interphase cells could not be accurately estimated without more information on the duration of stages in colchicine. As some diploid cells result after one hour's treatment the effect must be postulated in the later part of interphase, leaving cells in early interphase unaffected. This possibility would mean that the effect of colchicine is the same on all stages of division rather than one action on pre-metaphase stages and another on anaphase and telophase spindles. If spindle formation begins in interphase then the effect of colchicine is to destroy the spindle from the time of its initiation to telophase.

The nuclear material of cells in which the spindle is destroyed moved towards the centre of the cell. Apparently at anaphase and telophase in normal cells the spindle overcomes the forces which hold the nucleus at the centre of the cell, and keeps daughter nuclei apart until the new cell plate is formed. If the spindle is destroyed the original forces predominate once more and the nuclear material takes up a central position.

A diagrammatic representation of the effect of colchicine on cells in all stages of mitosis is shown in Figure 1.

Cell wall formation is prevented by colchicine, probably as a result of spindle suppression. No cell plates are formed if the spindle disappears at telophase. When the cell recovers, cell plates are formed after the spindle reappears, but not before, and a cell which becomes binucleate during treatment remains in that condition till it divides again during recovery. The observation that numerous cross walls form in recovered colchicine treated cells supports the view that cell plate formation is dependent on the spindle. The division figures of polyploid cells produced by treatment are frequently too wide to fit in the cell in the usual way, so they turn length-wise or from corner to corner in the cell. The cell plate in these cells forms across the spindle wherever it may be, not in the normal position across the cell.

In addition to altering the normal arrangement of chromosomes, colchicine affects their contraction since prophase and metaphase chromosomes are shorter and thicker than in normal cells. Two suggestions have been made to explain this aspect of the colchicine effect. Levan and Ostergren (1943) believe that colchicine, by destroying the spindle, prolongs metaphase and as a result spiralization continues for a longer time. This means thicker chromosomes are secondary effects of spindle destruction.

Ostergren (1944) rejected this explanation because he found thick chromosomes in prophase as well as metaphase, and also that chromosome contraction began at lower concentration than spindle suppression. He observed thickened chromosomes in some cells with normal or nearly normal spindles and concluded from this that colchicine must have a direct effect on the spiralization process. It is difficult to decide between these two views, especially since thickened chromosomes have been observed during this investigation in cells at anaphase after the spindle has been destroyed by colchicine. There seems to be some evidence to indicate a slowing down of some stages of the cell division process by colchicine. Metaphase is longer than normal when colchicine removes the spindle (Levan 1938; D'Amato 1948) and Barber and Callan (1943) found blocked metaphase chromosomes in swollen vacuolated newt cells treated with colchicine. Vacuolation normally occurs at the end of anaphase. Gaulden and Carlson have shown that colchicine not only prolongs metaphase but also prophase; so that extra spiralization at prophase could be due to a prolonged division with chromosome contraction proceeding at the normal rate. However, it is not clear how this could account for thicker chromosomes at anaphase.

All the observed irregularities indicate a disorganized cell division mechanism and can be explained by the absence of the spindle. The spindle appears to be responsible for metaphase plate formation, anaphase separation, holding the chromosomes apart at anaphase and telophase and for cell plate formation. Possibly it controls also the timing of the cell division process. In other words the spindle is responsible for the organization of the cell division and when it is removed the chromosomes continue their part in the division cycle but without the usual organization. It should be stressed that the formation of a tetraploid nucleus during colchicine treatment is not a reversal of any part of the division process, but a forward sequence of events following the normal path as closely as is possible without the spindle.

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EXPLANATION OF PLATE XI.

All photographs \times ca. 350.

A, B.—Normal cells showing spindles. C, D.—Abnormal metaphase. Treated for 30 and 45 minutes with colchicine. E, F.—Colchicine treated telophase. E shows a partly developed cell wall but the spindles have been destroyed in both cells. G.—Two nuclei close together in the cell after colchicine treatment for 45 minutes. H.—Abnormal interphase nuclei—a dumb-bell-shaped nucleus and a binucleate cell. Thirty minutes' treatment. J, K.—Prophase in irregular nuclei after one hour in colchicine followed by 19 and 48 hours' recovery respectively in water. L.—Prophase showing early development of the spindle on either side of the nucleus. One hour in colchicine and 48 hours in water. M.—Spindle and cell plate in colchicine induced tetraploid telophase. One hour in colchicine, 48 hours in water.

A STUDY OF THE MICROFLORA OF WHEAT GRAINS IN NEW SOUTH WALES.

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Synopsis.

The microflora of surface sterilized wheat grains from 49 samples harvested in 1949 and 1950 was examined by means of plating tests. Germination tests in soil and brief non-quantitative examinations of the surface flora were also carried out.

Bacteria and *Penicillium* spp. constituted a large part of the surface flora, while *Alternaria* spp. were the fungi most commonly isolated from surface sterilized grains, exceeding the total of the other organisms isolated by almost three times. Of the other organisms isolated, only *Septoria nodorum*, *Helminthosporium sativum* and *H. tritici-repentis* are known to be pathogenic to wheat, and of these only *H. sativum*, which was isolated from approximately 0.5% of the grains, has been observed to cause a seed-borne disease. *Fusarium* spp. were isolated only very rarely and these isolates were not pathogenic to wheat under glasshouse conditions.

Studies were made of the distribution of mycelium within the grain, and of the internal floras of various atypical types of grain, viz., pinched, mustard, pink and black-pointed grains. A marked association was observed between a pink discoloration of the grain, and the presence of *H. tritici-repentis* within it. *Alternaria* spp. were isolated from a greater proportion of black-pointed grains than from apparently normal ones, but further work is needed to establish the cause of this condition as it occurs in New South Wales.

The factors affecting the population present and the economic importance of the microflora are discussed.

INTRODUCTION.

Numerous organisms have been recorded on and in wheat grains from all parts of the world. The literature relating to this subject is extensive and in this study is reviewed as briefly as possible, an attempt being made to discuss the various aspects in the light of results obtained from investigations on grain samples from New South Wales. The work is concerned mainly with organisms isolated from surface sterilized grains.

The aims of the study were

1. to examine the microfloras of samples from the 1949 and 1950 harvest, noting differences, if any, between samples from different parts of the State;
2. to observe any relationships which might exist between the organisms present, the appearance and germination of the samples, and any diseases which might develop on seedlings grown from these samples; and
3. to determine the position of fungi within the grain.

ORGANISMS PREVIOUSLY RECORDED.

One of the earliest observations was made by Bolley (1913) who stated that certain fungi could be obtained from the surface and interior of wheat grains from almost any wheat-growing region of the world.

The surface flora has usually been determined by shaking the grain with water and examining the washings under the microscope. Various workers have recorded numerous common moulds, mainly species of *Alternaria*, *Aspergillus*, *Cladosporium*, *Penicillium* and bacteria, together with pathogens such as *Tilletia caries*, *T. foetida*, *Ustilago tritici*, *Helminthosporium sativum*, *Septoria nodorum*, *S. tritici*, *Fusarium* spp. and rusts (Carter and Young, 1950; Christensen, 1951; Crosier, 1936; Greaney and Machacek, 1942, 1946; James et al., 1946; Pollack, 1945; Rice, 1939; Russell and Ledingham, 1941; Schnellhardt and Heald, 1936). The fungi are usually present as spores and generally are regarded

* Work undertaken while a student in the Faculty of Agriculture, University of Sydney.

merely as contaminants, but James et al. (1946) suggest that since bacteria occur in such large numbers they constitute an epiphytic flora.

The organisms recorded within wheat grains include species of *Alternaria*, *Aspergillus*, *Botrytis*, *Cephalosporium*, *Chaetomium*, *Cladosporium*, *Colletotrichum*, *Curvularia*, *Epicoccum*, *Fusarium*, *Helminthosporium*, *Mucor*, *Nigrospora*, *Penicillium*, *Phoma*, *Podosporella*, *Pullularia*, *Rhizoctonia*, *Rhizopus*, *Sclerotium*, *Septoria*, *Stemphylium*, *Torula*, *Trichoderma*, *Trichothecium*, *Verticillium*, together with various other moulds, yeasts, bacteria and actinomycetes (Atanasoff, 1920; Blair, 1937; Bolley, 1924; Brentzel, 1944; Brittlebank and Adam, 1924; Carne, 1927; Christensen, 1951; Curzi, 1926, 1929; Dastur, 1928, 1942; Davidson and Den Shen Tu, 1950; Drechsler, 1923; El-Helaly, 1947; Fomin and Nemlienko, 1940; Galloway, 1936; Greaney and Machacek, 1942, 1946; Hagborg, 1936; Henry, 1923; Laumont and Murat, 1934; Machacek, 1945; Machacek and Greaney, 1938; Machacek et al., 1951; McCulloch, 1920; Milner et al., 1947a, 1947b; Minz, 1943; O'Gara, 1915; Peyronel, 1926; Rosella, 1930; Russell and Ledingham, 1941; Weniger, 1935; Ziling, 1932).

Most of the studies on the internal flora have been made using discoloured samples, *H. sativum* and *Alternaria* spp. of the *A. tenuis* type being the organisms most commonly present. The general finding with ordinary, sound, market samples has been that *Alternaria* spp. are the most common internal fungi, in some cases occurring in almost every grain (Christensen, 1951; Davidson and Den Shen Tu, 1950; Greaney and Machacek, 1942, 1946; Hyde and Galleymore, 1951; Laumont and Murat, 1934; Machacek et al., 1951; Milner et al., 1947a, 1947b).

Greaney and Machacek (1946) made a thorough study of a large number of samples from Manitoba over the period 1937-42, and found that 70.2% of the grains were infected with *Alternaria* spp., 3.5% with *H. sativum*, 0.6% with *Fusarium* spp., 3.2% with other fungi, and that 23.9% of the kernels were fungus-free. Bacteria, yeasts and actinomycetes were also found.

Pleosphaeria semeniperda, *Penicillium glaucum*, *Penicillium* sp., *Cladosporium* sp., *H. sativum*, *Alternaria* spp., *Fusarium* spp., *Pseudomonas atrofaciens* and other bacteria have been recorded in Australia, but little detail is given (Adam, 1950; Anon., 1939; Brittlebank and Adam, 1924; Carne, 1927; Noble, 1924, 1933)

MATERIALS AND METHODS.

Wheat samples were obtained from various parts of New South Wales. Samples 1-20 were from the 1949 harvest and samples 21-49 from the 1950 harvest. Samples 1-17 were from silos and were deliberately selected to contain a high proportion of discoloured grains, whereas Nos. 18, 19 and 20 were random samples. Numbers 21-49 were random samples collected from various sources.

The 1949 samples were subjected to an agar plate test six months after harvest. The 1950 samples were examined one month after harvest and, following Canadian proposals (Greaney and Machacek, 1946; Machacek and Wallace, 1942; Mead et al., 1950; Russell and Ledingham, 1941), were subjected to the following:

- (a) a macroscopical examination to observe the degree of pinching and the proportion of discoloured, shot, sprung and mechanically injured grains;
- (b) a qualitative examination of seed washings;
- (c) an agar plate test;
- (d) a non-sterile soil test to determine the germination and to observe any seed-borne diseases.

No attempt was made to detect loose smut infection.

The presence of the groove and the brush mark on the wheat grain admirably suited for carrying a large surface load of organisms, and for this reason a method of thorough surface sterilization is needed if the internal flora is to be examined by means of an agar plate test.

Various techniques have been employed (Machacek and Greaney, 1938; Mead, 1933; Simmonds, 1930a; Simmonds and Mead, 1935) and their relative merits are discussed

by Machacek and Greaney (1938) who devised what they describe as a simple, practical and efficient method, which they later (Greaney and Machacek, 1946) modified slightly. Except where otherwise indicated, this modified method, which is described below, has been adopted throughout this study.*

The grains were immersed in a solution of alcohol and mercuric chloride (1 part of 95% ethyl alcohol to 3 parts of 1:1000 mercuric chloride solution) for four minutes, washed in three changes of sterile water, and planted in freshly poured P.D.A. plates, 10 grains per dish. The dishes were held at room temperature for 8-10 days. At the end of this period the organisms growing out from each kernel were either identified at once or isolated for further study and identification.

The germination tests in non-sterile soil were carried out according to the method described by Machacek and Wallace (1942) and Mead et al. (1950). 100 grains from each sample were planted in pots in a glasshouse and left for 10 days, the temperature ranging from 20 to 30° C. during that period. The seedlings were then counted, taken from the soil, washed, and examined for lesions. The diseased tissue, where present, was then surface sterilized and planted in P.D.A. plates, to determine the organisms responsible.

GENERAL RESULTS.

Only a brief qualitative examination was made of the surface flora. Microscopic examination of the washings revealed spores of *Alternaria*, *Cladosporium*, *Epicoccum*, *Stemphylium*, numerous unicellular spores, uredospores and hyphal fragments. Occasional spores of *Tilletia* were also found. When the washings were streaked on to P.D.A., the organisms which developed were mainly bacteria and species of *Penicillium*, and it is probable that these constitute a large part of the surface flora.

The results of the plating tests to determine the internal flora of samples 1-17 are shown in Table 1. Species of *Alternaria* were the organisms most commonly isolated, exceeding the total of the other organisms isolated by almost three times. *Helminthosporium tritici-repentis* was isolated from 8.5% of the grains, *Septoria nodorum* from 2% and *H. sativum* from only 0.4%, while *Fusarium* spp. were not isolated at all. There appears to be little relation for these samples between germination in agar, the proportion of grains from which organisms were isolated, and the number and nature of the organisms, except that the two lowest germination figures were obtained with samples 11 and 12, from which were isolated the most colonies of *Aspergillus* spp. This is in keeping with the work of various authors (Laumont and Murat, 1934; Thomas, 1937) who found that *Aspergillus* spp. were able to reduce germination. Samples from which *H. tritici-repentis* was isolated were all from the northern half of the State, and it is interesting to note the high figure for *S. nodorum* obtained with the sample from Ladysmith.

The results obtained with random samples from the 1949 harvest are shown in Table 2, and are much the same as those obtained with samples 1-17, except for the high figure for *Penicillium* spp. in sample 18.

In Table 3 are grouped the results obtained with samples from the 1950 harvest. The population of organisms isolated was similar to that isolated from samples of the previous harvest, *Alternaria* spp. again exceeding the total of other organisms isolated by almost three times. *H. tritici-repentis* was prominent as before, being second in frequency to the *Alternaria* spp., this time, however, sharing the position with *Epicoccum* sp. *S. nodorum* was isolated from 2.7% of the grains, *H. sativum* from 0.5%, and a *Fusarium* sp. from only 0.1%.

It is clear, therefore, that the microflora of wheat grains in New South Wales, as revealed in these samples, is, except for the presence of *H. tritici-repentis*, very similar to that found overseas.

Alternaria spp. occurred in every sample examined, the percentage of grains from which they were isolated in any sample ranging from 16 to 95. Nearly all the isolates

* For justification of its use see the appendix.

TABLE 1.

The Organisms Isolated from, and the Germination in Agar of Samples 1-17 from the 1949 Harvest.

Sample.	Source.	Germination in Agar.	Number of Grains Giving—								
			<i>Alternaria</i> spp.	<i>H. tritici-repentis</i> .	<i>Aspergillus</i> spp.	<i>Septoria nodorum</i> .	<i>Penicillium</i> spp.	<i>Rhizopus nigricans</i> .	<i>H. sativum</i> .	Miscellaneous.*	No. Organisms.
1	Westdale	38	29	13	—	1	1	—	—	—	6
2	Emerald Hill	46	30	12	2	—	—	1	1	—	5
3	Breeza	37	29	8	3	3	—	—	1	—	5
4	Manilla	41	16	7	—	—	1	—	—	—	27
5	Delungra	42	30	5	—	—	—	1	—	—	15
6	Warialda	42	38	7	—	1	—	—	—	7	1
7	West Tanworth	40	24	14	—	—	—	2	—	1	10
8	Inverell	39	31	—	—	—	—	4	1	7	9
9	Quirindi	34	37	6	—	—	—	4	1	1	2
10	South Harefield	32	33	—	7	—	3	1	—	2	8
11	Brushwood	19	28	—	18	—	—	—	—	1	3
12	Corobimilla	16	20	—	16	—	1	—	—	1	12
13	Ladysmith	31	25	—	14	10	—	—	—	4	2
14	Arajoel	32	37	—	5	—	2	—	—	—	7
15	Illabo	29	48	—	—	—	1	—	—	1	—
16	Old Junee	38	39	—	—	—	—	—	1	2	10
17	Coolamon	32	36	—	—	1	3	1	—	5	10
	Average	34.6	31.2	4.2	3.8	1.0	0.8	0.8	0.2	1.9	7.7
	Average (%)	69.2	62.4	8.5	7.6	2.0	1.6	1.6	0.4	3.8	15.4

50 grains plated from each sample.

* Includes *Epicoccum* sp., *Cladosporium* sp., *Pullularia pullulans*, *Stemphylium* sp., *Botrytis* sp., *Phoma* sp., *Helminthosporium avenae*, together with unidentified fungi, bacteria, and yeasts.

TABLE 2.

The Organisms Isolated from, and the Germination in Agar of Samples 18-20 from the 1949-50 Harvest.

Sample.	Source.	Germination in Agar.	Number of Grains Giving—								
			<i>Alternaria</i> spp.	<i>Penicillium</i> spp.	<i>H. tritici-repentis</i> .	<i>Septoria nodorum</i> .	<i>Aspergillus</i> spp.	<i>H. sativum</i> .	Miscellaneous.	No. Organisms.	
18	Castle Hill (Federation)	39	24	18	—	—	—	1	—	2	5
19	Gunnedah (Gabo)	42	40	—	6	—	—	—	—	3	3
20	Inverell (Gabo)	37	35	1	—	4	2	—	1	4	12
	Average	39.3	33.0	6.3	3.3	0.7	0.3	0.3	0.3	3.0	7.7
	Average (%)	78.7	66.0	12.7	6.7	1.3	0.7	0.7	0.7	6.0	15.4

50 grains plated from each sample.

could be placed in *A. tenuis* auct. as described by Mason (1928), Wiltshire (1933), Groves and Skolko (1944), which is a little more comprehensive than Neergaard's (1945) *A. tenuis* auct. sensu stricto. Some isolates, however, produced only short chains of conidia and there seems to be little provision made in the literature for these forms.

They may fit *A. peglionii* as described by Curzi (1926) but, except for their shorter chains of conidia, they are similar to *A. tenuis* and could be regarded as extreme types of this very heterogeneous form-species. Simmons (1952), however, warns that the increasingly common practice of treating morphologically similar populations of the Fungi Imperfecti as genetically similar or identical species is based on false premises, in that such similar populations need not necessarily have any great degree of genetic similarity. This is illustrated by his work on three different isolates coming within the modern descriptive limits of *A. tenuis*, each having been derived from an ascospore of a different perfect stage.

Helminthosporium tritici-repentis was found in 34 of the 49 samples, being most abundant in those from the north-west. The percentage of grains from which it was isolated, for any sample in which it occurred, ranged from 2 to 46. This fungus has been recorded in wheat grains only once previously (Galloway, 1936).

A species of *Epicoccum* producing an orange pigment in culture and jet black sporodochia, was isolated from most samples, being obtained from up to 70% of the grains. The highest figures were obtained from samples 39 and 40 from the central coast, the only ones from which *Alternaria* spp. were not the fungi most frequently isolated.

Cladosporium herbarum was isolated from most samples. Frequently it grew out from the brush end of the grain, which suggests that it may not always have been inside the grain but was present deep in the brush and able to withstand the surface sterilization.

Septoria nodorum was found in 22 of the 49 samples, the percentage of grains from which it was isolated in any of these ranging from 1 to 45. It was more abundant in samples from the northern half of the State than the southern, and it is interesting to note that the highest figure was obtained with grain from a crop showing exceptionally bad glume blotch.

Helminthosporium sativum was found in 14 of the samples, highest percentage of grains found to be infected in any sample being 4. The occurrence of *H. avenae*, which was found as frequently as *H. sativum*, is interesting. This is perhaps analogous to the occurrence of *H. avenae* and *H. teres* in wheat grain in Canada (Machacek and Greaney, 1938, Machacek et al., 1951). In inoculation tests the *H. avenae* isolates infected only oats.

Of the fungi isolated, only *H. sativum*, *H. tritici-repentis* and *Septoria nodorum* are known to be actively parasitic on the growing wheat plant. The rest are rarely of any importance though it appears that some may discolour the grain and others, under special circumstances, reduce the viability. *Fusarium* spp. were isolated only very rarely and the isolates were not pathogenic to wheat under glasshouse conditions.

From Table 3 no obvious relation can be seen between the number and nature of the organisms isolated from any sample and the degree of pinching, percentage of smudged grains, percentage of pink grains, or number of grain fragments encountered during the macroscopic examination of 300 whole grains.

When the samples showing no shot or sprung grain and those containing such grain are compared, as in Table 4, no very obvious differences can be observed when the variability within each group is considered. However, it does appear that samples with no shot or sprung grains germinated better and contained more grains from which no organisms were isolated and fewer grains from which *Aspergillus* and *Penicillium* spp. were isolated than those samples with shot or sprung grain. This is to be expected when it is considered that the latter samples must have been subjected to moister conditions than the former. Various authors (Christensen and Gordon, 1948; Laumont and Murat, 1934; Milner et al., 1947a, 1947b; Thomas, 1937) report observations which indicate that invasion of the grain by such fungi as *Aspergillus* and *Penicillium* spp. is associated with high moisture content and cracking of the epidermis.

From Table 3 it can be seen that, except for the difference pointed out above, germination in agar or in soil bore very little relation to the appearance of the grain or its content of organisms. Germination in agar varied enormously from sample to

sample, often differing considerably from the corresponding germination in soil, usually being considerably smaller. This finding is similar to that of Rosella (1930), who found that the germination of mouchété (smudged) grains, with which *Alternaria* spp. were associated, was lower in agar than in sand.

The reason for the enormous variation between the germinations of different samples in agar, particularly between those whose germinations in soil were much the same, is obscure. It may perhaps be related to the depth of the agar, the attitudes in which the grains were placed therein, the overgrowing of the grain by fungal colonies, or the effect of the surface sterilizing agent.

The number and nature of the lesions developing on the seedlings seemed to bear little relation to the presence, prevalence, or absence in the grain samples of the fungi concerned. If, however, the number of grains infected with these organisms had been higher, no doubt a more clear-cut result would have been obtained. Mead *et al.* (1950) point out that production of lesions was somewhat erratic in their experiments owing to differences in temperature, moisture, and other conditions. Hence, until the optimum conditions for development are known for each organism, it is not clear how far the

TABLE 4.

Derived from Table 3 to Show the Average Populations and Germinations of Samples Containing no Shot or Sprung Grains and Samples Containing 14% or More of such Grains.

Samples.	Germination (%)		Percentage of Grains Giving—							
	In Agr.	In Soil.	<i>Alternaria</i> spp.	<i>Epicoccum</i> sp.	<i>H. tritici-repentis</i> ,	<i>S. nodorum</i> .	<i>Penicillium</i> spp.	<i>Aspergillus</i> sp.	Miscellaneous.	No Organisms.
Containing no shot or sprung grain	47.7	85.1	74.4	11.4	14.6	3.6	0.7	—	8.3	7.0
Containing shot or sprung grain	55.6	74.5	82.2	11.2	8.5	1.3	4.1	3.6	7.0	0.5

number and nature of the lesions developing in the glasshouse can be relied upon as a guide to the amount of seed-borne disease. The lesions developed mainly on the coleoptiles, and, as all the samples were sown and examined at the same time and under the same conditions, the results are comparative. The only pathogens isolated from these lesions were *Helminthosporium sativum* and *Septoria nodorum*.

Little is known of the importance of *S. nodorum* in grain. Machacek (1945) found lesions on the coleoptiles and first leaves of seedlings developing from infected grains, but it has not been shown that the disease can progress beyond this stage. In this study lesions have been observed on the coleoptiles only, and of all the organisms isolated from surface sterilized grain, *H. sativum* is the only one known to cause a seed-borne disease.

It appears from the literature that although fungi can remain viable within the grain for long periods, many species lose their viability relatively quickly (Machacek and Greaney, 1938; Machacek and Wallace, 1952). As can be seen from Table 5, there was a considerable reduction in the viability of the internal flora in sample 20 over a period of seven months. However, the main species were still viable in many of the grains 13 months after harvest.

As samples 1-20 were examined six months after harvest it seems probable that the internal flora had already undergone a decrease in viability. This may explain why these samples contained a higher percentage of grains from which no organisms were isolated than those of the 1950 harvest.

DISTRIBUTION OF MYCELIUM WITHIN THE GRAIN.

Most work on this subject has been carried out with discoloured grains in which the mycelium has been observed to be most abundant in the pericarp (Bolley, 1910; Curzi, 1926; Fomin and Nemlienko, 1940; Laumont and Murat, 1934; Machacek and Greaney, 1938; Minz, 1943; Rosella, 1930; Weniger, 1935). Where *Alternaria* spp. are the main fungi present the mycelium has usually been found to be restricted to the pericarp, but *H. sativum* has been observed penetrating the embryo and endosperm (Fomin and Nemlienko, 1940; Weniger, 1935).

Dastur (1935), when studying black-pointed grains, with which several organisms were associated, found hyphae in great abundance in the funicle and in the pericarp in the central region of the grain furrow, and observed that they creep between the pericarp and seed coat, where they form a kind of stroma, but were not found in the embryo or endosperm.

TABLE 5.

A Comparison of the Viability of Organisms within Grain Before and After a Storage Period of Seven Months at Room Temperature.

Time of Plating.	Number of Grains Giving—					
	<i>Alternaria</i> sp.	<i>H. tritici- repentis.</i>	<i>H. sativum.</i>	Bacteria.	Miscel- laneous.	No Organisms.
June, 1950	52	15	—	4	5	23
January, 1951	16	4	1	2	1	75

Sample 20 used, harvested December, 1949. 100 grains were plated on each occasion.

Bockmann (1933) inoculated wheat and barley seeds with *Cladosporium herbarum*, *Alternaria tenuis* and *A. peglioni* and found that they grew in the pericarp but did not penetrate the testa. He observed hyphae of *C. herbarum* to pass from cell to cell through the wall pits. Rosella (1930) observed hyphae of an *Alternaria* sp. to progress in a similar way.

Curzi (1926) found that the mycelium was not restricted to the discoloured area and that it occurred in clean grains as well, while Laumont and Murat (1934) found hyphae in the pericarp of both clean and discoloured grains belonging to a number of wheat varieties of different origins.

Oxley and Jones are reported by Hyde (1950) to have found mycelium in normal wheat grains in the space between the epidermis and the cross layer, and Hyde found subepidermal fungi in a similar position in normal wheat grains from almost all the wheat growing areas of the world, there being, however, a wide variation in the density of the mycelium and the area of the pericarp invaded.

Hyde quotes Marcus as finding mycelium between the pericarp and testa, growing in particular abundance in the large cavities at the side of the crease, which suggests a similar position, and it may be that Marcus and Dastur (1935) mistook the position of the mycelium.

Christensen (1951) found mycelium between the cell layers of the pericarp, on the inner side of the pericarp, and occasionally within the cells of the pericarp. However, as he peeled strips of "pericarp" from the grain, it is possible that the bulk of the mycelium he observed was actually in the space between the epidermis* and the cross layer, as it is usually the epidermis which is detached where grains are peeled.

* The epidermis according to J. M. Hector, Introduction to the Botany of Field Crops, Vol. I, Johannesburg, 1936, fig. 42, includes all layers outside the cross layer.

In this study, when the epidermis was stripped from grains which had been soaked in hot water for 30-60 minutes, hyphae were observed attached to the inner surface over its whole area in all cases, even in grains from the cleanest samples, whether the grains were discoloured or apparently normal. There was, however, considerable variation in the density of growth which was particularly dense in shot, discoloured grains from sample 44. The mycelium was usually most dense at the tip and along the crease, was branched, septate, usually hyaline, and apparently intercellular.

Examinations of cross sections showed mycelium occurring abundantly between the epidermis and cross layer, being very strongly developed in the large cavities between these layers along the crease, in the funicle and around the embryo. Occasionally hyphae were also observed between the cells of the epidermis.

In no case was any mycelium detected in the endosperm or embryo. However, it is possible that in some cases it was present in these tissues as hand sections only were examined.

TABLE 6.

A Comparison of the Results Obtained with Pink and Apparently Normal Grains from Samples from the 1950-51 Harvest.

Sample.	Pink Grains.						Clean Grains.					
	Number of Grains Plated.	Germination in Agar.	Number of Grains Giving—				Number of Grains Plated.	Germination in Agar.	Number of Grains Giving			
			<i>Alternaria</i> spp.	<i>H. tritici-repentis</i> .	Miscellaneous.	No. Organisms.			<i>Alternaria</i> spp.	<i>H. tritici-repentis</i> .	Miscellaneous.	No. Organisms.
21	20	9	1	19	1	—	20	8	12	7	—	1
22	20	3	6	14	5	—	20	2	16	2	13	—
23	20	—	4	17	2	—	20	2	13	2	6	—
24	20	4	3	20	2	—	20	6	15	2	4	—
25	20	13	8	13	4	—	20	16	16	1	2	—
26	20	11	2	18	1	—	20	15	15	5	1	—
37	20	13	2	19	3	—	20	13	18	1	3	—
Total ..	140	53	26	120	18	—	140	62	105	20	29	1
Average (%)		37.9	18.6	85.7	12.6	—		44.3	75.0	14.3	20.7	0.7

INVESTIGATIONS WITH ATYPICAL GRAINS.

Pinched Grains.

In a test carried out using sample 20, no differences were detected between the microfloras of a group of pinched grains and a group of plump grains.

Mustard Grains.

A small proportion of the grains in certain samples showed a mustard coloration, and in a similar test to the above, using samples 22, 29 and 21, no obvious differences were observed between these grains and those which were apparently normal.

Pink Grains.

It can be seen from Table 6 that, while *Alternaria* spp. were the fungi most commonly isolated from apparently normal grains, *Helminthosporium tritici-repentis* was the main organism isolated from pink grains, being found in 85.7% of these, as opposed to 14.3% of the clean grains. Preliminary tests carried out with samples from the 1949-50 harvest indicated a similar relationship.

This association, supported by the fact that the fungus secretes a pink pigment when grown on agar media and sterile wheat straw, indicates that it is almost certainly responsible for the pink pigmentation of the grain.

When the epidermis was peeled off pink grains it appeared to be more or less colourless, the remainder of the grain being as strongly coloured as before. In transverse sections of the grain the pink colour seemed to be most intense in the aleurone layer and did not extend far into the endosperm. It seems probable that the fungus develops in the pericarp and produces a pigment which is absorbed mainly by the outer layers of the endosperm.

H. tritici-repentis was not isolated from some pink grains. In these cases, the coloration might have been due to some other cause, or the fungus might have been killed by the sterilizing agent, or have been unable to grow out of the grain and compete with the other organisms present. On the other hand, the presence of the fungus in a grain was not always associated with the development of a pink colour.

No other record of the association of *H. tritici-repentis* with a pink grain colour has been found. The most common fungi associated elsewhere seem to be *Fusarium* spp., but Atanasoff (1920) reports that *Alternaria* and *Macrosporium* spp. can cause similar discolorations, while Curzi (1929) records *Acremoniella* sp. associated with reddened caryopses.

The *Epicoccum* sp. so frequently isolated produces an abundance of orange pigment on P.D.A., but no evidence was obtained that it was responsible for any discoloration of the grain. Ito and Iwadare (1934), however, record that *Epicoccum* spp. caused a reddening of rice grains.

H. tritici-repentis has never been recorded as causing a seed-borne disease, or reducing germination. Of 100 pink grains from sample 22, 92 germinated in soil, all seedlings being healthy, while 94 of 100 apparently normal grains germinated under the same conditions. Hence, apart from the discoloration which it might cause, the presence of this fungus is apparently unimportant. There is, of course, the possibility that, with different environmental conditions, germination might be reduced and seedling lesions develop.

Black-pointed Grains.

Numerous plating tests were carried out with black-pointed grains, on samples from different sources, and at various times after harvest. The results showed (a) that fungi were isolated more frequently from black-pointed grains than from clean normal grains, and (b) that black-pointed grains yielded more *Alternaria* spp. than normal grains. It is clear, nevertheless, that the presence of *Alternaria* spp. in a grain is rarely associated with a discoloration, since the proportion of black-pointed grains in the samples was low, whereas the proportion of grains containing *Alternaria* species was high (Table 3).

Examination of black-pointed grains showed that the cell walls in the dark area were a diffuse dark brown colour, the discoloration being limited to the pericarp and not extending below this into the embryo or endosperm, a finding similar to that of Peyronel (1926). The distribution and density of mycelium in the pericarp of the black-pointed grains was apparently the same as that in clean grains from the same samples.

The literature concerning black-point is in many cases conflicting and inconclusive and so extensive that it cannot be reviewed here. It is known that *Helminthosporium sativum* and *Pseudomonas atrofaciens* can cause it, and that a less clearly defined discoloration may be produced by *Xanthomonas translucens* var. *undulosum*, and it seems that *Alternaria* spp. and perhaps other fungi are often responsible. Also the possibility of a non-parasitic cause must not be overlooked.

The evidence obtained from this study suggests that the type of black-point commonly occurring in New South Wales is associated with species of *Alternaria*, but a more thorough study is needed to establish the cause of this condition.

FACTORS AFFECTING THE POPULATION PRESENT.

The Surface Flora.

The presence of most organisms, except perhaps for certain bacteria which multiply on the surface, is accidental. The grain is contaminated with air-borne fungi and bacteria and, mainly during harvesting operations, with those growing on the wheat plant.

The Internal Flora.(a) *Air-borne inoculum.*

Machacek and Greaney (1938) and El-Helaly (1947) conclude that, in Manitoba and Egypt respectively, infection of the grains with fungi which cause black-point arises from air-borne spores which are usually deposited in the largest numbers about the time the kernels are maturing. During the period 1932-36, Machacek and Greaney found large numbers of *Alternaria* spores in the air at this time, whereas those of *Helminthosporium sativum* occurred in an appreciable quantity only in 1935; but nevertheless, *Alternaria* spores were always found to outnumber these by at least four times.

Spores of a *Helminthosporium* similar to those of *H. tritici-repentis*, *H. sativum*, *Epicoccum*, *Alternaria*, *Stemphylium*, and *Cladosporium*, together with uredospores and numerous unidentified spores, were found on slides exposed in the north-west of the State in November, 1950, so it seems probable that infection of wheat grains in New South Wales also arises largely from air-borne inoculum, and that the fungi which are not actively parasitic enter the grains as they mature.

(b) *Mutual relations between micro-organisms.*

Machacek and Greaney (1938) found that over the period 1931-34 *Alternaria* spp. were the predominating fungi in discoloured kernels. In 1935, however, most of the discoloured wheat kernels in the samples examined were found to be infected with *H. sativum*, while *Alternaria* spp. were recovered much less frequently than in previous years. As there was no shortage of inoculum of *Alternaria* spp., it was suggested that an antagonism between the two fungi in the seed was responsible for this, and the hypothesis was supported by the fact that such an antagonism was observed in agar plate cultures.

That such effects are important has been demonstrated further by Niethammer (1938). She found that when *Penicillium expansum* and *Cladosporium herbarum* were simultaneously inoculated into wheat seed grain, the latter gains the upper hand and rapidly suppresses the former. In the case of *C. herbarum* and *Trichoderma koningi*, the latter was found to be the more active.

In the present work numerous antibioses have been observed in agar plates, although, as the colonies were usually some distance apart, some of the less pronounced effects may have been overlooked. *Penicillium* spp., *Trichoderma* sp., *Rhizopus nigricans*, *Mucor* sp., *Botrytis* sp., *Fusarium* sp., one colony of *H. sativum*, and certain bacteria were observed to have a detrimental effect on *Alternaria* spp. and most other fungi. It is not known whether the position is the same within the wheat grain.

Pullularia pullulans and *Epicoccum* sp. showed a very weak antibiosis to *Alternaria* spp. In the case of *Epicoccum* sp. it is possible that this was responsible for the relative freedom of samples 39 and 40 from *Alternaria* spp., although other factors could have been operating.

(c) *Amount of disease in crop concerned.*

With active parasites such as *Septoria nodorum*, *Fusarium* sp., and certain bacteria, it seems certain that infection is brought about by these organisms developing on the crop concerned. The same may be true, at least in some cases, for the *Helminthosporium* spp., if only in that amount of disease in the crop influences the concentration of spores in the air in the immediate vicinity.

(d) *Climatic conditions.*

El-Helaly (1947) claims that an outbreak of black-point depends, amongst other things, on atmospheric humidity and rainfall, while Adam (1950) noted that a wet spell

after flowering seemed associated with an outbreak. Hyde (1950) found a correlation between the amount of subepidermal mycelium and the atmospheric humidity during the ripening of the grain.

Greaney and Machacek (1946) found in Manitoba that if climatic conditions favoured early ripening and harvesting, the incidence of seed pathogens was low, but if warm, humid weather occurred during ripening and harvesting the incidence of infection was high.

Undoubtedly climatic conditions have a similar influence here. After the 1949 and 1950 samples, which had ripened and been harvested under exceptionally humid conditions, had been examined, it was supposed that in a drier season more of the grain would be free of internal fungous infection, and that of the fungi present a smaller proportion would be pathogens. This supposition was supported by the fact that samples 48 and 49, from Finley, which had ripened under comparatively dry conditions, were very clean and bright, contained the largest percentages of grain from which fungi were not isolated, and were almost free, internally, of pathogenic species.

A brief examination of samples from the 1951 harvest has confirmed this supposition. Conditions during ripening and harvesting were abnormally hot and dry and microscopic and plating tests revealed that only occasional grains contained fungi, these almost invariably being *Alternaria* spp. The mycelium beneath the epidermis, where present, was sparse and confined to the regions over the embryo and at the brush end. The surface flora of the samples examined consisted almost entirely of bacteria and the grains carried very few mould spores.

(e) *Conditions after harvest.*

Investigations overseas have shown that *Aspergillus* spp., *Penicillium* spp., and certain other common moulds do not enter sound wheat stored under normal conditions, but enter when the epidermis is cracked, as sometimes occurs in the course of threshing operations, or when the grain is stored with a high moisture content. Milner et al. (1947a, 1947b) found *Alternaria* to be the main fungus in sound samples, but that *Aspergillus* and *Penicillium* spp. were predominant in samples from the same lots stored with a high moisture content.

ECONOMIC IMPORTANCE.

The organisms occurring on or in wheat grains may be important because:

- (i) They cause discolorations which may lower the commercial value of the grain;
- (ii) they cause damage during storage, particularly species of *Aspergillus* and *Penicillium*, which cause heating when grain is stored with a high moisture content (Christensen and Gordon, 1948; Hyde, 1950); and
- (iii) they may affect the yield and quality of the subsequent crop.

The general opinion in the literature seems to be that while certain organisms, particularly *Helminthosporium sativum* and *Fusarium* spp., may reduce germination and seedling emergence, and cause root rots, *Alternaria* spp. have no effect, and, from the standpoint of seed-borne disease, are not considered important (Brentzel, 1944; El-Helaly, 1947; Fomin and Nemlienko, 1940; Greaney and Machacek, 1942, 1946; Henry, 1923; Machacek and Greaney, 1938; Minz, 1943; Rosella, 1930; Ziling, 1932). There have been two reports in New South Wales of reduced germination in black-pointed grain (Anon, 1939; Stening, 1935), but it is interesting to note from the work of Russell and Ledingham (1941) and Waldron (1936) that a reduced emergence is not necessarily followed by a reduced yield.

Although seed-borne pathogens were rarely detected in the samples used in this study, it is quite possible that there may be important variations in the grain microflora in future years. Also, it is clear that the value of a sample for seed cannot be assessed from its appearance, for a badly discoloured sample may carry less pathogenic organisms and germinate better than an apparently clean one.

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APPENDIX.

Methods of Isolation.

Before adopting the procedure recommended by Greaney and Machacek (1946), tests were carried out to determine the effect of time and nature of surface sterilization, and the nature of the agar medium on the number and nature of the organisms isolated. In each test the germination in agar was also recorded. Platings in the first two tests were made in P.D.A. An untreated control was included in each test. Grain used was from samples 20 and 22.

1. *Time of treatment with alcoholic mercuric chloride solution.*

Times of treatment were as follows: 5 sec., 10 sec., 15 sec., 30 sec., 1 min., 2 min., 3 min., 4 min., 15 min., 30 min., 1 hr., 3 hr., 6 hr., 12 hr., 24 hr.

Bacteria, *Aspergillus*, *Penicillium*, and *Cephalosporium* were virtually eliminated after five seconds' treatment, indicating that they were occurring largely as surface contaminants. As the time of treatment increased beyond 30 seconds, the other organisms continued to be isolated in the same proportions, although the total number of fungi, the number of grains giving organisms, and the germination gradually declined when times of treatment extended beyond four minutes. It was considered, therefore, that nothing would be gained by departing from the recommended sterilization time of four minutes.

2. *Method of sterilization.*

Grain was treated as follows:

- (i) Immersed for ten minutes in calcium hypochlorite;
- (ii) Immersed for four minutes in alcoholic mercuric chloride solution, followed by washing three times in sterile water;
- (iii) As (ii), but without subsequent washing.

Very much the same results were obtained with these three methods, both as to the number and nature of the organisms isolated, and the germination in agar.

3. *Nature of agar medium.*

The media used were malt agar, nutrient agar, and P.D.A. at pH 5-6 and 7-8. Again, very little difference was detected.

After the above tests, it was considered that the sterilization procedure of Greaney and Machacek (*loc. cit.*) was satisfactory, and was followed in all the subsequent work.

When the study was completed the work of Oelofsen* came to the notice of the writers. He concluded that the fungi which grew from kernels treated by methods similar to that used here "were so numerous and so different in nature that they could not possibly all have been borne internally by the seed". The number of fungi isolated was much smaller and fewer genera were encountered when the suture was opened before sterilization, a measure which is claimed to give the mercuric chloride better

* O. N. Oelofsen, Investigation of Cereal Diseases in the Western Cape Province, Science Bulletin No. 289, Department of Agriculture, Stellenbosch-Elsenburg, 1950.

access to the fungi lodged in the groove. He stated that the fact that the pericarp is torn as a result of the treatment makes no appreciable difference to the effect of the disinfectant. He soaked the grains for 12 hours in water before opening the suture, and also removed the embryo.

When grains from local samples were treated without removal of the embryo, by Oelofsen's method, there was, as in his work, a marked reduction in the number of the fungal colonies isolated.

However, as very often a large proportion of the internal mycelium occurs in the cavities between the epidermis and cross layer along either side of the base of the suture and above the embryo, it is felt that Oelofsen's treatment must have some effect on the subepidermal fungi.

YELLOW SPOT DISEASE OF WHEAT IN AUSTRALIA.

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(Plate xii; one Text-figure.)

[Read 26th November, 1952.]

Synopsis.

Yellow Spot of wheat is recorded from New South Wales and Queensland. The symptoms, importance and distribution of the disease, and the morphology of the causal organism are discussed. Pathogenicity tests are reported, and, after an examination of the literature, it is concluded that the fungus concerned is *Helminthosporium tritici-repentis* Died. with the perfect stage *Pyrenophora tritici-repentis* (Died.) Drechs.

INTRODUCTION.

Recently a species of *Helminthosporium*, differing markedly from any previously described on wheat in Australia, has been found causing a disease of wheat in New South Wales and southern Queensland. It also differs considerably from all the species described on wheat except *H. tritici-repentis* Died. and *H. tritici-vulgaris* Nisikado.

Although the fungus was isolated from grains of the 1949 harvest, it was not until August, 1950, that infected plants were recognized in the field. These were observed near Gunnedah, and since then the disease has been found to be widespread in the northern half of New South Wales and has been recorded on specimens from southern Queensland.

It seems probable that this disease has been present for some time but has remained inconspicuous until the 1949 and 1950 seasons, which were unusually wet and favoured its spread and development.

SYMPTOMS.

The disease develops mainly on the leaves. The lesions in the early stages are small oval to oblong spots, which gradually increase in size, becoming light brown to dark brown with a yellowish zone at the margin (Plate xii, 1), and may easily be confused with lesions caused by *Septoria nodorum*. The lesions are usually small, but may reach a length of 1-2 cm., although they are rarely more than 0.5 cm. wide, sometimes becoming irregular owing to the coalescence of several spots. Severely attacked leaves wither from the tips, and conidiophores and conidia are produced on the dead tissue. Small black sclerotia frequently develop, particularly on the base of the stem and the sheathing leaf bases.

The presence of the fungus within the grain is often associated with a pink pigmentation, and it seems to have been responsible for almost all of the pink or reddish discolorations observed in New South Wales in 1949 and 1950 (Shaw and Valder, 1952). A similar pigmentation has occasionally been observed on dead glume, leaf and stem tissue.

CHARACTERISTICS OF THE CAUSAL FUNGUS.

1. *Culture.*

On P.D.A. the fungus gives rise to pale grey, low-growing, cottony, non-sporing colonies, sometimes producing deposits of orange and pink pigment in the medium. These may occur uniformly over the whole colony, in rings, or only where the mycelium runs up against the edge of another colony.

As the colonies age, they darken, becoming almost black at the surface of the agar, although the aerial mycelium remains grey. The submerged mycelium shows an abundance of anastomoses, and some of the cells involved in these hyphal fusions swell

* Work undertaken while a student in the Faculty of Agriculture, University of Sydney.

into sub-globose bodies similar to those described by Drechsler (1923) for various species of *Helminthosporium*. In plate cultures these are found in abundance near the lower surface of the agar. Frequently certain of these develop into small black sclerotia, either scattered throughout the colony or aggregated where two colonies have met.

Where the mycelium meets the glass wall of a Petri dish or culture tube, numerous grey fascicle-like structures, usually 1-3 mm. but up to 5 mm. high, and reminiscent of minute bracket fungi, develop. Luttrell (1951) in describing the cultural characters of *H. dictyoides* states that a fringe of tiny, erect clavae, composed of compacted hyphae, develop around the margin of the colony where it comes in contact with the walls of the culture tube. Apart from this record there appears to be no mention of such structures in the literature concerning the genus *Helminthosporium*. However, the writers have observed them in cultures of other species, though they were not formed as abundantly as in cultures of the fungus from wheat.

Drechsler (1923) and Connors (1940) report no conidia in culture for *H. tritici-repentis*, while Mitra (1934) states that this species spored in a day or two when mycelium with a little agar from culture was incubated in a moist chamber, and when it was grown on sterilized straw. Nisikado (1929) reports conidial production by *H. tritici-vulgaris* when it was grown on Beijerinck's or plain agar. Local isolates produced no conidia under any of these conditions, nor on nutrient, malt or maize meal agars.

Cultures that have been kept for some time seem to lose their ability to form sclerotia and clavae, become paler, and often produce more pink or orange pigment than when they were first isolated.

2. Occurrence of the Perfect Stage.

The perfect stage of the local fungus was first observed in a culture obtained from grain of the 1949 harvest in which, after some weeks, perithecia of the type described by Wehmeyer (1949) for *Pleospora trichostoma* (Fr.) Ces. and de Not. matured. Single ascospore cultures were obtained and shown to be pathogenic to wheat on which the conidia were later produced. Perithecia, however, have not been observed in culture since.

In the springs of 1950 and 1951, perithecia were observed to be abundant on stubble in the north-west of New South Wales, frequently intermingled with pycnidia of *Septoria nodorum*.

3. Morphology.

a. Conidiophores.—The conidiophores are unbranched, dark brown, have a swollen basal cell and occasionally show geniculations (Text-fig. 1, E). Those from leaves collected in the field measured $75-270 \times 8-10 \mu$ with 3-11 septa (20 measured). Those produced on leaves kept in a humid atmosphere were somewhat paler and measured $190-280 \times 10-11.5 \mu$ with 2-7 septa (20 measured).

Andrews and Klomparens (1952) and Sprague (1950) state that the conidiophores of *H. tritici-vulgaris* show a characteristic light colour towards their tips. This has been observed with local collections, particularly when the conidiophores are produced on leaves kept in a humid atmosphere.

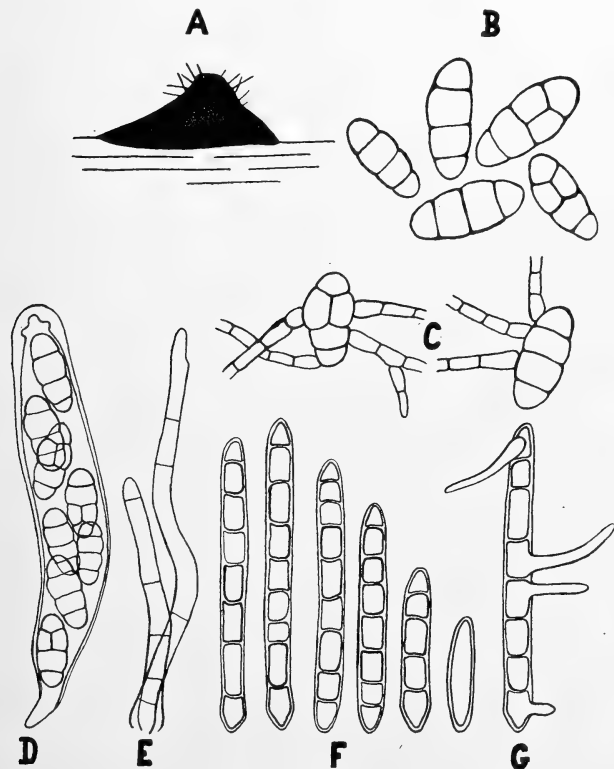
b. Conidia.—The conidia from leaves collected in the field were pale brown, pale olivaceous or subhyaline, thin walled, straight or occasionally slightly curved, more or less cylindrical, often tapering a little towards the distal end, the distal cell hemispherical or hemiellipsoidal, the proximal (basal) cell bearing an inconspicuous hilum and often characteristic in shape, there being a slight constriction at the septum with the basal portion of the cell tapering abruptly in the manner of a cone (Plate xii, 5; Text-fig. 1, F). This shape suggested the appearance of the head of a snake as described for *H. tritici-repentis* by Drechsler (1923).

Drechsler notes that departures from this type are not infrequent, and the same holds for the local fungus (Plate xii, 4). Cultures derived from single spores showing

and not showing the "snake's head" appeared identical, were all pathogenic, and all produced both types of conidia when inoculated on to the host.

Conidia produced under natural conditions in the field measured $23\text{--}307 \times 13\text{--}26 \mu$ (mean $116 \times 18.3 \mu$) with 0-13 (most frequently 6) septa (50 measured). Only five conidia were longer than 156μ .

Conidia produced on diseased tissue kept in a humid atmosphere were subhyaline, straight and cylindrical, with the basal cell often exhibiting, either weakly or strongly, the "snake's head" appearance, and measured $52\text{--}216 \times 11.5\text{--}23 \mu$ (mean $160 \times 15 \mu$) with 0-9 (most frequently 7) septa (50 measured).



Text-figure 1.

A. Sclerotoid perithecium of *P. tritici-repentis* showing setae in the neck region. $\times 50$.
 B. Mature ascospores. $\times 350$. C. Germinating ascospores. $\times 350$. D. Immature ascus. $\times 350$.
 E. Conidiophores. $\times 350$. F. conidia. $\times 350$. G. Germinating conidium. $\times 350$.

Secondary conidia were sometimes produced from the tips of the primary ones when diseased tissue was held in a humid atmosphere.

In general appearance, the conidia with the "snake's head" character resemble very much those figured by Drechsler (1923), Mitra (1934) and Dennis and Wakefield (1946) for *H. tritici-repentis*, and those not showing the "snake's head" appearance resemble those figured by Nisikado (1929) and Andrews and Klopmparens (1952) for *H. tritici-vulgaris* and by Drechsler (1923) for *H. bromi*.

The conidia germinate from any of their cells (Text-fig. 1, G) and frequently show anastomoses between the germ tubes. When two germinating conidia lie side by side, pairs of germ tubes are proliferated from approximately opposite positions and immediately anastomose giving rise to scalariform figures (Plate xii, 5). A similar phenomenon is described by Drechsler (1923) for *H. bromi*, Mitra (1934) for *H. tritici-repentis* and Graham (1935) for *H. gramineum*.

c. Perithecia.—The development of sclerotoid perithecia of the *Pleospora trichostoma* type has been well described by Drechsler (1923), Wehmeyer (1949), and Webster (1951). When mature the perithecia develop a conical beak (occasionally two) and the beak and other portions of the wall bear stiff black hairs (Plate xii, 2; Text-fig. 1, A).

The asci (Plate xii, 3; Text-fig. 1, D) show an internal annular thickening at the top and each contains eight irregularly biseriate, pale olivaceous ascospores, each with three transverse septa and often with one vertical septum in the second or third cell, there usually being constrictions at the septa (Text-fig. 1, B). These ascospores germinate readily in tap water from either the central or end cells or both (Text-fig. 1, C).

The perithecia measured $0.4-0.7 \times 0.25-0.4$ mm. (20 measured) and the asci $80-310 \times 37-53 \mu$ (mean $245 \times 41 \mu$) (20 measured). Ascospores from different sources varied considerably in size, the difference no doubt being due to differences in maturity, environment and perhaps to variation within the fungus itself. Those which matured in culture were the smallest observed, measuring $42-49 \times 14-18 \mu$ (20 measured), while those collected in the field measured $42-65 \times 14-30 \mu$ (50 measured).

4. Tests of Pathogenicity.

Owing to the fact that no spores were produced in pure culture, mycelium taken from young cultures, and macerated in water, was used as inoculum. After inoculation, the plants were held in a humid atmosphere for 48 hours.

Plants inoculated were seedlings of "Federation" wheat, "Kinver" barley, "Algerian" oats, "Black Winter" (open-pollinated) rye, "Milo" sorghum, "Fitzroy" maize and plants of *Agropyron repens*, *Bromus inermis*, *Cynodon dactylon*, *Elymus canadensis*, *Hordeum leporinum* and *Lolium multiflorum*.

A heavy infection was obtained on wheat and *Elymus canadensis*, a moderate infection on *Agropyron repens* and minute lesions only on *Bromus inermis*. The fungus was re-isolated from all these plants. No infection was obtained on any of the others.

IDENTIFICATION OF THE CAUSAL FUNGUS.

Drechsler (1923) reviewed the early history of *H. tritici-repentis* and related species and transferred their perfect stages from *Pleospora* to *Pyrenophora*. He stated (1934) that excessive emphasis on the presence or absence of setose outgrowths had obscured the important differences between these genera and that, rehabilitated as a natural genus through the elevation of *Chaetoplea* to generic rank, *Pyrenophora* again conformed to Fuckel's definition, being properly reserved for the hard sclerotoid perithecial forms having their asexual stages in the *Helminthosporium* series with indiscriminate germination. Until recently this decision of Drechsler's seems to have been followed.

Nisikado (1929) described *H. tritici-vulgaris* on wheat in Japan. It apparently differed from *H. tritici-repentis* in its ability to sporulate easily in culture and in the shape of the basal cells of the conidia, which did not present the "snake's head" appearance. *H. tritici-vulgaris* has since been recorded by Raabe (1937) in Germany, and Barrus (1942), Johnson (1942), Miller (1947), Sprague (1950), and Andrews and Klomparens (1952) in the United States. This fungus has only been recorded on wheat and no cross inoculation tests with grasses are reported.

Sprague (1950) and Weiss (1950) record *H. tritici-repentis* on wheat, rye and numerous grasses in the United States.

Garbowski (1932) recorded *H. tritici-repentis* on rye in Poland, and after preliminary reports (McRae, 1932, 1933; Mitra, 1931), Mitra (1934) described it as it occurred on

wheat in India. The Indian fungus produced sclerotia in culture, could infect *Agropyron repens*, and produced conidia showing the "snake's head" appearance of the basal cell. Galloway (1936) recorded its presence in black-pointed wheat grain in Pusa.

Conners (1938) records that *H. tritici-repentis* caused a severe leaf blotch and spotting of durum wheat near Melita, Manitoba, in 1937, and later (1940) states that it reached epidemic proportions over most of the wheat-growing area in Manitoba in 1934. He records that it has been found on *Elymus canadensis* in Manitoba, but not on *Agropyron repens*, and states (1950) that the disease on wheat was known at least as early as 1923 in Canada.

H. tritici-repentis has been recorded on *Agropyron repens* in England (Dennis and Wakefield, 1946), but apparently neither this nor *H. tritici-vulgaris* has been reported on wheat in that country.

The descriptions by these various authors of the diseases of wheat reported to be caused by *H. tritici-repentis* and *H. tritici-vulgaris* show great similarity. Conners (1940) considers that these fungi, as they have been described on wheat, are probably synonymous. Luttrell (1951b) describes them as "two nearly identical species" and it would be very difficult to differentiate them using his key. It is clear that they have not been shown to be different.

Of the species of *Helminthosporium* other than these two, the local fungus seems closest in its morphology and cultural characteristics to *H. bromi* as described by Drechsler (1923) and Chamberlain and Allison (1945). *H. bromi* is, however, apparently confined to species of *Bromus*.

Through the kindness of Professor Waterhouse, cultures were obtained from the United States labelled *H. tritici-repentis*, *H. tritici-vulgaris* and *H. bromi*, and another *H. tritici-vulgaris* from Japan. These were all non-sporing, showed varying degrees of production of pink pigment, and in general habit were similar to the local fungus. Unfortunately, they were old cultures, and had lost their pathogenicity. Hence, side-by-side comparisons could not be made.

Owing to the variation observed in the morphology of the local fungus when studied under differing environmental conditions and probable variation within the fungus itself, it is not considered to exhibit any outstanding differences from *H. tritici-repentis* as described overseas. It may, however, show differences in pathogenicity from the fungus as it occurs on *Agropyron repens*.

Wehmeyer (1949) includes the *Pyrenophora* spp. with imperfect stages in *Helminthosporium* in *Pleospora trichostoma* (Fr.) Ces. and de Not., pointing out that there is a great deal of variation in the size of the perithecium, ascus and ascospore within individual collections of this species group, and that there may be some correlation between these characters and host occurrence, which would be a basis for varietal separation, but that so far no such evidence has been seen. Webster (1951) follows Wehmeyer, including the ascigerous stage of *H. teres* in *P. trichostoma*.

The imperfect stages of the fungi placed in this species, however, show quite marked morphological and physiological differences and, even if their perfect stages are almost identical morphologically, show apparent differences in the ease with which these stages are formed. In the case of *H. avenae* as described by Dennis (1939) and a species of *Helminthosporium* described from Italian ryegrass by Dovaston (1948) the ascospores are predominantly five-septate. Hence even if certain species are reduced to varietal status it is considered that there are differences present sufficiently large to warrant the recognition of more than one species. It seems to the writers that Drechsler's (1934) claims for the genus *Pyrenophora* still carry considerable weight and that the species placed therein constitute a natural group best considered apart from *Pleospora*.

To arrive at a satisfactory conclusion concerning this nomenclature a thorough study of all the perfect and imperfect stages is needed, and until this has been done it is thought that following Drechsler's nomenclature will cause the least confusion. It is proposed, therefore, to consider the local fungus to be *Pyrenophora tritici-repentis* (Died.) Drechs. with the imperfect stage *Helminthosporium tritici-repentis* Died.

TABLE 1.

Comparison of the Conidial Characters of the Local *Helminthosporium* sp. with Various Descriptions of *H. tritici-repentis*, *H. tritici-vulgaris* and *H. bromi*.

Fungus.	Authority.	Conidial Characters.		
		Size. (μ .)	Number of Septa.	Presence of "Snake's Head".*
Local.	Present authors	23-307 \times 13-26 (mean 116 \times 18.3)	0-13	+
<i>H. tritici-repentis</i> .	Drechsler (1923)	45-175 \times 12-21	1-9	+
	Mitra (1934)	45-201.5 \times 13-22 (mean 117.17 \times 16.6)	2-11	+
	Conners (1940)	Longer than <i>H. teres</i> .	Not given	+
	Dennis and Wakefield (1946)	98-160 \times 12.18	2-8	+
<i>H. tritici-vulgaris</i>	Nisikado (1929)	28.5-183 \times 8.9-21.9 (mean 118.6 \times 17.4)	0-10	-
	Raabe (1937)	80-270 \times 15-19	3-13	-
	Andrews and Klomparens (1952)	30-156 \times 14-24 (mean 18.8 \times 110.6)	Not given	Not mentioned
<i>H. bromi</i> .	Drechsler (1923)	45-265 \times 14-26	1-10	-
	Diedicke (1902)	108-150 \times 13-20	4-6	-
	Chamberlain and Allison (1945)	57-201 (up to 400 on leaves kept in humid atmos- phere) \times 13-19	Not given	-

* In Luttrell's (1951b) key the basal cells of the conidia of *H. tritici-repentis* and *H. tritici-vulgaris* are regarded as similar.

TABLE 2.

Comparison of Measurements of the Ascigerous Stage of the Local *Helminthosporium* sp. with Measurements Given in Published Descriptions of the Ascigerous Stages of *H. tritici-repentis* and *H. bromi*.

Fungus.	Authority.	Size of Perithecia. (mm.)	Size of Asci. (μ .)	Size of Ascospores (μ .)
Local.	Present authors	0.4-0.7 \times 0.25-0.4	80-310 \times 37-53 (mean 245 \times 41)	42-65 \times 14-30
<i>H. tritici-repentis</i>	Diedicke (1902)	Not given	165 \times 45 (mean)	46.8 \times 18 (mean)
	Drechsler (1923)	0.20 \times 0.35	170-215 \times 43-50	45-70 \times 18-28
<i>H. bromi</i> .	Diedicke (1902)	Not given	189-288 \times 36-58.5 (mean 244 \times 48.5)	42.5-49 \times 16.4 23 (mean 45 \times 20)
	Drechsler (1923)	0.3-0.4	Up to 300 \times 65	45-72 \times 20-30
	Chamberlain and Allison (1945)	Not given but stated to be similar to those observed by Drechsler (1923).	190-300 \times 36-60	48-77 \times 22-30

DISTRIBUTION AND ECONOMIC IMPORTANCE.

The disease has been recorded only in the northern half of New South Wales, and from southern Queensland, although the causal fungus has been isolated on a few occasions from grain produced in southern New South Wales in 1950 (Shaw and Valder, 1952).

In 1950 it was widespread in the north-west of New South Wales, but as *Septoria nodorum*, *S. tritici* and *Puccinia triticina* were present also, it is hard to estimate the extent to which *P. tritici-repentis* was responsible for the damage. It was observed, however, causing a severe leaf blight on seedling wheat at Burburgate in August, 1950, in September near Tamworth, and also in a late sown crop at Edgeroi in November.

In 1951 it was very severe in the seedling stage, in many localities in the north-west, the first and second and sometimes the third leaves being affected. The subsequent dry conditions, however, prevented further development of the disease. In the 1952 season it was again observed in the field, in some cases causing severe blighting.

Cases of epidemics and severe infections have been reported from overseas, but the general opinion seems to be that the disease is inconspicuous except in years particularly favouring its development. The position here will probably prove to be similar, and it is unlikely that the need for control measures will arise. No doubt much could be done, however, by eliminating the source of inoculum with altered cultural practices and by breeding resistant varieties should the disease become serious.

Connors (1940) states that there are differences in the susceptibility of varieties. He reports that the durum wheats seemed more susceptible than the common wheats. All durum varieties, however, were not equally susceptible, some being practically free of the disease.

PERSISTENCE FROM YEAR TO YEAR.

Although the fungus is able to enter the grain, as far as is known the disease is not seed-borne. Under experimental conditions infected seed has given rise to healthy seedlings only.

The conidia are thin walled, short lived, and those produced during the wheat-growing season are probably of little importance as far as carry-over of the fungus is concerned. Connors (1940) states that in Canada it apparently overwinters on infected straw and stubble of wheat, and on the leaves and culms of certain grass hosts, the perithecia maturing in June. He suggests that the factors responsible for the epidemic in Manitoba in 1939 were the ease with which perithecia develop, and the considerable increase in the use of one-way discs which fail to cover the stubble with soil.

Drechsler (1923) states that with the advent of suitable conditions the developing sclerotia or perithecia begin to proliferate conidiophores, and conidia are produced at the expense of further development of the perithecia. The production of such conidia, he states, is large in the case of *P. teres*, moderate for *P. tritici-repentis*, and small for *P. bromi*. He suggests that the latter species is probably the only one in which the production of ascospores plays an essential part in the resumption of growth in the spring.

Under local conditions, however, as in Canada, the fungus on wheat produces normal perithecia readily on straw and stubble. These mature in the spring, so that there is an abundance of inoculum when the wheat is in the seedling stage. The production of some conidia from sclerotia and perithecia has been observed.

It has not as yet been observed overwintering on self-sown wheat, or infecting any grass hosts in New South Wales, but the possibility of such occurrences should not be overlooked.

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EXPLANATION OF PLATE XII.

- 1.—Leaves of "Gabo" wheat with lesions caused by *P. tritici-repentis* after artificial inoculation. $\times \frac{1}{2}$.
- 2.—Wheat straw with perithecia. $\times 4$.
- 3.—Immature asci with the eight irregularly biserial ascospores. $\times 550$.
- 4.—Conidium not showing the "snake's head" appearance of the basal cell. $\times 550$.
- 5.—Germinating conidia showing the "snake's head" appearance and anastomoses. $\times 550$.

AUSTRALIAN RUST STUDIES. X.

FURTHER BREEDING WORK WITH "KHAPLI" EMMER WHEAT, AN OUTSTANDING SOURCE
OF STEM RUST RESISTANCE.

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[Read 26th November, 1952.]

Synopsis.

In continuation of earlier work, studies have shown that the very resistant "Khapli" emmer wheat usually shows strong incompatibility in crosses with vulgare wheats. Three hundred and forty-seven vulgare varieties have given this result. A detailed study of crosses with "Federation", made year after year since 1921, has shown that seasonal influences do not affect its incompatibility.

Compatibility was shown with "Steinwedel" and twelve of its progeny which were available as named varieties, although eleven others were incompatible. Seven other unrelated vulgare varieties from various overseas sources also show high compatibility. Tests of F1 plants with several races of stem rust showed that dominance of resistance is general. From "Steinwedel" crosses, vulgare types having "Khapli" resistance have been obtained. A preliminary study of the mode of inheritance of the compatibility character was made.

Numerous crosses of 14-chromosome wheats with "Khapli" have also been made. There is urgent need for cytogenetical studies of the happenings.

INTRODUCTION.

Earlier work (Waterhouse, 1930, 1933) showed that despite repeated failures by many workers to get satisfactory crosses between vulgare wheats and the very resistant "Khapli" emmer, some success came from using a group of varieties which gave very limited F1 growth and high sterility. But normal vegetative F1 growth was found when a second group of three particular varieties was used, although low fertility occurred. These varieties were found as a result of studying (McMillan, 1933) the pedigrees of members of the first-named group. "Steinwedel" was a common parent of the three varieties which showed this compatibility.

Since summarizing the work done up to 1932, numerous other "Khapli" crosses have been made each year in a search for additional information on the happening.

VULGARE CROSSES.

In this work, certain varieties of 21-chromosome wheats such as *T. compactum* Host. and *T. sphaerococcum* Perc. have been included under the general name of "vulgare".

Again it has been usual to find that vulgare pollinations gave small, sterile, short-lived F1 plants. In all, 347 varieties have given this result. They are as follows:

A115, Akagomoughi, Allora Spring, Alpha, American Club, Anchor, Apex, Argentine 1026 (2 strains), Argentine 1059, Argentine 1060, Argentine 1061.

E.I.C., Baringa, Barwang, Basil, Bencubbin, Birdproof, Bobin (3 strains), (Bobin × Gaza × Bobin) (3 strains), Bobs, Bokveld, Bomen, Bonus, Boomey (2 strains), Bordan, Brevit. (2 strains), Bruce, Bunge, (Bunge × Emmer 19), Bungulla, Bunyip.

Cadia, Cailloux, Californian Club, Caliph, Canaan, Canberra, Canimbla, Canrock (2 strains), Canus, Carina, Carrabin, Cedar, (Cedar × Florence), Celebration (2 strains), Ceres, (Ceres × Hope × Florence), Champlain, Chinese Red, Chinese White, Chinese White Hybrid Hard, Chinese White Hybrid Soft, Clarben (4 strains), Clarendon, Clarke's, Cleveland, Club C.I. 4534, Club E.A.S., Currawa.

Daphne, Dindiloa, Duchess, Dundee (2 strains), (Dundee × Nabawa).

Early Bird, Early May, Early Purple Straw, Early Red Chief, Eng. 3, Eureka (4 strains), Euston (4 strains), (Euston × Hope), (Euston × Hope × Federation), Exquisite.

Farmer's Friend, Federation, (Federation × Cleveland), (Federation × Hope), (Federation × Kenya 744), (Federation × Khapli) (5 strains), Fedweb 1, Fedweb 2, Fedweb 3, (Fedweb × Hofed) (2 strains), Felix, Firwhill, Flèche d'Or, Flora, Florence, Ford (3 strains), Forelock, Free Gallipoli, Frondoso, Fronteira, Fulcaster.

Gabo, Galgalos, Galgalos E.A.S., Gallipoli, Geeralying, Gem, Genoa, Ghurkha, Girral, Gluclub, Gluford (2 strains), Gluyas, Gluyas Early, (Golden Grain × Bobs), Grassland, Gresley,

Gular, Gullen, Gunnedah 3, Gunnedah 6, Gurkha.

(H44-24 × Marquis) (2 strains), (H44 × Reward × Ford × Dundee), Hard Federation, (Hard Federation × Clarendon)⁴, Harfedko, Haynes' Blue Stem, Hochzucht, Hofed 1, Hope, Hope Crossbred (2 strains), (Hope × Marquis × Yaroslav), (Hope × Reliance × Reward), (Hope × Yandilla King) (3 strains), (Hope × Yandilla King × Geeralying), Hornbill, Hudson's Early Purple Straw, (Huguenot × Federation × Federation), Hume, Hurst's 11.

Imperial Amber, Indiana Swamp.

Japanese Bearded, Jonathan, Jones Fife.

Kanred, Kendee, Kenya 743, Kenya 744, Kenya 745, Kenya 778, Kenya 1033, Kenya 1035, Kenya 1037, Kenya 1038, Kenya 1039, Kenya 1049, Kenya 1050, Kenya 1052, Kenya 1053, Kenya 1054, Kenya 1055, Kenya 1056, Kenya 1057, Kenya 1058, Kenya 1304, Kenya 1348, Kenya 1349, Kenya 1350, Kenya 1351, Kenya 1445, (Kenya × Dundee), Kenya Governor, (Kenya × Gular), Kenya White, Klein 33, Klein 157, Klein Cometa, Klein Exito, Kleintrou, Koorda, Kota, Kruger.

La Estanzuela, Lambert, Lawson, Linden, Loros.

Mabrook, Major, Majorica Rossa, Mallan, Marquillo, Marquis (2 strains), (Marquis × Vernal), Marshall's No. 3, Mediterranean, Mentana, Minflor, Minister, Mitchell (2 strains), Mona, Morocco, Mudyā, (Mudyā × Khapli).

N 716 (2 strains), (Nabawa × Duchess), (Nabawa × Egyptian 4), (Nabawa × Hope)⁷, Nebraska 28, Nevertire (2 strains), Ngachen (2 strains), Niloc, Nizam, Nullar, Numba.

Ojirua.

P 1068, Petatz Surprise, Pilot, Poole, (Poole × Medeah), Portugal 909, Portugal 912, Pringle's Champlain, Puglu, Puora, Purple Straw, (Purple Straw × Medeah), Pusa 4 (2 strains), Pusa 6, Pusa 31, Pusa 45, Pusa 107, Pusa 110, Pusa 111, Pusa 190.

Quantity.

Ranee, Red Egyptian (2 strains), Red May, Red Rock, (Red Russian × Florence)⁷, Red Wave, Reliance, Renown, Rerraf, Rhodesian (5 strains), Riverina, Russian 861, Rymer.

S.H.J., Salter's 85, Scimitar, Secalotrichum, Sepoy, (Steinwedel × Khapli) 1451, (Steinwedel × Timopheevi) (5 strains), (Steinwedel × Timopheevi × Bena), (Steinwedel × Timopheevi × Dundee × Dundee × Nabawa), Stewart, Sultan, Sunset, Suprezo, Sweden, Sword, Sword 2, Sword 50, (Sword × Kenya) (2 strains).

Talberg, Talgai, Thatcher, Thew, Totadgin, *T. sphaerococcum* S.B., *T. sphaerococcum* B.L., Turvey.

Union 17, Union Stranger, Uruguay 1064, Uruguay 1065, Uruguay 1066, Uruguay 1067, Uruguay 1068.

Wagga White Lemmas, Walmer, Waratah, Warden, Warigo, Warrah, Warren, (Warren × Florence × Huguenot × Nyngan 2)⁸, (Warren × Florence × Huguenot × Nyngan 2)⁷, Webster, Whillan, White Federation, Wilfred.

Yalta, Yandilla, Yandilla King, (Yandilla King × C24)⁸.

Zaff, Zealand, Zealand Blue.

The variety "Federation" has been used in each of the years. The size of the F1 plants has shown some variation in different seasons, the range of total growth being from 6 inches to 10 inches in height at the time of death. In all, some 366 F1 plants, representing 30% seed-setting, have been tested, but in no case has anything been obtained other than a scanty vegetative growth which soon yellowed and died. In no instance was there any evidence of spike formation. This is at variance with the result reported by Hynes (1926) in which he found normal growth and some fertility in F1 and succeeding generations. "Federation" has subsequently been crossed with "Vernal" several times. F1 plants have shown normal growth with partial fertility and intermediacy of morphological characters. In the F2 and F3 generations the wide segregation usual in a vulgare × dicoccum cross has been found.

A degree of seasonal variation has also been shown by the sterile F1 plants derived from other vulgare parents, but this has been slight. In the same way, the degree of development attained by the F1 plants has shown some variation depending upon the particular vulgare parent used, but this has not been great, the height ranging from 6 inches to about 15 inches. Small inflorescences have been formed in certain cases.

In all, 347 vulgare parents have given 7,221 sterile progeny, which represents a 38% seed-setting. Six hundred and thirty-one crosses have been involved. In many cases the same cross has been made in different seasons in order to check behaviours.

Special attention was given to the variety "Geeralying", which has shown the remarkable compatibility with rye (Waterhouse, 1939). But this is completely absent in "Khapli" crosses.

Quite different results have come from certain other crosses. Following upon the initial successes with the three varieties "Steinwedel", "Improved Steinwedel" and

"Garra", as reported in 1933, crosses between them and "Khapli" have been made each year since then. In all cases the F1 plants have given normal vegetative growth with about 1% setting of grain when selfed, and up to 20% when open-pollinated. Seasonal variations in each have been noted, plant height ranging from 4 feet to 5 feet 6 inches in particular cases.

In addition to the 39 F1 plants already recorded (Waterhouse, 1933), subsequent crosses using these three varieties have yielded a total of 865 F1 plants. This represents a 39% seed-setting. Wide variation was found from season to season, low figures coming from dry seasons. As much as 80% was obtained in two seasons.

Having established the value of "Steinwedel" as a parent, other varieties listed (McMillan, 1933) as its derivatives were given special attention. In all, 23 accessions were available for crossing. Of them the following 12 gave normal F1 progeny of the same nature as those from the "Steinwedel" crosses: "Bald Early", "Boonoo", "Currimp", "Dan", "Eligulate", "Fan", "Fane", "Garra" (3 strains, morphologically different), "Improved Steinwedel", and "Queen Fan".

The other 11 "Steinwedel" derivatives gave the usual small short-lived sterile F1 plants. They were: "Alpha", "Basil", "Bobin", "Canaan", "Daphne", "Girral", "Lambert", "Niloc", "Sultan", "Walmer", and "Whillan".

Thus there is evidence of transmissibility and segregation of the "Steinwedel" compatibility. An effort was made to trace this further back. Its pedigree is given as (a) "Selection from 'Farmer's Friend'"; and (b) "Selection from 'Champlain's Hybrid'". Seed of "Farmer's Friend" was obtained from the N.S.W. Department of Agriculture, and of "Champlain" from the U.S.D.A. Numerous crosses with each variety failed to give any fertile F1s. At the present time it would appear that of the group, "Steinwedel" is the ultimate source of the compatibility characteristic.

In addition to "Steinwedel" and its derivatives, seven other vulgare varieties have given F1 plants of normal vegetative growth. These are: "Egyptian W1228", "Guinea W572", "Kenya W1347", "Russian W674", "Sabanero W1231", "Solid Straw Tuscan" (two strains). Of these, the only one whose pedigree is available is "Guinea", listed as (a) "Selection by Mr. Kroker, Uranquinty", and (b) "Supposed natural cross between 'Federation' and 'Minister'". Both "Federation" and "Minister" have been found to produce sterile F1s. It is not impossible for "Steinwedel" to have been involved in the parentage of the selection made by Mr. Kroker, since this variety was in common cultivation at that time.

So far as the other six varieties are concerned, there is no evidence to point to "Steinwedel" being involved in their parentage, nor to their being parents of it.

Summating the total results in which compatibility was shown, the 2,920 crossed grains set represent a 38% seed-setting. Where "Steinwedel" appears in the pedigree, the 13 varieties yielded 2,632 grains, representing 42% seed-setting, as compared with 288 grains or 18% seed-setting where the other seven varieties were parents of the crosses. The numbers are sufficient to show that there are significant differences between the degree of compatibility shown by the two groups of varieties. Cytological investigations are clearly required to give further information on this as well as on other happenings in this work.

STUDIES OF F1 PLANTS.

The morphological characters of the various F1 plants showed, in general, intermediacy between the particular vulgare and "Khapli".

Crossed grains from "Steinwedel" and its derivatives were inoculated with *Urocystis tritici* Keke. and others with a mixture of *Tilletia caries* (D.C.) Tul. and *T. foetida* (Wallr.) Liro. They produced smutted plants. "Khapli" was resistant throughout.

Tests of the various F1 plants with *Puccinia graminis tritici* E. and H. were made with races 34, 43, 45, 46, 126, 126B, and 222. "Khapli" shows strong resistance to all. Where the vulgare parent was resistant, the F1 was fully resistant. In other cases there was some seasonal variation within a particular cross, but this could be related

directly to the temperature-light conditions prevailing at the time the test was carried out. The reaction was a resistant one which in general was lower with r.43 than with the other races used, ranging from ; to \times . With the other races the range was from ; to \times +. In all cases it was lower than the reaction of the vulgare parent.

In a few cases F1 tests were made with *P. triticina*. Using races 26 and 95 which show respectively susceptible and resistant reactions on "Thew", and "Kenya 744", whilst "Khapli" shows susceptibility to both, the F1 seedlings gave the same reactions as the vulgare parents, that is to say, there was clear dominance of resistance to r.95. When the varieties "Argentine 1060" and 'Rhodesian 1237' which gave resistant reactions with these two races were used, there was clear dominance of susceptibility.

Because of the incompatibility with "Khapli" shown by all these varieties and the consequent early death of the F1 plants, no further leaf rust studies were possible.

LATER GENERATION STUDIES.

Many F2 generations from selfed and open-pollinated grain of the "Steinwedel" crosses were grown, but detailed studies could not be made. The widest segregation for morphological characters, sterility, and stem rust resistance occurred.

Selections designed to give useful vulgare material were grown in the F3 and succeeding generations, and one of the resistant vulgare types originating in a 1931 cross has been maintained and has proved valuable in further crossing work designed to give stem rust resistance. It is not in itself a satisfactory agronomic variety.

INHERITANCE OF COMPATIBILITY.

A preliminary study was made of the mode of inheritance.

From an F2 of ("Federation" \times "Steinwedel") derived from an F1 which had been proved on morphological grounds to be a true cross, a number of plants taken at random were pollinated with "Khapli". The resultant plants were inoculated with *P. graminis tritici* 222 and afterwards planted out. Notes taken during growth showed that at a time when near-by F1 plants of ("Federation" \times "Khapli") were yellowing, this condition showed up in many of the plants, whereas adjacent ones were quite healthy. These differences became accentuated as the season proceeded, and by spring many individuals were already dead. At harvest time their number had increased.

Counts showed that five plant progenies were homozygous for the normal condition (compatibility), eight for the lethal (incompatibility), and 16 were heterozygous. These numbers are too small for genetic analysis and it is unlikely that the semblance of a 1:2:1 ratio is real.

These same plants were tested in the seedling stage for resistance to *P. graminis tritici* 222 and showed wide segregation with reactions varying between "Fleck" and "3". Again the numbers were insufficient for a genetic interpretation. There was no correlation with the compatibility characteristic.

CROSSES WITH 14-CHROMOSOME WHEATS.

Results of crosses involving several species are summarized in Table 1:

TABLE 1.
Seed-setting in Crosses between certain 14-chromosome Wheats and "Khapli" Emmer.

Species.	Number of Varieties Tested.	Grains Set.	Pollinations.	Percentage Grain-Setting.
<i>T. durum</i>	25	1,652	2,361	70
<i>T. dicoccum</i>	5	245	457	53
<i>T. turgidum</i>	2	44	100	44
<i>T. persicum</i>	2	87	158	55
<i>T. orientale</i>	1	77	108	71
Totals	35	2,105	3,184	66

In this series, the "durum" group comprises two or three varieties that might better be listed as *T. pyramidale* Perc., a species not everywhere recognized as valid.

Of the varieties, the durum known as "Gaza" was used most extensively, crosses being made in most of the years since 1929. On three occasions there was 100% seed-setting, although in one of the very dry seasons it fell as low as 30%. No significant differences were found between varieties in regard to their compatibility with "Khapli".

Fertility of the F1 was general. Dominance of resistance was shown when these plants were tested with the same races of *P. graminis tritici* as were used with the vulgare F1s. A considerable amount of work was done on later generations, but this will be reported separately.

In addition to the 14-chromosome wheats listed, certain other species were used in preliminary tests, and gave the following results.

TABLE 2.
Seed-setting in certain Species Crosses with "Khapli" Emmer.

Species.	Grains Set.	Pollinations.
<i>T. Timopheevi</i>	21	24
<i>T. Vavilovi</i>	15	24
<i>T. Timococum</i>	3	38
<i>T. Sovieticum</i>	1	34

Complete sterility was shown. The Timopheevi F1s gave normal vegetative growth and intermediacy of morphological characters. Leaf rust tests showed dominance of the resistance carried by the Timopheevi parent: with stem rust, to which both parents are resistant, complete resistance was shown.

Crosses were attempted with several rye varieties and with *Aegilops squarrosa*, but in no case was any grain set.

BACK-CROSSES.

Since 1924 more than 100 back-crosses have been made. Many have involved F1s from the "Steinwedel" derivatives crossed with "Khapli" and with the vulgare parent. In other cases this F1 has been crossed with other vulgares having greater agronomic value, and in yet others, the F1 from the 14-chromosome parent crossed with "Khapli" has been back-crossed with a selected vulgare parent.

Again, material of cytogenetical value has been obtained and at the same time evidence got that the "Khapli" resistance can be transferred to vulgare wheats.

It was clearly realized from the outset that detailed cytogenetical studies were called for, and much material has been saved for this purpose. Up to the present all efforts to have these investigations made have failed. The problem is now clearly delimited, and steps should be taken to have this cytogenetical work carried out.

ABERRATIONS IN "KHAPLI".

In the many sowings of "Khapli" made for control purposes, three albinotic plants have shown up: all died in the early stages of development.

Two striped seedlings have also been found. Both retained the striping of the leaves and came to maturity. In each case, grain gave rise to normal green seedlings, and from these at maturity bulk grain was saved which in the next generation again produced normal green seedlings.

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AUSTRALIAN CLOVER RUSTS.

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Synopsis.

The morphology, life histories and host ranges of rusts occurring on *Trifolium* spp. in Australia, have been studied. Biometrical analyses of measurements of spore dimensions have been made. The occurrence of physiologic specialization in the rust of subterranean clover is recorded, and its importance discussed. A classification of the rusts is attempted from the results obtained.

The influence of temperature and humidity on the longevity of uredospores of subterranean clover rust has been determined.

The results are given of an experiment designed to demonstrate the effect of strains of *Rhizobium* on clover rust development.

I. COMPARATIVE STUDIES.

Introduction.

For many years, the rusts of *Trifolium* spp. have been studied by workers in Europe and North America. Three principal clover rust species have been differentiated on the basis of life history studies, and within one of these, three distinct subspecies differing in spore morphology and host specialization are known. The species are designated by Arthur (1934):

1. *Uromyces flectens* Lagerh., a microcyclic form on *T. repens* L.;
2. *U. nerviphilus* (Grognot) Hotson, a demicyclic form on *T. repens*;
3. *U. trifolii* (Hedw. f.) Lév., an autoecious eu-form having the following three subspecies:
 - (a) *U. t. trifolii-repentis* (Liro) Arthur on *T. repens*;
 - (b) *U. t. hybridi* (Davis) Arthur on *T. hybridum* L.;
 - (c) *U. t. fallens* (Desm.) Arthur on *T. pratense* L. and *T. medium* L.

Similar studies have not been made in Australia, and since some of the predominant host species differ from those of Europe and North America, a detailed comparison of their rusts is warranted. Physiologic specialization has not been demonstrated within any clover rust subspecies. Statistical data on spore dimensions are not available.

Life Histories and General Morphology.

Literature Review

A detailed description of the macrocyclic species *U. trifolii* is given by Arthur (1934). The differentiation of the three subspecies is set out in Table 1. Other workers, including Liro (1906), Sydow (1909), Kern (1911) and Davis (1924), have considered these rusts as distinct species, but the production of the aecidial stages of *U. t. hybridi* (Davis, 1917) and of *U. t. fallens* (Kobel, 1920) clearly established the relationship of these rusts to the macrocyclic species *U. trifolii*. For this reason, the simpler species concept adopted by Arthur is used in this paper.

The short-cycle forms on *T. repens*, viz., *U. nerviphilus* and *U. flectens*, differ little from *U. t. trifolii-repentis* in spore morphology; however the former lacks the uredospore generation, and the latter lacks spermogonia, aecidia, and uredosori. The teleutosori of the short-cycle forms are large, elongated, and mainly confined to the veins and petioles, whereas those of the macrocyclic form are small, rounded and restricted to the leaf blades.

Clover Rusts Present in Australia.

During the period from March, 1951, to January, 1952, five species of *Trifolium* were found rusted under field conditions, viz., *T. subterraneum* L., *T. fragiferum* L.,

T. glomeratum L., *T. repens* and *T. pratense*. Field, glasshouse and microscopic comparisons of the rusts showed that they differ considerably in their life cycles and general morphology. A description of each rust is given below. Brackets placed about a subspecies designation indicate that the complete classification of the rust is still in doubt.

(a) *U. trifolii trifolii-repentis*. *

The rust most commonly found on *T. repens* produces uredospore, teleutospore, spermogonial and aecidial stages. The transient uredosori, typically small, rounded, and red-brown in colour, rapidly give place to black teleutosori. The teleutospores germinate at maturity, giving rise to the spermogonial and aecidial stages. Aecidiospores play the primary rôle in the dissemination of the organism.

The uredospores are finely echinulate, light cinnamon-brown, $19-27 \times 18-21 \mu$,* with 2-4 equatorial germ pores. The spore wall is $1-1.5\mu$ thick. The single-celled teleutospores are smooth, cinnamon-brown, $20-30 \times 16-23 \mu$, with a single terminal pore. The spore wall is $1-2\mu$ thick.

This rust has been recorded in Australia by McAlpine (1906) under the name *U. trifolii* (Alb. & Schw.) Winter.

TABLE 1.
Differentiation of Subspecies of *U. trifolii*.

Subspecies.	Principal Host Species.	Occurrence of Aecidia.	Uredospore Germ pores.	
			Number.	Distribution.
<i>U. t. trifolii-repentis</i> ..	<i>T. repens</i> .	Common.	2-4	Equatorial.
<i>U. t. hybridi</i> ..	<i>T. hybridum</i> .	Rare.	2-4	Equatorial.
<i>U. t. fallens</i> ..	<i>T. pratense</i> .	Rare.	4-7	Scattered.

(b) *U. trifolii (glomerati)*.

The rust on *T. glomeratum* resembles *U. t. trifolii-repentis* in its life history and morphology. The uredosori, teleutosori, spermogonia and aecidia all occur frequently throughout the growing season, often on the same plant. The uredosori, as in *U. t. trifolii-repentis*, do not persist.

The uredospores are finely echinulate, light cinnamon-brown, $19-27 \times 15-22 \mu$, with 2-4 equatorial germ pores. The spore wall is $1-1.5\mu$ thick. The single-celled teleutospores are smooth, cinnamon-brown, $20-35 \times 14-21 \mu$ (somewhat longer and narrower than in *U. t. trifolii-repentis*), with a single terminal pore. The spore wall is $1-2\mu$ thick.

(c) *U. trifolii fallens*.

T. pratense is parasitized by a rust which predominates in the uredospore stage. The uredosori are typically rounded, dark-brown, and medium in size on the leaf blades, and larger and elongated on the stems. Teleutospores are produced only under unfavourable conditions, usually towards the end of the growing season. Attempts to germinate teleutospores immediately have failed. However, material exposed to winter conditions at Glen Innes, N.S.W., showed a small proportion of viable spores. Neither the spermogonial nor the aecidial stage has been found under natural conditions.

The uredospores are finely echinulate, cinnamon-brown, $21-29 \times 20-24 \mu$, with 4-7 scattered germ pores. The spore wall is $1-3\mu$ thick. The single-celled teleutospores are smooth, cinnamon-brown, $20-29 \times 15-21 \mu$, with a single terminal pore. The spore wall is $1-2\mu$ thick.

The occurrence of the aecidial stage on *T. pratense* has not yet been demonstrated in Australia, but the rust corresponds in all other respects to *U. t. fallens*.

* Further details of spore dimensions are given below.

(d) U. trifolii subterranei.

The rust occurring on *T. subterraneum* is similar to *U. t. fallens*. It persists almost exclusively in the uredospore stage, the rounded, dark-brown uredosori occurring on the leaflets and petioles, and on the cotyledons of young seedlings. Teleutospores are rarely produced, having been detected in only one of 46 field collections. This collection was made from a plant which had overwintered in a favourable position at Black Mountain, A.C.T. Germination tests with the teleutospores were unsuccessful, but a portion of the material exposed to winter conditions at Glen Innes showed some viable teleutospores. Inoculations of young shoots of susceptible plants in the glasshouse gave negative results. Neither the spermatogonial nor the aecidial stage of the rust has been observed under natural conditions. However, the rust collection from Black Mountain contained viable uredospores, which presumably carry the rust from season to season.

The uredospores are finely echinulate, cinnamon-brown, $19-27 \times 16-23 \mu$, with 2-4 equatorial germ pores. The spore wall is $1-3\mu$ thick. The single-celled teleutospores are smooth, cinnamon-brown, $20-30 \times 16-22 \mu$, each with a single terminal pore. The spore wall is $1-2\mu$ thick.

The presence of the aecidial generation on *T. subterraneum* has not yet been recorded, but other characteristics of the rust provide strong presumptive evidence for its inclusion in the species *U. trifolii* (Radel, 1935; Loftus Hills, 1942). Of the three subspecies, *U. t. hybridi* is most like the Australian rust, having uredospores with 2-4 equatorial germ pores, and a life history in which the aecidial stage plays an unimportant part.

(e) U. flectens (repentis).

A rust has been found on *T. repens* under Australian conditions which is distinct from *U. t. trifolii-repentis*, being restricted to the teleutospore generation. The sori are very large, black in colour, and confined mainly to the petioles and to the midribs of the leaflets. The teleutospores germinate at maturity, the resulting sporidia causing further infection of the host. Four successive generations of teleutosori have been induced during glasshouse testing.

The single-celled teleutospores are smooth, cinnamon-brown, $18-29 \times 15-23 \mu$, each with a single terminal pore. The spore wall is $1-2\mu$ thick. The spores germinate to give hyaline, 3-4 septate promycelia, $6-9\mu$ in breadth, with sterigmata $4-8 \times 1.5-3 \mu$; the sporidia are smooth, hyaline, globular to kidney-shaped, and $10-18 \times 5-8 \mu$.

(f) U. flectens (fragiferi).

There is an Australian rust on *T. fragiferum* which resembles *U. f. (repentis)* very closely. Successive generations of teleutosori of the same general type have been produced under glasshouse conditions without the appearance of other spore stages. Details of spore morphology correspond to those recorded for *U. f. (repentis)*.

In Table 2 a summary is given of the differences between the rusts parasitizing different species of *Trifolium* in Australia.

Distribution of the Rusts.

A total of 164 rust samples has been examined between March, 1951, and January, 1952. Of these, 140 were collected in New South Wales, 10 in Victoria, 3 in South Australia, 1 in Queensland, 1 in Tasmania, 6 in Western Australia, and 3 in the Australian Capital Territory. The localities from which the samples of each rust came are given below:

U. t. trifolii-repentis: Springbrook, Qld., Glen Innes, Murwillumbah, Byron Bay, Lismore, Grafton, Oxley Island, Taree, Maitland, Lawson, Sydney, Nowra and Bega, N.S.W.

U. t. (glomerati): Gosford and Castle Hill, N.S.W.

U. t. fallens: Glen Innes, Gosford, Richmond, Castle Hill and Bega, N.S.W.

U. t. subterranei: See Table 8.

U. f. (repentis): Leeton, Sydney, Castle Hill, N.S.W., Melbourne, Vic., and Canberra, A.C.T.

U. f. (fragiferi): Melbourne, Vic., and Meningie, S.A.

Cultural Studies.

Literature Review.

The range of *Trifolium* spp. attacked by each of the three subspecies of *U. trifolii* has been studied by Liro (1906), Davis (1924), Kobel (1920), and Mains (1935). Liro and Davis attempted cross-inoculations involving the three host species, viz., *T. repens*, *T. hybridum* and *T. pratense*, and demonstrated that each subspecies is incapable of attacking the hosts of the other two. More extensive tests by Kobel and Mains have shown them to differ on a number of other species of *Trifolium*. The two workers' results do not in all instances agree, but the lack of correspondence is probably due to the use of different strains of the *Trifolium* spp.

The host specialization of *U. fectens* has not been determined.

TABLE 2.

Summary of Differences in Life History and Spore Morphology shown by Australian Clover Rusts.

Organism.	Spore Stages Commonly Present.	Uredospore Morphology.			
		Germ pores.		Spore Wall.	
		Number.	Distribution.	Colour.	Thickness in Microns.
<i>U. t. trifolii-repentis</i> ..	{ Uredospore. Teleutospore. Spermogonial. Aecidial.	2-4	Equatorial.	Light cinnamon-brown.	1-1.5
<i>U. t. (glomerati)</i>	{ Uredospore. Teleutospore. Spermogonial. Aecidial.	2-4	Equatorial.	Light cinnamon-brown.	1-1.5
<i>U. t. fallens</i>	{ Uredospore. (Teleutospore).	4-7	Scattered.	Cinnamon-brown.	1-3
<i>U. t. subterranei</i>	{ Uredospore. (Teleutospore).	2-4	Equatorial.	Cinnamon-brown.	1-3
<i>U. f. (repentis)</i>	Teleutospore.				
<i>U. f. (fragiferi)</i>	Teleutospore.				

Materials and Methods.

Seed of 35 species of *Trifolium* and nine species of related genera was obtained from the United States Department of Agriculture; the Pasture Research Station, Burnley Gardens, Melbourne; the Division of Plant Industry, C.S.I.R.O., Canberra; and the Department of Agriculture, N.S.W. For many of the species a number of different strains was available, and each has been studied individually.

A single rust isolate was used to represent each Australian rust type, with the exception of *U. t. subterranei*. Owing to the occurrence of physiologic specialization within this rust subspecies (to be considered in detail in a later section), two isolates were used in studies of its host range, one to represent each of the two most abundant physiologic races. The localities from which the selected isolates originated are given in Table 3.

Cultures of the rust isolates were maintained on plants of the species from which they were collected. Inoculations were made in separate glasshouses between August, 1951, and February, 1952. Seed was germinated between moist sheets of blotting paper in a 25° C. incubator, as this was found to speed up the testing work. Scarification of the seed coat with coarse emery paper improved the percentage germination. Approximately 20 seedlings were raised in sterilized soil in each 4" pot. When six or more leaves had developed, the plants were atomized with water, and spores dusted

on the upper surfaces of the leaves by shaking abundantly rusted plants over them. A period of incubation of 48 hours in a saturated atmosphere was found to be satisfactory. When infection had reached its maximum development (14-18 days after inoculation), notes on the reactions were taken according to the following infection types:

- I *Host immune*: no trace of mycelial invasion.
 R+ *Host very resistant*: small hypersensitive flecks shown.
 R *Host resistant*: hypersensitive flecks shown on the upper surface of the leaf blade; corresponding development of minute pustules on the lower leaf surface.
 R- *Host moderately resistant*: light-brown necrotic spotting of the upper surface of the leaf blade; corresponding development of small to medium pustules on the lower leaf surface.
 S- *Host moderately susceptible*: pustules on the upper surface medium in size, surrounded by a chlorotic halo; corresponding development of pustules medium in size on the lower surface.
 S *Host susceptible*: pustules on both leaf surfaces medium in size, coalescence infrequent; no visible expression of antagonism between host and parasite.
 S+ *Host very susceptible*: pustules on both surfaces large and confluent; often associated with crinkling of the leaf tissue.

TABLE 3.
Origin of Isolates Used in Studies of the Species Host Ranges of Australian Clover Rusts.

Rust.	Origin of Isolate.
<i>U. t. trifolii-repentis</i>	Grafton, N.S.W.
<i>U. t. glomerati</i>	Gosford, N.S.W.
<i>U. t. fallens</i>	Castle Hill, N.S.W.
<i>U. t. subterranei</i> r. A.	Castle Hill, N.S.W.
<i>U. t. subterranei</i> r. B.	Bombala, N.S.W.
<i>U. f. (repentis)</i>	Sydney, N.S.W.
<i>U. f. (fragiferi)</i>	Melbourne, Vic.

The series of reaction types based on a scale of 0-4, so commonly employed in cereal rust work (Stakman and Levine, 1922), was not found satisfactory here. The symbols I, R, S, were used to avoid confusion with the more common numerical designations. No host reaction comparable with the "mesothetic" reaction was encountered.

Results and Discussion.

In Tables 4 and 5 are given the reactions of species of *Trifolium* and related genera to the Australian clover rusts under test, and the number of strains tested within each host species. The information concerning *U. t. trifolii-repentis* and *U. t. (glomerati)* was limited by the small amount of uredospore inoculum produced.

In most instances, the reactions of the plants within a given strain showed little variation, but a few strains contained plants showing marked differences in reaction to a given rust isolate, and for these the range in reaction is given. In general, different strains of the one host species behaved similarly in their reactions to a given rust isolate, though there were exceptions. Five strains of *T. glomeratum* were susceptible to *U. t. fallens*, whereas the remaining nine strains were very resistant. One strain of *T. glomeratum* was very resistant to both races of *U. t. subterranei*, while the remaining 13 were susceptible. The reaction of one strain of *T. incarnatum* to *U. t. fallens* (R+) also differed from that of the other six strains (S). The two strains of *T. resupinatum* tested gave contrasting reactions to infection by *U. t. fallens*.

The following conclusions can be drawn from the experimental results recorded:

1. The two physiologic races of *U. t. subterranei* induce almost identical reactions in all host species.

TABLE 4.

Reactions of Species of *Trifolium* and Related Genera to Australian Clover Rusts.

Species.	Number of Strains.	Reaction Induced by				
		<i>U. f.</i> (<i>repentis</i>).	<i>U. f.</i> (<i>fragiferi</i>).	<i>U. t.</i> <i>fallens</i> .	<i>U. t. subterranei</i> .	
					r. A.	r. B.
<i>Trifolium agarium</i> L.	2	I	S-	S-	S+	S+
<i>T. alexandrinum</i> L.	3	I	I	R+	R	R
<i>T. angustifolium</i> L.	2	I	I	S+	S+	S+
<i>T. arvense</i> L.	2	I	I	I	I	I
<i>T. balansae</i> Boissier	2	S+	S+	S+	S+	S+
<i>T. carolinianum</i> Michx.	1	I	I	I	I	I
<i>T. cernuum</i> Brot.	2	S	S	S+	S+	S+
<i>T. dubium</i> Sibth.	3	I	I	I	I	I
<i>T. fragiferum</i> L.	9	S	S	R+	S	S
<i>T. globosum</i> L.	2	I	I	R	I	I
<i>T. glomeratum</i> L.	14	S+	S+	R+	S	S
<i>T. hirtum</i> All.	2	S	S-	R+ & S-	S+	S+
<i>T. hybridum</i> L.	6	S	S-	I	S	S
<i>T. incarnatum</i> L.	7	S	S-	S	S	S+
<i>T. lappaceum</i> L.	1	I	I	I	I	I
<i>T. lupinaster</i> L.	1	I	I	R+	I	I
<i>T. maritimum</i> Huds.	1	I	I	S-	S-	S- & R-
<i>T. medium</i> L.	1	I	I	I	R+	R+
<i>T. nigrescens</i> Viv.	2	S	S	I	S+	S+
<i>T. pallidum</i> Waldst. and Kit.	2	I	I	S+	I	R+
<i>T. pratense</i> L.	3	S-	S	S+ & R+	S	S
<i>T. procumbens</i> L.	1	I	I	I	R+	R+
<i>T. reflexum</i> L.	1	R+	R+	R+	R+	R+
<i>T. repens</i> L.	10	S+	I	I	I	I
<i>T. resupinatum</i> L.	2	S	S	S+ & R+	S+	S+
<i>T. scabrum</i> L.	1	S-	S-	S	S+	S
<i>T. squarrosum</i> Bieb.	1	I	S+	S	S+	S+
<i>T. stellatum</i> L.	1	I	I	I	R+	R+
<i>T. striatum</i> L.	1	S	S	S+	S+	S+
<i>T. subrotundum</i> Steud. and Hochst.	1	I	I	I	S+	S+
<i>T. subterraneum</i> L. (Mt. Barker)	1	I	I	I	S+	S+
<i>T. tomentosum</i> L.	1	S	S	S	I	I
<i>T. tridentatum</i> Lindl.	2	I	I	I	I	R+
<i>T. wormskjoldi</i> Lehm.	1	I	I	I	I	I
<i>T. xerocephalum</i> Fenzl.	1	I	I	I	I	I
<i>Lotus americanus</i> Bisch.	1	I	I	I	I	I
<i>L. corniculatus</i> L.	1	I	I	I	I	I
<i>L. hispidus</i> Desf.	1	I	I	I	I	I
<i>L. major</i> Sm.	1	I	I	I	I	I
<i>Medicago sativa</i> L.	3	I	I	I	R+	I
<i>Melilotus alba</i> Desr.	2	I	I	I	I	R+
<i>M. officinalis</i> Lamk.	1	I	I	I	I	I
<i>Trigonella suavissima</i> Lindl.	1	I	I	I	S	S
<i>Vicia atropurpurea</i> Desf.	1	I	I	I	I	I

- Only three species, viz., *T. agarium*, *T. repens*, and *T. squarrosum*, differ appreciably in their reactions to *U. f. (repentis)* and *U. f. (fragiferi)*.
- The host ranges of *U. t. fallens* and *U. t. subterranei* differ markedly, 10 of the 35 species of *Trifolium* giving contrasting reactions.
- The host ranges of both *U. t. fallens* and *U. t. subterranei* differ in many respects from those of *U. f. (repentis)* and *U. f. (fragiferi)*.
- U. t. subterranei* is able to attack a species of *Trigonella*. In no other instance has the host range of a clover rust extended beyond the genus *Trifolium*.

U. t. trifolii-repentis and *U. t. (glomerati)* cannot be compared owing to the meagre information available, but the inability of the latter to attack the two strains of *T. repens* on which it was tested is interesting and might be carried further.

The host ranges of *U. t. hybridi* (Kobel, 1920; Mains, 1935) and *U. t. subterranei* show some similarity, the former being able to attack *T. subterraneum* and the latter *T. hybridum*. However, the rusts give contrasting reactions on *T. agrarium*, *T. arvense*, *T. resupinatum* and *T. pratense*. Of particular significance is the susceptibility of seedlings of *T. pratense* to *U. t. subterranei*; extensive cross-inoculation studies (Liro, 1906; Davis, 1924) have demonstrated the resistance of *T. pratense* to attack by *U. t. hybridi*.

The Australian rust, *U. f. (repentis)*, has a host range which is similar to that of the macrocyclic form on the same host species, *U. t. trifolii-repentis*, as given by Kobel and Mains. However, the microcyclic form is able to attack both *T. pratense* and *T. hybridum*; these two species are recorded by Liro (1906), Davis (1924), Kobel (1920) and Mains (1935) as resistant to *U. t. trifolii-repentis*.

TABLE 5.
Reactions of Species of Trifolium to Australian Clover Rusts.

Species.	Number of Strains.	Reaction Induced by	
		<i>U. t. trifolii-repentis</i> .	<i>U. t. (glomerati)</i> .
<i>T. glomeratum</i> L. . .	4	S	S
<i>T. pratense</i> L. . . .	1	I	I
<i>T. repens</i> L.	2	S	I
<i>T. subterraneum</i> L. . .	1	I	I

Physiologic Specialization of Subterranean Clover Rust.

Introduction.

Leaf rust (*U. t. subterranei*) appears to be the most destructive of the diseases of subterranean clover in Australia. During favourable seasons, serious losses in grazing potential may result owing to the widespread cultivation of susceptible varieties. Resistant varieties are available, but in general their yielding capacity is not high. The incorporation of rust resistance into susceptible but prolific commercial varieties would therefore be an important step in reducing such losses.

Continued freedom from the disease, however, must be based on an understanding of the physiologic specialization shown by the pathogen. No evidence of specialization in *U. t. subterranei* has yet been recorded. Little information is available on the reactions of subterranean clover varieties to rust, and the observations recorded by different workers are not completely concordant.

Accordingly, the present study was undertaken with the following objectives:

1. To search for evidence of specialization in the pathogen;
2. To determine the distribution in Australia of any physiologic races detected;
3. To determine the reactions of all available varieties to each physiologic race.

Review of Literature.

Australian, American and European varieties of subterranean clover have been classified by Aitken and Drake (1941). Observations were made of more than 200 samples grown year after year at Burnley Gardens, Melbourne, and more than 50 varieties differentiated, each exhibiting an extreme stability of type. Levy and Gorman (1937) classified 25 varieties for resistance to leaf rust during plot trials at Palmerston North, New Zealand. Radcliff (1935), in discussing Tasmanian field trials, mentioned the relative resistance to leaf rust of several varieties. Loftus Hills (1942) has summarized the

results of field observations on the reactions to leaf rust of 24 varieties grown at Moss Vale, N.S.W., and Canberra, A.C.T. The observations at the two localities did not in all instances agree, and discrepancies were found between these results and those recorded by Radel, and Levy and Gorman.

A satisfactory technique for the hybridization of subterranean clover varieties has been developed by McMillan (1937). From field observations on the F₂ generation of a cross between Mt. Barker and the immune early-maturing variety Mulwala, Loftus Hills (1944) concluded that resistance to leaf rust was an inherited character in which susceptibility was dominant, and that a variety could probably be evolved which would combine the desirable agronomic characters of Mt. Barker with the rust resistance of Mulwala.

Materials and Methods.

Seed of 70 varieties of subterranean clover was obtained from the Pasture Research Station, Burnley; the Division of Plant Industry, C.S.I.R.O., Canberra; and the Department of Agriculture, N.S.W. In some instances seed of a given variety was received from more than one source, and each seed sample has been studied individually.

TABLE 6.
Reactions of Selected Varieties of *U. subterraneum* to Three Physiologic Races of *U. t. subterranei*.

Test Variety.	Reaction to Physiologic Race.		
	"A."	"B."	"C."
Bacchus Marsh	R & S	S	S
Clare	R	S-	R
Dwalganup	R-	S	R-
Madrid	S	S+	S
Mt. Barker	S+	S+	S+
Mulwala	I	I	I
Tallarook	S	S	S
Yarloop	R+	S+	R-

Isolates of *U. t. subterranei* have been collected from 27 localities throughout the subterranean clover areas of Australia. Cultures of the rust isolates were maintained on plants of the variety from which they were collected. A technique was developed involving the use of seedlings grown in 6" x 1" glass tubes stoppered with loose cotton wool plugs, a method most useful for the initiation of cultures from specimens collected during surveys of country areas. A large number of cultures was thus maintained, without fear of mixing, until glasshouse space became available. In the bottom of each tube were placed a few small pebbles covered with a piece of cotton wool, to drain excess water from the sifted soil above. Watering was necessary only according to the amount of water visible in the bottom of the tubes. The roots of the seedlings were kept in darkness by means of a strip of brown paper around the base of each tube.

Because of the manual work involved, seedlings grown under tube conditions were unsatisfactory for the general testing work, and the method described in the previous section was used. The testing period was from May, 1951, to February, 1952.

Results.

A set of eight subterranean clover varieties was selected arbitrarily for the comparison of isolates of *U. t. subterranei* (Table 6). As each isolate came to hand it was built up on susceptible plants and tested on the selected varieties. The individual plant reactions within each variety except Bacchus Marsh were completely uniform, and 15-20 seedlings of a given variety provided a most satisfactory basis for comparative studies.

By this means three physiologic races of the pathogen were differentiated. The reactions of the selected host varieties to the races, recorded under uniform environmental conditions, are given in Table 6. The races are most easily recognized by use of the variety Yarloop. A summary is given in Table 7 of the number of times each race has been isolated from material collected in each State. Table 8 lists the localities within each State from which isolates have been collected, together with racial designations.

From a breeding viewpoint, it is important to know not only the distribution of each physiologic race, but also the relative susceptibility of all available host varieties.

TABLE 7.

Frequency of Isolation of Physiologic Races of U. t. subterranei from Material Collected in the States of Australia.

Race.	Number of Isolations in Each State.					Total.
	N.S.W.	Vic.	Tas.	S.A.	W.A.	
A	16	1	1	1	5	24
B	1	4				5
C	1					1
Totals ..	18	5	1	1	5	30

TABLE 8.

Localities Throughout Australia from which Isolates of U. t. subterranei have been Obtained.

Locality.	Race.	Locality.	Race.
Glen Innes, N.S.W.	A	Bombala, N.S.W.	B
Wingham, N.S.W.	A	Lang Lang, Vic.	B
Oxley Island, N.S.W.	A	South Gippsland, Vic.	B
Gloucester, N.S.W.	A	Burnley, Vic.	B
Tuncurry, N.S.W.	C	Box Hill, Vic.	B
Maitland, N.S.W.	A	Moorooduc, Vic.	A
Capertee, N.S.W.	A	Cressy, Tas.	A
Castle Hill, N.S.W.	A	Glen Osmond, S.A.	A
Goulburn, N.S.W.	A	Esperance, W.A.	A
Canberra, N.S.W.	A	Manjimup, W.A.	A
Leeton (M.I.A.), N.S.W.	A	Marybrook, W.A.	A
Griffith (M.I.A.), N.S.W.	A	Waterloo, W.A.	A
Bodalla, N.S.W.	A	Bullsbrook, W.A.	A
Bega, N.S.W.	A		

The reactions of 70 varieties to race A from Castle Hill, N.S.W., race A from Manjimup, W.A., race B from Bombala, N.S.W., and race B from Box Hill, Vic., were therefore determined. The results are summarized in Table 9. With the varieties listed in Table 6, the seedling reactions under glasshouse conditions correspond to those of three-months-old plants raised out of doors.

Discussion.

Physiologic specialization in *U. t. subterranei* must influence the problem of breeding rust resistant varieties. On the basis of the evidence at hand, race B appears to be restricted to Victoria and southern New South Wales, but it must be considered capable of spreading to all subterranean clover areas in Australia. Presumably the race has

TABLE 9.
Reactions of Varieties of T. subterraneum to Physiologic Races of U. t. subterranei.

Variety.	Number of Samples.	Reaction to Physiologic Race.			
		"A." N.S.W.	"A." W.A.	"B." N.S.W.	"B." Vic.
Amber-seeded Mt. Barker	1	S	S+	S	S
Bacchus Marsh	5	R & S	R & S-	S	S
Bass	3	R-	R-	S	S
Baulkamaugh North	1	I	I	I	I
Bena	2	S	S	S+	S
Benalla	1	S-	S	S+	S
Berlin	1	R+	R+	S	S
Burnerang	2	S-	S	S+	S+
Burnley	2	S-	S-	S	S
Casterton	2	R	R	S	S
Clare	3	R	R	S-	S-
Cranmore	1	S+	S+	S	S
Daliak	2	R+	R+	S	S
Derrinal	1	R	R+	S	S
Dwalganup	5	R-	R-	S	S
Edenhope	2	S	S	S	S
Flinders	1	R+	R	S	S
Gin Gin	1	R+	R+	S	S
Hexham Hairy Stem	2	R	R	S+	S+
Hexham Smooth Stem	2	R	R	S+	S
Hill's Small	2	R	R-	S	S
Horsham	1	R-	R	S	S
Kilmore	2	R+	R+	S	S
Kyabram	2	S-	S-	S+	S+
Kybybolite	1	S+	S+	S	S
Kyneton	1	R+	R	S	S
Lake Midgeon	2	S	S-	S+	S+
Leige	1	R-	S-	S	S
MacArthur	1	S	S-	S	S
Madrid	3	S	S+	S+	S
Mansfield	2	S-	S-	S+	S+
Merino	1	S-	S	S	S
Milton	2	R-	R	S	S
Mt. Barker	5	S+	S+	S+	S+
Mulwala	2	I	I	I	I
Muresk	1	R	R	S	S
Nangeela	5	R	R	S	S
New Northam Early	1	R-	R	S	S
Northam	1	R-	R-	S	S
Northam B	1	R-		S	
Northam C	1			S-	
Northam D	1			S-	
Orford	1	S+	S+	S	S
Pahantamu	1	R-	R-	S	S
Phillip Island	1	S-	R-	S+	S
Pink Flowered	2	R-	R-	S	S
Port Fairy	1	S	S-	S+	S+
Portugal	1	S+	S+	S+	S+
Portugal A	1	R	R	S	S
Redleaf	1	S	S	S	S
Romsey	1	S-	S-	S	S
Rouen	1	R+	R	S	S
Ruakura Farm	1	R+	R+	S+	S
Ruakura Selection	1	R+	R+	S	S+
Samaria	2	R	R	S	S
Seaton Park	2	S-	S	S	S
Smeaton	2	R	R+	S	S
Springhurst	2	R	R+	S	S
Tallarook	7	S	S	S	S
Turkish	1	R	R	S	S-
Wallendbeen	1	S+	S+	S	S

TABLE 9.—Continued.

Reactions of Varieties of U. t. subterranean to Physiologic Races of U. t. subterranei.—Continued.

Variety.	Number of Samples.	Reaction to Physiologic Race.			
		"A." N.S.W.	"A." W.A.	"B." N.S.W.	"B." Vic.
Wangarrata	1	S-	S-	S+	S+
Wenigup	2	R+	R+	R+	R+
White-seeded Mt. Barker .. .	1	S+	S+	S+	S
Williams	1	R+	R	S	S
Wodonga	1	R+	R	S	S
Yabba North	1	R	R	S	S
Yarloop	6	R+	R+	S+	S+
Yea	2	R	R+	S	S

arisen in Victoria during recent years, its greater aggressiveness having resulted in a progressive widening of its distribution.

Breeding programmes in States other than Victoria cannot be based solely on the principle of "field-exposure" to rust attack. Varieties developed by such a method would carry resistance to race A of *U. t. subterranei*, but not necessarily to race B, and might be rendered "field-susceptible" by the subsequent introduction of race B to the area.

Physiologic specialization in *U. t. subterranei* has some significance from a mycological viewpoint as well, being the first recorded instance of specialization within a subspecies of *U. trifolii*.

The available sources of resistance to leaf rust are shown in Table 9. There are 19 varieties which show strong resistance (I or R+) to race A, but only three which are resistant to race B, viz., Baulkamaugh North, Mulwala and Wenigup. Since each of the three varieties shows immunity to both races of the pathogen, its value as a resistant parent in breeding work is obvious.

The host ranges of the isolates of race A from New South Wales and Western Australia are identical; this is also the case with the isolates of race B from New South Wales and Victoria. The series of eight test varieties used in the comparative studies was apparently adequate.

There appears to be no strict correlation of the flowering date of a given host variety to its rust reaction, though the rust incidence under field conditions is no doubt affected by seasonal factors.

Much more must be learned before our knowledge of the physiologic races of *U. t. subterranei* in Australia is complete. An intensive survey of each State to detect all physiologic races, and to provide information about the distribution in space of each, should ideally be made annually. The most urgent question arising from the present investigation concerns the distribution in space and time of race B.

Biometrical Studies of Spore Dimensions.

Literature Review.

Comparative biometrical studies of spore morphology have been recorded for few species of plant rusts. Levine (1923) presented the first statistical information on the spores of subspecies of *Puccinia graminis*, all of which showed significant differences in uredospore, teleutospore, and aecidiospore dimensions when cultured under uniform conditions. A comparative study of the uredospores of eight physiologic races of *P. g. tritici*, made by Levine (1928), detected significant differences in their size and shape. The differences were often found to be similar in magnitude to those between subspecies of *P. graminis*.

Waterhouse (1930) made biometrical studies of the spore morphology of cereal rusts in Australia. Significant differences were shown between subspecies of *P. graminis*, between physiologic races of *P. g. tritici*, and between races of *P. triticina*.

The spore forms of rusts of *Trifolium* spp. have hitherto been characterized by the ranges within which measurements of length and breadth have fallen.

Methods and Material.

To ensure representative spore samples, efforts were made to standardize the conditions under which the rusts developed, and the procedures of spore sampling and measurement. The spores were produced on fully susceptible host plants under glasshouse conditions, and all measurements were made during a period of two months. Closely related rusts were cultured simultaneously.

All rust cultures were initially derived from field collections. Teleutospores of *U. t. subterranei* and *U. t. fallens* could not be induced under glasshouse conditions, and those from field collections were used in these studies.

To ensure the complete maturity of the spore sample, heavily infected leaves of the host were lightly shaken over a large drop of 50% aqueous lactic acid on a slide. After mounting, a constant period was allowed before measurement. All measurements were

TABLE 10.
Dimensions of Teleutospores of Subspecies of U. flectens and U. trifolii.

Subspecies.	Teleutospore Dimensions.		
	Mean Length in Microns.	Mean Breadth in Microns.	Mean Ratio.
<i>U. f. (repentis)</i>	23.55±0.13	19.01±0.09	1.25±0.009
<i>U. f. (fragiferi)</i>	22.90±0.12	18.79±0.09	1.23±0.009
<i>U. t. trifolii-repentis</i>	23.16±0.12	19.16±0.08	1.22±0.008
<i>U. t. subterranei</i> A	23.83±0.15	18.96±0.09	1.27±0.010
<i>U. t. fallens</i>	24.24±0.13	18.22±0.09	1.34±0.011
<i>U. t. (glomerati)</i>	25.80±0.19	17.57±0.10	1.49±0.017

made with the same Watson "Service" microscope, and the same combination of ocular and objective used with an ocular micrometer. The same artificial light intensity was used throughout.

To avoid unconscious selection of spores, every spore encountered in passing was considered for measurement, but with teleutospores, and with all uredospores except those of *U. t. fallens*, it was possible to reject for measurement those spores orientated with their long axes at right angles to the plane of the slide, by careful observation of the germ pore distribution. The greatest length and breadth were taken for uredospores. For teleutospores, the greatest breadth was taken, and the length was measured from the tip of the hyaline papilla covering the apical pore to the point of attachment of the pedicle. The ratio of length to breadth was calculated for each spore.

The procedure adopted by Levine (1928) for the determination of the size of an adequate spore sample, related to the particular rusts studied, and to the conditions of rust culture, spore sampling and spore measurement was applied, and it was found that a sample of 50 spores, collected and measured in the manner described, was adequate. In the comparative studies, a spore sample of 200 was used; the ability of the resulting statistics to characterize the rusts is thus assured.

Results.

(a) Teleutospore comparisons.

In Table 10 the statistics resulting from the measurement of 200 teleutospores of each of the two subspecies of *U. flectens*, and of the four subspecies of *U. trifolii*, are

presented. Teleutospores of race B of *U. t. subterranei* could not be induced under glasshouse conditions, nor were they present in any field collection. Errors given for the means are the standard errors. A summary of the differences between means is given in Table 11. Test statistics are obtained by dividing the difference to be tested by its standard error. For a one-sided *t*-test, a test statistic greater than 2.3 is significant at the .01 level of probability.

The rusts can be seen to show significant differences in teleutospore length and breadth. Teleutospores of *U. f. (repentis)* have a mean length which exceeds that of the teleutospores of *U. f. (fragiferi)* by $0.65 \pm 0.18 \mu$. The means obtained for the subspecies of *U. trifolii* vary by as much as $2.64 \pm 0.22 \mu$ in length, and $1.59 \pm 0.13 \mu$ in breadth.

In Table 10 the subspecies of *U. trifolii* are arranged in order of increasing average length and decreasing average breadth of the teleutospores, showing the consistent negative correlation between the two dimensions. Teleutospores of subspecies of *U. flectens* do not conform to the same pattern.

The non-significant differences between the teleutospores of *U. f. (repentis)* and *U. t. trifolii-repentis* are summarized in the last line of Table 11. Such similarity favours theories of a common origin of the two species on *T. repens*.

TABLE 11.

Summary of Differences between Means of Dimensions of Teleutospores of Subspecies of *U. flectens* and *U. trifolii*.

Rusts Compared.	Length.		Breadth.		Ratio.	
	Difference in Means in Microns.	Test Statistic.	Difference in Means in Microns.	Test Statistic.	Difference in Means.	Test Statistic.
<i>U. f. (repentis)</i> and <i>U. f. (fragiferi)</i>	0.65 ± 0.18	3.6*	0.22 ± 0.13	1.7	0.02 ± 0.013	1.5
<i>U. t. trifolii-repentis</i> and <i>U. t. subterranei</i> A	0.67 ± 0.19	3.5*	0.20 ± 0.12	1.7	0.05 ± 0.013	3.8*
<i>U. t. trifolii-repentis</i> and <i>U. t. fallens</i>	1.08 ± 0.18	6.0*	0.94 ± 0.12	7.8*	0.12 ± 0.014	8.6*
<i>U. t. trifolii-repentis</i> and <i>U. t. (glomerati)</i>	2.64 ± 0.22	12.0*	1.59 ± 0.13	12.2*	0.27 ± 0.019	14.2*
<i>U. t. subterranei</i> A and <i>U. t. fallens</i>	0.41 ± 0.20	2.1	0.74 ± 0.13	5.7*	0.07 ± 0.015	4.7*
<i>U. t. subterranei</i> A and <i>U. t. (glomerati)</i>	1.97 ± 0.24	8.2*	1.39 ± 0.13	10.7*	0.22 ± 0.020	11.0*
<i>U. t. fallens</i> and <i>U. t. (glomerati)</i>	1.56 ± 0.23	6.8*	0.65 ± 0.13	5.0*	0.15 ± 0.020	7.5*
<i>U. f. (repentis)</i> and <i>U. t. trifolii-repentis</i>	0.39 ± 0.18	2.2	0.15 ± 0.12	1.3	0.03 ± 0.012	2.5*

* Significant at $P=0.01$.

(b) Uredospore comparisons.

In Table 12 are presented the dimensions of uredospores of subspecies of *U. trifolii* and of races of *U. t. subterranei*. There are considerable differences in uredospore dimensions within the rust species, the subspecies differing by up to $1.54 \pm 0.13 \mu$ in length and $2.00 \pm 0.11 \mu$ in breadth. Race A of *U. t. subterranei* has a mean uredospore which is $0.54 \pm 0.14 \mu$ longer than that of race B. The difference in the average ratio of length to breadth shown by the two races was noticeable from a direct visual comparison of groups of uredospores.

In Table 12 the mean uredospore lengths are arranged in order of increasing magnitude. A negative correlation between length and breadth is apparent among all subspecies except *U. t. fallens*, whose average uredospore is longer and wider than that of any other subspecies. *U. t. fallens* has uredospores with 4-7 scattered germ pores, while the other subspecies all have 2-4 equatorial germ pores.

The inter-subspecies differences in uredospore dimensions, and the difference in mean length shown by races A and B of *U. t. subterranei*, are of a similar order. Levine (1928) and Waterhouse (1930) record similar properties of cereal rusts. Since physiologic races showing similar morphological differences may occur within other subspecies, the statistics given in Tables 10 and 12 are characteristic only of the entities tested, and not necessarily of the subspecies of which the entities are representative.

TABLE 12.
Dimensions of Uredospores of Subspecies of U. trifolii.

Subspecies.	Uredospore Dimensions.		
	Mean Length in Microns.	Mean Breadth in Microns.	Mean Ratio.
<i>U. t. subterranei</i> B	21.85 ± 0.09	20.28 ± 0.07	1.09 ± 0.004
<i>U. t. subterranei</i> A	22.39 ± 0.11	20.25 ± 0.08	1.11 ± 0.005
<i>U. t. trifolii-repentis</i>	22.70 ± 0.10	20.02 ± 0.07	1.14 ± 0.006
<i>U. t. (glomerati)</i>	22.80 ± 0.10	19.42 ± 0.09	1.18 ± 0.007
<i>U. t. fallens</i>	23.39 ± 0.09	21.42 ± 0.06	1.08 ± 0.004

TABLE 13.
Summary of Differences between Means of Dimensions of Uredospores of Subspecies of U. trifolii.

Subspecies Compared.	Length.		Breadth.		Ratio.	
	Difference in Means in Microns.	Test Statistic.	Difference in Means in Microns.	Test Statistic.	Difference in Means.	Test Statistic.
<i>U. t. subterranei</i> B and <i>U. t. subterranei</i> A	0.54 ± 0.14	3.9*	0.03 ± 0.11	0.3	0.02 ± 0.006	3.3*
<i>U. t. subterranei</i> B and <i>U. t. trifolii-repentis</i>	0.85 ± 0.13	6.5*	0.26 ± 0.10	2.6*	0.05 ± 0.007	7.1*
<i>U. t. subterranei</i> B. and <i>U. t. (glomerati)</i>	0.95 ± 0.13	7.3*	0.86 ± 0.11	7.8*	0.09 ± 0.008	11.3*
<i>U. t. subterranei</i> B and <i>U. t. fallens</i>	1.54 ± 0.13	11.8*	1.14 ± 0.09	12.7*	0.01 ± 0.006	1.7
<i>U. t. subterranei</i> A and <i>U. t. trifolii-repentis</i>	0.31 ± 0.15	2.1	0.23 ± 0.11	2.1	0.03 ± 0.008	3.8*
<i>U. t. subterranei</i> A and <i>U. t. (glomerati)</i>	0.41 ± 0.15	2.7*	0.83 ± 0.12	6.9*	0.07 ± 0.009	7.8*
<i>U. t. subterranei</i> A and <i>U. t. fallens</i>	1.00 ± 0.14	7.1*	1.17 ± 0.10	11.7*	0.03 ± 0.006	5.0*
<i>U. t. trifolii-repentis</i> and <i>U. t. (glomerati)</i>	0.10 ± 0.14	0.7	0.60 ± 0.11	5.5*	0.04 ± 0.009	4.4*
<i>U. t. trifolii-repentis</i> and <i>U. t. fallens</i>	0.69 ± 0.13	5.3*	1.40 ± 0.09	15.6*	0.06 ± 0.007	8.6*
<i>U. t. (glomerati)</i> and <i>U. t. fallens</i>	0.59 ± 0.13	4.5*	2.00 ± 0.11	18.2*	0.10 ± 0.008	12.5*

* Significant at P=0.01.

(c) Comparison of uredospore and teleutospore dimensions.

Tables 10 and 12 show that inter-subspecies differences in teleutospore dimensions are not correlated to corresponding differences in uredospore dimensions. A similar case was recorded by Waterhouse (1930) for Australian physiologic races of *P. g. tritici*. However, within each subspecies of *U. trifolii*, the average teleutospore is both longer

and narrower than the corresponding average uredospore. This seems to be characteristic of the species.

Differences between the spore dimensions of subspecies of *U. trifolii* are in no instance as great as those found by Levine (1923) between subspecies of *P. graminis*. However, subspecies of *U. trifolii* are differentiated by species within the genus *Trifolium*, whereas subspecies of *P. graminis* are specialized largely to different genera of the Gramineae, and a lower order of morphologic variation in the former species would therefore be anticipated.

Conclusions.

Studies of the rusts occurring on five species of *Trifolium* in Australia have distinguished seven biological and morphological entities, viz.: *U. trifolii trifolii-repentis*, *U. trifolii (glomerati)*, *U. trifolii fallens*, *U. trifolii subterranei* races A and B, *U. flectens (repentis)*, *U. flectens (fragiferi)*. *U. trifolii* and *U. flectens* are recognized clover rust species, but only *U. t. trifolii-repentis* and *U. t. fallens* correspond to previously recognized subspecies.

Since physiologic races of a subspecies of *P. graminis* are differentiated by species and varieties within the host genus, comparable biological entities within a subspecies of *U. trifolii* would be differentiated by varieties within the host species. Races A and B of *U. t. subterranei* do not differ in reaction on the range of *Trifolium* spp. tested, but are separated by varieties of *T. subterraneum*.

Of the three previously recognized subspecies of *U. trifolii*, subterranean clover rust resembles *U. t. hybridi* most closely. Though material of *U. t. hybridi* has not been available for comparison with *U. t. subterranei*, the two rusts apparently differ in their ability to parasitize *T. pratense*. The recognition of *U. t. subterranei* as a fourth subspecies of *U. trifolii* therefore seems justified.

The Australian rust of *T. glomeratum* clearly belongs to the species *U. trifolii*, and closely resembles *U. t. trifolii-repentis*. Limited glasshouse tests have shown the ability of *U. t. trifolii-repentis* to attack *T. glomeratum*, and the resistance of *T. repens* to *U. t. (glomerati)*. The rusts also differ markedly in teleospore dimensions. However, the information available is not yet sufficiently extensive to warrant the recognition of *U. t. (glomerati)* as a distinct subspecies.

The short-cycle rusts on *T. repens* and *T. fragiferum* belong to the species *U. flectens*. The teleospores of *U. f. (repentis)* are $0.65 \pm 0.18 \mu$ longer than those of *U. f. (fragiferi)*. While *U. f. (repentis)* attacks all strains of *T. repens* and *T. fragiferum* tested, *U. f. (fragiferi)* is unable to attack available strains of *T. repens*. The reactions of the rusts correspond on the majority of *Trifolium* spp. tested. Classification of the rusts is difficult at this stage. The species *U. flectens* was originally described by Lagerheim as occurring on *T. repens*; the inability of *U. f. (fragiferi)* to attack *T. repens* may therefore warrant separation of the rust as a subspecies, implying a lower order of variation in *U. flectens* than in *U. trifolii*. Alternatively, the two microcyclic rusts may be considered as physiologic races of the rust of their common host, *T. fragiferum*, but since the rusts are differentiated by features of their species host ranges, such a concept of racial difference is not comparable with that proposed for *U. trifolii*. It is felt that the rusts are best considered as distinct subspecies of *U. flectens*, but until more is known no decision can be made.

II. LONGEVITY OF UREDOPORES OF SUBTERRANEAN CLOVER RUST.

Introduction.

Oversummering of uredospores of *U. t. subterranei* in a viable condition has been described. In view of the apparent importance of uredospores in carrying the rust over from season to season, some information is desirable on the longevity of the spores under controlled conditions of temperature and humidity.

Materials and Methods.

Uredospore inoculum freshly produced under glasshouse conditions was stored in small desiccators, the humidity within each of which was regulated by an $H_2SO_4:H_2O$

mixture. Three levels of relative humidity were used, 30%, 50% and 70%, corresponding to specific gravities of 1.43, 1.34 and 1.24 of the mixture. Three desiccators, one representing each level of relative humidity, were stored in the absence of light in incubators at the six temperatures shown in Table 14.

Germination tests of the material were made at regular intervals, the most satisfactory germination resulting when the spores were dusted on to the surface of tap water in a syracuse dish. Germinations were made at a temperature of 20–23° C.

Results and Discussion.

The results are given in Table 14. A 100% germination is represented by +++, 50% by ++, and 5% by +. Failure of germination is designated by –.

It can be seen that conditions of low temperature and low humidity (30%) are the most favourable for storage of the uredospore inoculum. At 2° C. and 30% relative

TABLE 14.

Longevity of Uredospores of U. t. subterranei at Various Combinations of Temperature and Relative Humidity.

Temperature.	Relative Humidity.	Viability at Progressive Storage Periods.			
		36 Days.	61 Days.	97 Days.	145 Days.
2° C.	30%	+++	+++	+++	+
	50%	+++	+++	+++	–
	70%	+++	+++	+	–
5° C.	30%	+++	+++	+++	–
	50%	+++	+++	+++	–
	70%	+++	+++	+	–
10° C.	30%	+++	+++	+++	–
	50%	+++	+++	+++	–
	70%	+++	+++	–	–
15° C.	30%	+++	+++	+++	–
	50%	+++	+++	+++	–
	70%	++	+	–	–
20° C.	30%	+++	+++	–	–
	50%	++	+	–	–
	70%	–	–	–	–
25° C.	30%	++	+	–	–
	50%	–	–	–	–
	70%	–	–	–	–

humidity, the maximum period of storage is approximately five months. Though conditions in the field are not directly comparable with those prevailing in a controlled experiment of this nature, it can be concluded that repeated infection of volunteer plants throughout the summer period is necessary for the carry-over of subterranean clover rust.

III. THE INFLUENCE ON RUST DEVELOPMENT OF STRAINS OF RHIZOBIUM TRIFOLIUM.

Introduction.

Among the several nutrients which influence the disease disposition of host plants, nitrogen occupies a central position. Its influence on the development of plant rusts is well established (Chester, 1946). Attention is immediately drawn to the part played by symbiotic nitrogen-fixing bacteria in conditioning rust susceptibility in legume species. An experiment was therefore designed to determine the extent to which the presence of a bacterial symbiont in the root system of a host plant influences rust development.

Materials and Methods.

Seedlings of three varieties of *T. subterraneum* were raised in 6" x 1" specimen tubes stoppered with light cotton wool plugs, on a basic agar medium of the following composition: CaHPO₄ 1 gm., K₂HPO₄ 0.2 gm., MgSO₄ 0.2 gm., NaCl 0.2 gm., FeCl₃ 0.1 gm., agar 8 gm., water 1 litre. The pH of the medium was adjusted to 6.5 by the addition of 8 ml. of N/10 NaOH per litre.

The following four treatments were compared:

1. Inoculation with an ineffective strain of *Rhizobium*;*
2. No nitrogen source;
3. Inoculation with an effective strain of *Rhizobium*;*
4. Inorganic nitrogen supplement.

Commercial seed of the three host varieties was sterilized with 1/500 HgCl₂ and germinated aseptically, after the fifth washing, on yeast-mannitol-agar. For treatments 1 and 3 a suspension was prepared by "rubbing-up" the growth of the bacterial strain with a few ml. of sterile water. The germinated seeds were then mixed with a little of the suspension under aseptic conditions, and sown on the surface of the basic agar medium at two seeds per tube. In the case of treatment 2, seedlings were grown from sterilized and germinated seeds in the basic agar medium described above. A supplement of 0.05% KNO₃ was used in treatment 4.

Two physiologic races of *U. t. subterranei* were employed. Seedlings were inoculated when the first signs of nitrogen deficiency became apparent in seedlings grown under the conditions of treatment 2. The experiment was replicated three times, so that a sample of six seedlings of each variety was available for the determination of the influence of each treatment on the development of each rust race.

The experiment was conducted under laboratory conditions throughout the period October to December, 1951. Lighting was adequate for healthy seedling growth and for satisfactory rust development. The mean daily temperature ranged from 60 to 70° F. Measurements of pustule diameters were made under the low power objective of the microscope, by means of an ocular micrometer. Care was taken not to disturb the uredosori.

Results.

(a) Development of the seedlings.

Seedlings subjected to treatments 1 and 2 began to show symptoms of nitrogen deficiency 27 days after germination; it was at this stage that the seedlings were inoculated with the appropriate leaf rust race. By the time the uredosori reached maximum development the deficiency symptoms were acute; the cotyledons were yellow and withering, the leaflets mottled, and the seedlings stunted. No consistent difference in appearance could be detected between the seedlings of treatments 1 and 2.

Seedlings inoculated with an effective strain of *Rhizobium* made normal growth but showed a faint mottling of the leaflets; those grown with a nitrate supplement maintained a healthy dark-green appearance throughout.

(b) Nodulation.

Root nodules induced by the ineffective bacterial strains were typically poorly developed, white in colour, and produced in large numbers scattered throughout the root system. With the effective strains a smaller number of large pigmented nodules was formed, usually aggregated towards the surface of the growth medium.

(c) Rust development.

The reactions given by the three host varieties to each rust race under the conditions of each nitrogen treatment are indicated in Table 15, expressed in terms of the approximate mean pustule diameter in millimetres on the lower surfaces of the second seedling leaves. Microscopic measurements of pustule diameter were made for all seedlings of the Mt. Barker variety (Table 16). The maximum diameter of each pustule

* These cultures were made available by Mr. J. M. Vincent, to whom thanks are tendered.

was taken, approximately 50 measurements contributing to each mean. Readings for the varieties Dwalganup and Yarloop were estimated by visual comparison with the Mt. Barker series.

An analysis of variance technique (Snedecor and Cox, 1935) was applied to the data (Table 17). It can be concluded that pustule diameter is significantly influenced by the treatment given the host seedlings, and though the two rust races do not appear to differ inherently in pustule size, they do differ in the magnitude of their response to different treatments (significant interaction)

TABLE 15.
Reactions of Varieties of *T. subterraneum* to Races A and B of *U. t. subterranei*.

Treatment.	Host Variety.					
	Mt. Barker.		Dwalganup.		Yarloop.	
	Race A.	Race B.	Race A.	Race B.	Race A.	Race B.
1. Ineffective <i>Rhizobium</i> ..	0.3* ^c	0.3	0.3	0.3	;	0.4
2. Non-nitrogen ..	0.4 ^c	0.4	0.3	0.3	;	0.4
3. Effective <i>Rhizobium</i> ..	0.5	0.5	0.4	0.4	;	0.5
4. Inorganic nitrogen ..	0.7	0.5	0.7	0.7	;	0.7

* Approximate mean pustule diameter in millimetres.

"c" Denotes the presence of a halo of slightly chlorotic tissue.

"C" Denotes an advanced chlorotic condition in the tissue surrounding the uredosori.

;

TABLE 16.

Mean Diameters of Uredosori of Races A and B of *U. t. subterranei* on *Mt. Barker*.

Treatment.	Mean Pustule Diameter in Microns.		
	Race A.	Race B.	
1. Ineffective <i>Rhizobium</i> {	Strain L89*	332 ± 8	310 ± 10
	Strain L90	322 ± 19	334 ± 13
2. Non-nitrogen	415 ± 21	446 ± 20
3. Effective <i>Rhizobium</i> {	Strain L91	554 ± 28	460 ± 31
	Strain L92	530 ± 20	474 ± 25
4. Inorganic nitrogen	695 ± 23	503 ± 18

* Accession numbers at Faculty of Agriculture, University of Sydney.

In Table 18 are shown differences between the treatment means together with the results of tests of their significance. The between-treatment differences shown by race A on Mt. Barker are all highly significant, while the differences between strains within treatments are non-significant. The corresponding differences for race B are somewhat less marked but a similar pattern is evident in the results. Two important observations are:

1. Rust development is more vigorous on seedlings grown in a non-nitrogen medium than on seedlings grown in the same medium in the presence of an ineffective strain of *Rhizobium*. The difference in vigour appears to be independent of the quantitative response to available nitrogen, since in both cases the seed proteins are the only nitrogen source.

2. Seedlings supplied with inorganic nitrogen promote more vigorous rust growth than those inoculated with an effective strain of *Rhizobium*. However, this may be due to a difference in the level of nitrogen available to the rust under the conditions of the two treatments.

These effects can be seen to vary in degree with the rust race and host variety considered. Of particular interest is the stability of the resistant reaction of Yarloop to rust race A.

TABLE 17.

Analysis of Variance of Mean Pustule Diameters of Races of U. t. subterranei on Mt. Barker.

Source of Variation.	Degrees of Freedom.	Sum of Squares.	Mean Square.	F.
Between treatments	5	120,066	24,013	7.2*
Between rust races	1	8,587	8,587	2.6
Interaction	5	16,626	3,325	8.0**
Total	11	145,279		
Experimental error	676		416	

* Significant at $P=0.05$, tested against Interaction.

** Significant at $P=0.001$, tested against Experimental error.

TABLE 18.

Tests of Significance of Differences between Treatment Means.

Comparison.	Race A.		Race B.	
	Difference in Means in Microns.	Test Statistic.	Difference in Means in Microns.	Test Statistic.
Ineffective <i>Rhizobia</i> L89 and L90	10 ± 21	0.5	24 ± 16	1.5
Ineffective <i>Rhizobium</i> L89 and Non-nitrogen ..	83 ± 22	3.8*	136 ± 22	6.2*
Ineffective <i>Rhizobium</i> L90 and Non-nitrogen ..	93 ± 28	3.3*	112 ± 24	4.7*
Non-nitrogen and Effective <i>Rhizobium</i> L91 ..	139 ± 35	4.0*	14 ± 37	0.4
Non-nitrogen and Effective <i>Rhizobium</i> L92 ..	115 ± 29	4.0*	28 ± 32	0.9
Effective <i>Rhizobia</i> L91 and L92	24 ± 34	0.7	14 ± 40	0.4
Effective <i>Rhizobium</i> L91 and Inorganic nitrogen	141 ± 36	3.9*	43 ± 36	1.2
Effective <i>Rhizobium</i> L92 and Inorganic nitrogen	165 ± 31	5.3*	29 ± 31	0.9

* Significant at $P=0.01$.

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THE *CULEX PIPIENS* GROUP IN SOUTH-EASTERN AUSTRALIA. I.

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(Communicated by D. J. Lee.)

(Three Text-figures.)

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INTRODUCTION.

The mosquitoes of southern Australia have received little attention in the past, but recently work on them has been stimulated, firstly by the introduction, for the control of rabbits, of a myxoma virus, which is carried principally by mosquitoes, and secondly by the occurrence of a severe outbreak of encephalitis in the Murray Valley in 1950. The types of mosquitoes responsible for the transmission of these diseases are not fully known, but the possibility that the *C. pipiens* group might be involved made a close study of this group necessary.

In south-east Australia the group comprises a *pipiens*-complex of three forms and an additional undescribed species. This paper presents a description of this new species. A full account of the *pipiens* complex will be published later.

CULEX GLOBOCOXTUS, n. sp.

DESCRIPTION OF ADULT.

Holotype ♂.—The head is clothed with scales of the usual form. The flat scales around the eye-margins are white, the narrow curved scales are pale and the erect ones are whitish medially and black laterally. The proboscis is dark with pale scales on the ventral side. The palpi are longer than the proboscis by only two-thirds of the length of the last segment. They are dark with pale scales on the underside of the first three segments; the third segment is also pale laterally, on its distal third. The hairs on the last two segments are relatively short and sparse; the third segment has only 10 long hairs at its tip (Fig. 1).

The dorsum of the thorax is dark brown; the scutellum is lighter. The scutal scales are goldish, those of the scutellum are lighter. The bristles are black. The pleurae have the usual patches of whitish scales. There are no pre-alar scales on the tip of the sternopleuron.

The abdomen is black scaled above. The first tergite has two patches of black scales on its posterior border. The second to seventh tergites have wide unconstricted basal bands of creamy scales; the eighth is pale with two large round patches of black scales. The venter is creamy, with black scales forming median and lateral patches on the second to seventh sternites, and a posterior border to the eighth.

Genitalia.—The coxites are very broad and swollen, with dense yellowish hairs and a bunch of setae on the inner face (Fig. 2).

Legs.—The coxae are pale. The bristles and scales of the front and mid-coxae are black; those of the hind coxae are pale. The legs are blackish dorsally; the femora are pale ventrally. The tip of the hind tibia has a distinct ochreous spot. The tarsi are not ringed.

The wing scales are blackish. The upper fork-cell is twice the length of its stem. The distance between the cross-veins is twice as long as the posterior cross vein. Wing length, 3.0 mm. The halteres are pale with a dark knob.

Paratypes ♂.—The series of 30 paratype males show the following variations: Length of proboscis: 2.02 to 2.71 mm., mean 2.34 mm. On the tip of the third segment of the palpi there are from 6 to 15 long hairs. There is some variation in the width

of the basal tergal bands. On the sixth and seventh tergites the bands sometimes widen laterally to reach the posterior margin of the segments. The black patches on the eighth tergite are sometimes reduced to a few black scales.

Genitalia.—The coxites are swollen and broad with a bunch of setae on the inner face. The style is sickle-shaped, and very narrow distally. The paraproct is without a basal arm; it bears seven fine hairs. The ventral processes of the mesosome are narrow and bent outwardly. The dorsal processes are stout and pointed, and their tips, which are often slightly divided, are directed towards the tips of the ventral processes. The number of hairs on each lateral lobe of the ninth tergite varies from 3 to 6.

Wing length, 3.0–3.5 mm.

Allotype ♀.—This differs from the holotype as follows: The palpi are dark with some pale scales on the third segment. This segment is blunt and has a vestige of a fourth segment (Fig. 1). The proboscis is pale scaled ventrally to the tip. The legs are darker than in the male and dorsally are almost black. The abdomen is black above with wide creamy basal bands. Constrictions between the bands and lateral spots are present only on the second and third tergites. The lateral spots, which are whitish, have approximately the same width as the bands, except on the seventh segment where they are two-thirds the length of the tergite. The apical margin of the eighth tergite is black scaled. The venter has yellowish scales, with conspicuous median and lateral patches of black scales on the third to seventh segments.

Wing length, 3.8 mm. The upper fork-cell is 3.6 times as long as its stem. The distance between the cross-veins is twice the length of the posterior cross-vein.

Paratype ♀.—The series of 30 paratype females have the following variations: The black median and lateral patches on the venter may be conspicuous or may be reduced to a few black scales. Wing length 3.7–4.7 mm. The upper fork-cell is 3.5 to 5.6 times the length of its stem. The distance between the cross-veins is 2.0 to 2.8 times as long as the posterior cross-vein.

Types: The holotype male and allotype female were bred from larvae collected at Williamstown, Victoria, 4th December, 1951. A paratype series was bred from larvae collected in the suburbs of Melbourne. The holotype and allotype together with the associated larval and pupal skins, the paratype series with ten individually associated larval and pupal skins are in the collections of the National Museum, Melbourne.

PUPA.—The trumpet is almost cylindrical or slightly widened distally and is 6–7 times as long as broad. The opening is oblique and is about one-fourth the length of the trumpet. Seta O has 6–7 branches, P and R have 2–3 branches each; all are slightly plumose. Seta A has three plumose branches on segment III–VI, four on segment VII, 6–7 on segment VIII. Seta B on III has 5–6 weak branches; on IV has 3–4 branches, longer than the length of the segment; on V and VI has 2–3 branches about one and a half times the length of the segment; on VII has 2–3 weak branches equal to length of segment VIII. Seta C on IV–VII has 4–8 branches. The ratio of the paddle is about 1.5.

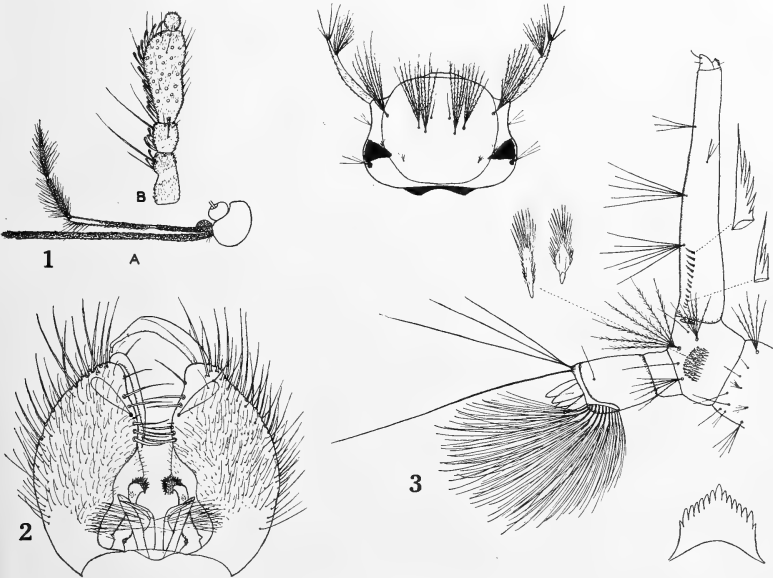
THE FOURTH STAGE LARVA (Fig. 3).—The head is yellow. It is one and a half times broader than long. The antennae are brown. They are about five-eighths of the length of the head, and two-thirds of their length from the base bear a tuft of about 23 plumose hairs. The anterior frontal setae are single, the inner frontal consists of five to seven plumose hairs, the mid frontal of three to six and the outer frontal of eight to twelve. The sutural seta (*e*) has three to five branches, the trans-sutural (*f*) four to seven. The mental plate has a large central tooth and seven to eight lateral teeth.

The chaetotaxy of the larval thorax is like that of *C. pipiens* L.; the posterior third of the thorax is sometimes blackish.

Abdomen.—The pentad hairs of the eighth segment: *a* has 5–7 plumose branches, *β* is single, *γ* has 6–9 plumose branches, *δ* is single and *ε* has 4–6 plumose branches. The comb consists of 44–50 scales arranged in four irregular rows. The dorsal brush usually consists of three inner hairs, rarely four or five, and a single long outer hair. The saddle hair is single. The ventral brush has about twelve tufts. The anal papillae are short, usually one-half to two-thirds the length of the saddle. The siphon is slender

with a very slight sigmoid curve. The siphonal index varies from 4.6 to 6.3, with a mean of 5.5. There are four siphonal tufts on each side. The first consists of three to seven single hairs, the second of three to six, the third of two to four, and the fourth of three to four. The hairs of the first two tufts are about twice the width of the siphon at its base. The third tufts are placed slightly towards the dorsal side. The number of pecten teeth varies from 11 to 15.

The egg-rafts are elongate-oval in shape with 190-302 eggs arranged in 11-14 rows; the number of eggs on the mid-longitudinal line varies from 23 to 31. The index of greatest width to length of the egg is about 0.27. Egg-rafts laid in the laboratory after a human blood meal are small and variable in shape, being triangular, oval or oblong. They contain from 70 to 100 eggs in 5-10 rows, with a median row of 9-17 eggs.



Text-figure 1. Palpi of *Culex globocoxitus*, n. sp.
A, male; B, female.

Text-figure 2. Terminalia of *Culex globocoxitus*, n.sp.

Text-figure 3. *Culex globocoxitus*, n.sp. Head, terminal segments and mentum of larva.

BIOLOGY.

This is a stenogamous species; mating will occur in a space as small as three cubic inches. In larger laboratory cages males may mate with resting females, but very commonly the initial coupling occurs when both sexes are in flight.

Reproductive activity is maintained throughout the year (homodynamy). During late July and early August of 1951, pools were found to contain second, third and fourth stage larvae, as well as pupae, from which adults were emerging. In 1952, in the early part of July, pools contained only fourth stage larvae and pupae; in August there were pupae and first stage larvae. It appears therefore that one or two generations are completed during the winter.

Mating would not be inhibited by normal winter temperatures. In the laboratory it has been observed at temperatures down to 13° C.

C. globocoxitus is anautogenous. It is not a man-biting mosquito. On many occasions females have been collected in a bedroom but were never caught freshly engorged. The reduction in the size of the egg rafts laid in the laboratory after engorgement with human blood also indicates that man is not a normal host. The species is probably ornithophilous.

Breeding habitat: Larvae are found in swamps, large and small pools in creek beds and in drainage pits. They will tolerate very polluted water. During the winter the larvae are found in small grassy pools together with *Aë. camptorhynchus* Tomson.

Distribution.—*C. globocoxitus* occurs throughout Victoria, in the neighbouring parts of South Australia and New South Wales, and in Tasmania. In addition to the type series from suburbs of Melbourne, specimens have been examined from Victoria: Yarram 1♀ 9.4.52, Ararat 1♂ 1.2.52, Ellangerin 1♂ and 1♀ 6.3.52, Lang Lang 2♀ 25.3.52, Cape Paterson 2♂ and 8♀ 5.4.52, Warrnambool 5♂ and 15♀ 29.1.52 and 13–14.2.52 (G. W. Douglas), Inglewood 2♂ and 1♀ 22.4.52, Merbein 2♂ 19.4.52; N.S.W.: Wentworth 1♂ and 1♀ 19.4.52 (N. V. Dobrotworsky); South Australia: Upper south east, nine localities, 4♂ and 6♀ April, 1952 (E. W. L. Lines), 22♂ and 26♀ 19.11–21.12.51, 9–28.2.52; Tasmania: Middleton 1♀ 12.5.48 (E. G. Cannah), Launceston 2♀ 29.3.52, Bothell 1♂ and 1♀ 30.3.52.

NOTE: *C. globocoxitus* is a member of *Culex pipiens* group but is readily distinguished from the other Australian members. The male can be recognized by the short palpi and by the swollen coxites. The distinctive features of the female are the vestigial fourth segment of palp, the pale scales on the underside of the proboscis and the broad creamy unconstricted tergal bands.

It may be noted that *C. globocoxitus* will inter-breed in the laboratory with the other members of the *pipiens* group in Victoria. In the field three male specimens were obtained whose terminalia were indistinguishable from that of a laboratory *globocoxitus* × *molestus* hybrid.

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Grateful acknowledgement is made to Dr. F. H. Drummond for his interest and valuable advice, to Mr. D. J. Lee for the loan of specimens collected in South Australia, to Mr. G. W. Douglas for permission to study specimens in his collections, and to Mr. E. W. L. Lines who presented some specimens from South Australia.

A COMPOUND *EUCALYPTUS* HYBRID.

By L. D. PRYOR.

(Plates xiii-xiv.)

[Read 26th November, 1952.]

Synopsis.

The existence of a compound hybrid derived from *Eucalyptus Rossii*,* *E. dives* and *E. macrorrhyncha* is deduced on the basis of a progeny test.

INTRODUCTION.

Numerous cases of hybrids between well defined *Eucalyptus* species have been detected in the field and some others have been synthesized under controlled conditions. During field examinations individuals and sometimes hybrid swarms have been examined in which it has been necessary, for a satisfactory explanation, to postulate that more than two species have been concerned in the parentage. Clearer evidence of this has so far been lacking, but an interesting progeny now two years old has disclosed distinct elements of three separate species in the make-up of the parent tree.

PROGENY TEST.

Seed was collected from an apparent hybrid at Black Mountain, A.C.T., and about 40 plants were raised in 1949 and planted out in 1950. The plants are now about two feet high and display very clearly the juvenile characters. The parent was assessed, before the progeny test, as a hybrid between *E. Rossii* and *E. dives*. No sign of *E. macrorrhyncha* was sufficiently clear to suppose at that stage that it was present in the hybrid combination. At two years of age, however, undoubted *E. macrorrhyncha* characters have appeared both in indumentum and leaf shape and are easily recognized in the progeny. Some segregates approximate closely in their juvenile form to each of the other presumed parents also. There are in addition various combinations amongst them of the characteristic juvenile forms of the three species (Pl. xiii, figs. 1, 2, 3).

The juvenile characters of the three species happen to be markedly distinct, which makes the material suitable for detection of such inheritance at an early age. *E. dives* has sessile, ovate-lanceolate, highly glaucous, opposite leaves (Pl. xiv, fig. 8); *E. Rossii* has, after two or three preliminary pairs of leaves beyond the cotyledons, alternate, petiolate, narrow-lanceolate grey-green leaves (Pl. xiv, fig. 9); *E. macrorrhyncha* likewise has alternate leaves but they are ovate with a distinctively tapered apex. In *E. macrorrhyncha* they are also petiolate and dull green, and in addition in the earlier stages are well covered with so-called stellate hairs (actually clusters of hairs on protuberances) which is a distinctive feature of the "stringybark" group of species to which *E. macrorrhyncha* belongs (Pl. xiv, fig. 7). All of these characters are strongly displayed in the progeny. Some individuals in the present stage are almost indistinguishable from *E. dives* (Pl. xiii, fig. 5), or alternatively from *E. Rossii* (Pl. xiv, fig. 6). Those approaching *E. macrorrhyncha* (Pl. xiii, fig. 4), however, are less close to the characteristic form of that species in the juvenile condition than the former two. Nevertheless the two distinctive characters of "stellate hairs" and leaf shape, as well as the general habit of the seedlings, are unmistakably present, and there is little doubt that *E. macrorrhyncha* has entered into the combination.

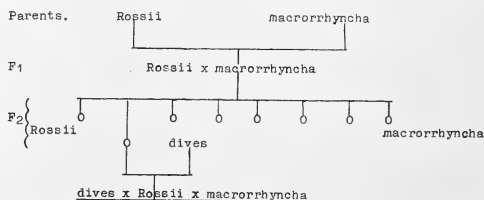
Other characters of diagnostic value will appear as the plants flower and fruit and as the mature type of bark develops which will allow more accurate assessment of the degree of contribution from each parent.

* Nomenclature and spelling as in Blakely, "A Key to the Eucalypts", 1934.

DISCUSSION.

There is no difficulty in finding a likely explanation for this combination. Hybrids between *E. Rossii* and *E. macrorrhyncha* have been located and substantiated by progeny testing. They also occur in the locality from which the seed was collected in this case. The minority representation of the *E. macrorrhyncha* characters in the progeny suggests that either some of its characters are suppressed by those of the other species, or, more likely, that one of the parents was a segregate with a preponderance of *E. Rossii* characters from an *E. macrorrhyncha* × *E. Rossii* hybrid swarm. One might say that it is equally possible that the *E. macrorrhyncha* entered the combination through a hybrid with *E. dives* and a subsequent segregate from this combined with *E. Rossii*. The *E. dives* × *E. macrorrhyncha* combination is, however, less frequent than the *E. Rossii* × *E. macrorrhyncha* combination.

There is still another aspect which is interesting and which may be significant. In some progenies of *E. pauciflora* × *E. dives* raised previously, "stellate" hairs have occasionally been noticed, suggesting, along with other general morphology, the rather faint presence of characters in the progeny derived from some stringybark species. The "stellate" hair character is very distinctive and one which is completely lacking in species other than stringybarks on the southern tablelands. It seems very probable that their presence indicates inheritance from a stringybark species, but the possibility must not be completely ruled out that these two characteristics from *E. macrorrhyncha*, tapered leaf at apex and stellate hairs, may both have arisen by some unusual gene interaction. It is easy to imagine the *E. macrorrhyncha* leaf shape arising by gene interaction between certain of the genes determining the narrow *E. Rossii* leaf and the broad *E. dives* leaf. However, it is much more difficult, although not impossible, to imagine such an origin for "stellate" hairs. For example, Saunders (*Jour. Genetics*, 10, 1920: 149) describes some complex interactions between four gene loci for hairiness in the stock (*Matthiola*). Full hairiness is obtained only by the presence of four dominants, two of which, C and R, are necessary for the development of anthocyanin in the flowers. It is possible that similar complex gene interaction could be responsible for the production of "stellate" hairs characteristic of *E. macrorrhyncha*. However, in three other progenies from the presumptive F1 hybrid *E. Rossii* × *E. dives*, no such "stellate"-haired plants have arisen, nor has there been any sign of the *E. macrorrhyncha* leaf shape. Thus probably the results are to be explained in the following way:



The cases in which "stellate" hairs have been observed in *E. pauciflora* × *E. dives* progenies have been with parents which were not growing close to any stringybark tree. This character has therefore appeared as a "phantom" preserved in the genetic makeup of the tree concerned.

It is possible in comparison with species like *E. dives*, *E. pauciflora* and *E. Rossii*, that *E. macrorrhyncha*, though a little more exacting species in its habitat requirements, has characters which, if preserved in hybrid combination with these species, would aid survival of the hybrid.

In particular, the character of "apical dominance" and rapid early growth favours the species possessing it over those which do not, at least for survival in the youthful stages. It is possible therefore that the presence of stringybark characters indicates a combination better adapted to survive under conditions which have developed since

settlement. It has been observed in some hybrid combinations of *E. dives* × *E. pauciflora* that the hybrids though fast growing are relatively short lived—say forty or sixty years. With the reduced average age of trees which has followed settlement and tree clearing, the preservation of hybrid combinations which are favourable to survival in the relatively early stages of growth would probably increase, and perhaps for this reason the appearance of the stringybark influence has become more prominent. The fact that *E. macrorrhyncha* (and even more so other stringybarks) requires a somewhat better site than the other species concerned, would make perhaps for shorter life on sites poorer than that which the stringybark normally occupies. This, however, would be less critical for survival when the average age of the stand is shortened.

The question is of considerable interest and its fuller investigation will be aided by the distinctive inherited condition of "stellate" hairs to provide rapid assessment of the genetic condition of the individuals examined.

EXPLANATION OF PLATES XIII-XIV.

Plate xiii.

1. A segregate in the progeny from the hybrid, showing mixed characters, especially the pointed broad leaf of *E. dives*, but other characters derived from the other species.
2. Segregate with some characters of *E. macrorrhyncha* in combination with *E. dives*.
3. Segregate with a preponderance of *E. Rossii* characters, but strongly influenced by *E. dives* in the preservation of almost opposite and rather broad leaves.
4. A segregate closely approaching *E. macrorrhyncha*.
5. A segregate almost identical with *E. dives*.

Plate xiv.

6. A segregate closely similar to *E. Rossii*.
 7. A seedling of pure *E. macrorrhyncha* of the same age.
 8. A seedling of pure *E. dives* of the same age.
 9. A seedling of pure *E. Rossii* of the same age.
-

VARIABLE RESISTANCE TO LEAF-EATING INSECTS IN SOME EUCALYPTS.

By L. D. PRYOR.

(Plate xv; one Text-figure.)

[Read 26th November, 1952.]

Synopsis.

Progeny tests and morphological analyses of *Eucalyptus* hybrids indicate that in some *Eucalyptus* species resistance to leaf-eating scarab beetles is a heritable character, probably with some capacity to assort independently in segregating populations.

INTRODUCTION.

Many species of *Eucalyptus* are very susceptible to attack by leaf-eating insects which at times completely defoliate them. Carne (1950) has studied in considerable detail the species involved and has found at least twenty kinds of scarab beetle belonging to several genera and also species in other orders which are commonly concerned. While there are fluctuations from season to season, it is clear that attack in general varies in intensity with different *Eucalyptus* species, some being almost resistant while others are regularly and heavily eaten.

Among the ornamental plantations in Canberra there have been some interesting cases of resistance, two of which have been selected for study. The first is that of one resistant individual among a susceptible population; the second, a tree heavily eaten while its companions were more or less untouched.

INDIVIDUAL RESISTANCE.

In a plantation of some 30 trees of *Eucalyptus rubida** about 25 years old, there was one tree which remained almost untouched while the remainder were completely defoliated. The plantation was attacked in the summer of 1949-50 by the scarab beetle, *Anaplognathus montanus* Macl. All leaves were eaten and the crown was reduced to a mass of twigs many of which died. A similar thing happened in the summer of 1947-48 due to the same insect, and it occurred about two years previously as well as on still earlier occasions, but the records before 1947-48 are not precise. On each occasion the one resistant tree referred to remained almost untouched and appeared quite unpalatable to the beetle. It is in a line of trees of *E. rubida* spaced about 60 feet apart and does not differ from that species in its general form and appearance in any way that can be detected easily. In the hand specimen, however, most of the umbels have more than three flowers. Sometimes there is a three-flowered umbel on a branch which has otherwise multi-flowered umbels and also small branches are found on which most of the umbels are three-flowered (Pl. xv, fig. 1). The three-flowered umbel is a highly distinctive feature of *E. rubida*. Care must be taken of course to distinguish between an umbel which emerges as a three-flowered umbel and one which, while originally containing more flowers, is reduced to three by dropping of some of the additional buds. In the latter case, the resultant scars at the top of the peduncle are seen with careful observation. Irregular departure from this three-flowered umbel has been found associated with hybridization in other species (Pryor, 1950). It was thought therefore that this individual might be a hybrid, and a progeny test was carried out.

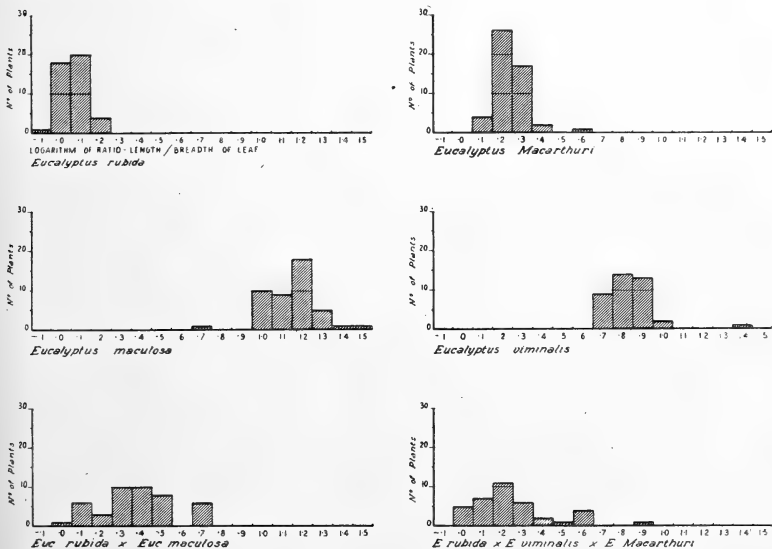
PROGENY TEST.

Seedlings were raised from the resistant tree using the method employed in a previous examination of some hybrids (Pryor, 1951). Fifty plants were raised in each case and in seven months provided the relevant information.

* Nomenclature and spelling as in Blakely "A Key to the Eucalypts" (1934).

The progeny from the resistant tree shows marked segregation in the juvenile foliage characters. Some of the plants are like *E. maculosa* and others like *E. rubida*, with a series of grading intermediates between them.

The juvenile foliage of *E. maculosa* is quite different from that of *E. rubida*. *E. maculosa* has narrow-lanceolate or almost linear juvenile leaves, with short petioles which are alternately placed after the first few pairs. They are not glaucous although sometimes greyish-green in colour. On the other hand, *E. rubida* has orbicular, highly glaucous juveniles which are sessile and strictly opposite one another for many pairs. The leaves are also generally somewhat emarginate.



Text-figure 1.

Histograms of numbers of individuals of different classes for the ratio, leaf length to leaf breadth. The arithmetical data were transformed to logarithms to reduce the variance in the progenies from the supposedly pure parents to the same order.

The seedlings in the progeny display a range of combinations which are at the extremes almost identical with the two species, but which grade from one to the other through a series of intermediate forms which show various combinations and blends of the various parental characters (Pl. xv. fig. 2). There is a preponderance of forms which approach that which is intermediate between the putative parents. Glaucousness seems to assort quite independently of the other characters with which it is normally associated in *E. rubida*.

The ratio length/breadth of leaf is a convenient measure of the difference in leaf shape. Simple histograms (Text-fig. 1) have been prepared based on the number of individuals with different ratios, which give expression simply to the kind of variation which occurs in the various progenies. It was found in preparing these data that the variance in progenies from the presumed parental species could be reduced to the same order by transforming the figures to logarithms in the manner suggested by Mather (1949). Two points are clear from the histograms. Firstly, the distinct separation of the parental types and the relatively small variation of each, and the wide variation in the hybrid progenies together with their intermediate characters.

The same kind of variation exists with at least some other characters, but measurement is less simple and has not been made.

It seems clear from the morphology of the mature trees and the kind of variation present in the progeny that the resistant individual is of hybrid origin with *E. rubida* and *E. maculosa* as parents. The kind of variation in the progeny suggests that the resistant individual is a segregate in an F₃ or later generation which approaches more closely to *E. rubida* than to *E. maculosa*, since the mean of the ratio of leaf measurements L/B falls nearer to that of *E. rubida* than *E. maculosa*. This impression is supported by evidence obtained elsewhere by Barber (1952) on a known F₁ hybrid, and other information which will be published later.

The character which confers resistance to *Anaplognathus* is apparently inherited from *E. maculosa*, as this species is highly resistant to *Anaplognathus* attack and survives almost untouched in areas in which alternating trees of *E. rubida* and *E. maculosa* occur and in which *E. rubida* is heavily defoliated.

INDIVIDUAL SUSCEPTIBILITY.

A plantation of some twenty trees of *E. Macarthurii* about 25 years old contained one tree which was susceptible to scarab attack. *E. Macarthurii* is at times fairly heavily eaten but in the summer of 1950-51 was only lightly eaten in the area in question. The test tree on the other hand, while not completely defoliated like the *E. rubida*, was nevertheless very heavily eaten.

It is somewhat distinct from the *E. Macarthurii* amongst which it is planted and may be distinguished from them at sight by the more open crown, lighter coloured leaves and relatively small amount of fibrous bark on the trunk. In the case of *E. Macarthurii* the rough bark extends over the main trunk to limbs of about six-inch diameter, while in the case of the tree in question the rough bark extends for a few feet only at the butt. At the same time the tree seems to have some of the characters of *E. Macarthurii*, and while it cannot be assigned to this species it cannot readily be placed with any other. In the hand specimen it shows characters which, like the previous case, indicate probable hybrid origin.

E. Macarthurii commonly has umbels with 6-8 flowers. The tree in question has many such umbels but it also has occasionally three-flowered umbels. The fruit is also small and nearer the size of *E. Macarthurii* than other species (Pl. xv, fig. 1).

As with the previous case a progeny test was carried out.

PROGENY TEST.

Fifty plants were again raised in the same way from open-pollinated fruits. They display very variable juvenile characters suggesting marked segregation in a rather complex hybrid combination. The parent is not so clearly intermediate between *E. Macarthurii* and another parent as in the former case; the *E. Macarthurii* characters are less prominent than might be expected in a simple blend between two species as in an F₁ hybrid. While this might be explained as due to dominance of some characters inherited from one parent, this would be quite unusual in *Eucalyptus* where seedling morphological characters generally show blending in hybrid combinations.

The progeny however discloses additional features of interest. There appear to be three parental types concerned in the combination, viz., *E. rubida*, *E. viminalis* and *E. Macarthurii*. The juvenile characters of *E. viminalis* are not widely different from those of *E. Macarthurii*. *E. viminalis* has opposite, sessile, narrow-lanceolate green leaves, while *E. Macarthurii* usually has a broad base giving a broad-lanceolate or ovate shape. Otherwise it is like *E. viminalis*. *E. Macarthurii* is characterized at all stages however by the highly distinctive oil which contains geranyl acetate and which, when present in sufficiently high concentration, can be detected readily by smell.

In the progeny from this susceptible individual there appears to be *E. viminalis*, there is clearly *E. rubida*, while *E. Macarthurii* is clearly represented in leaf shape but only faintly by the oil character (Pl. xv, fig. 3).

The presence of *E. viminalis* is interesting, as this species, or trees very much like it, appears quite often in progenies of *E. Macarthurii*. *E. Macarthurii* is one of those

species of limited geographic distribution which exhibit greater variation in their genetic makeup than some of the more widespread species. It is suggested that they are of comparatively recent origin—that they are polymorphs in which genetic variability has not yet been reduced to the level characteristic of more stable species. If this supposition is correct, *E. Macarthurii* might well be a polymorph derived partly from *E. viminalis* and the presence of the *E. viminalis* in the progeny might arise inherently from *E. Macarthurii*. As the progeny becomes older and other characters are available for assessing the biotypes present, this will become clearer.

In any case there is no doubt that the individual concerned is a somewhat complex hybrid and its susceptibility compared with *E. Macarthurii*, which is almost as resistant to *Anaplognathus* as *E. maculosa*, is probably a result of inheritance from *E. rubida*. The histogram (Text-fig 1) similar to that prepared for the first progeny illustrates the diversity and intermediate position in leaf shape of the hybrid progeny as compared with *E. Macarthurii*, *E. viminalis* and *E. rubida*.

While the genetic analysis is incomplete, since it is based on open-pollinated progeny tests and on juvenile characters of the plants, the evidence is so strong that there is little doubt that the individuals examined are of hybrid origin and that their susceptibility or resistance is a consequence of inherent qualities passed to them by one or other of their parents. The reliability of the progeny test in assessing the genetic makeup is perhaps greater than might at first appear. In the case of *E. rubida* × *E. maculosa* hybrid, the only *Eucalyptus* species within 800 yards of this tree is *E. rubida*. The nearest *E. maculosa* is further away. Self-fertility has been found in all species examined for this character and it is likely that the seed collected from the tree has resulted from self-pollination although probably from different flowers on the same tree. Crossing with adjacent *E. rubida* is unlikely because the flowering times of the two are well separated. In 1951 in this area the *E. rubida* flowered in January, and the supposed hybrid about the end of March. It is true that *E. maculosa* started to flower about the end of March also, but it seems that the distance to the nearest trees would at least reduce the amount of out-crossing, if not eliminate it, and favour a high proportion of self-pollination unless partial or complete self-sterility were the case. The kind of segregation disclosed by the progeny however is not as would be expected from a back-cross.

With regard to the possibility of out-crossing, it should be remembered that the distance as in this case, and the separation of the general flowering times, are probably not absolute bars to some cross-pollination, but the chance, if the individual is self-fertile, of other than a very small portion of the seed in the capsules arising from out-crossing is quite small.

It is true that complete confirmation can be obtained only after a progeny is obtained following controlled self-pollination, but in any case, apart from the theoretical possibility of the seed in the progeny test resulting from out-crossing with another as yet undiscovered hybrid individual in the same locality, it is likely the progeny obtained from the resistant tree is from self-pollinated capsules and fairly indicates the genetic constitution of the individual.

The position is somewhat similar with the susceptible individual amongst the *E. Macarthurii* trees. In 1951, it flowered in the latter half of March while the surrounding *E. Macarthurii* flowered in February. *E. rubida* is within 100 yards of the tree, but flowered still earlier in the year. *E. viminalis* and *E. maculosa* flowered at the same time, but are some 400–800 yards distant respectively. It is likely in this case also that the progeny is from seed resulting from self-pollination.

The mode of inheritance of resistance to insect attack should become clearer when the progenies are older. If in the progeny from the presumptive *E. rubida* × *E. maculosa* hybrid, susceptibility segregates to any degree independently of other characters, it should be possible to select various desired combinations with the resistance of *E. maculosa* which could be propagated vegetatively. In the presumptive hybrid it is interesting that the tree is as resistant as *E. maculosa* and therefore, instead of blending as is commonly the case with various morphological characters, the character

of resistance may be inherited as a dominant. However, if essential oil composition determines resistance, a lower proportion of the critical oil in the total oil content than in the case of the parent *E. maculosa* may still mean resistance, and inheritance may be still as with seedling morphological characters. If the selection of desirable segregates were possible, it would be of considerable benefit in ornamental plantings where beetle devastation is unsightly and costly to control.

In commercial planting of eucalypts on grazing lands, any means of incorporating resistance in desirable species would be of extreme importance, as it is now difficult to establish satisfactorily some of the most desirable species in heavily deforested grazing areas due to excessive beetle attack, and growth losses are often very heavy for this reason (Jacobs, 1951). There are also prospects of obtaining seed which, though not genetically uniform, may contain a high proportion of desirable combinations, and therefore which could be used effectively in rather closely spaced plantations.

The inheritance of resistance to insect attack in segregating or hybrid populations of other tree species is well enough known, for example that with Pines to Pine Weevil (Miller, 1950), and also the inheritance of resistance in susceptibility to leaf-eating insects in Poplars has been indicated.

While further experiment will be necessary to confirm the conclusions with more certainty, the evidence so far available indicates a likelihood of development in this field of study with *Eucalyptus* which may have valuable practical consequences.

SUMMARY.

Evidence from progeny tests and morphological analyses indicates that resistance to leaf-eating beetles in some *Eucalyptus* species is a heritable character and it appears this may assort in segregating populations independently of a number of other characters. In the re-establishment of *Eucalyptus* by planting on grazing lands where the beetle population has been very much altered as a result of tree clearing, the use of this factor by one means or another may be of critical importance for success.

Acknowledgement.

I am greatly indebted to Professor H. N. Barber for helpful suggestions in this study.

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 MATHER, K., 1949.—*Biometrical Genetics*, London.
 MILLER, J. M., 1950.—California Forest and Range Experiment Station, *Forest Research Notes*, 68.
 PRYOR, L. D., 1950.—*Australian Forestry*, XIV: 95-98:
 ———, 1951.—*PROC. LINN. SOC. N.S.W.*, 76: 140-148.

EXPLANATION OF PLATE XV.

1. Leaves, buds and fruits of the different species and hybrids. Note the three-flowered umbel on the *E. rubida* × *E. maculosa* specimen, and also a few on the *E. rubida* × *E. Macarthuri* × *E. viminalis* specimen. Note also the intermediate fruit size between the *E. rubida* × *E. Macarthuri* × *E. viminalis*. *E. Macarthuri*, *E. viminalis* types.

2. Progeny 50/724 of the supposed hybrid *E. rubida* × *E. maculosa*. Note the typical *E. rubida* form at the left, and the *E. maculosa* type at the right. Progenies approximately intermediate at the centre of the range.

3. Progeny 50/761 derived from a hybrid presumably containing *E. rubida*, *E. Macarthuri* and *E. viminalis*. *E. rubida* at the extreme left, *E. Macarthuri* in the centre and *E. viminalis* at the right, with various combinations in between.

AUSTRALASIAN CERATOPOGONIDAE (DIPTERA, NEMATOCERA).¹PART VI. AUSTRALIAN SPECIES OF *CULICOIDES*.By DAVID J. LEE, B.Sc., and ERIC J. REYE, M.B., B.S.²

(Plate xvi; 93 Text-figures.)

[Read 26th November, 1952.]

Synopsis.

This systematic review of the Australian *Culicoides* comprises a discussion of the six species previously recorded from the region together with descriptions of fifteen new species, all from eastern Australia. Separation of species is primarily based on wing patterns but such other useful details as are revealed in head structures, thoracic patterns, tarsi and spermathecae are illustrated for the majority of species. A key to the identification of species is presented and a brief summary of such details of the biology of the various species as are known.

Introduction, p. 369.

Method of Description, p. 370.

Genus *Culicoides*: Synonymy and Generic Characters, p. 370.

Grouping of Species, p. 371.

Key to Australian Species of *Culicoides*, p. 373.

Description of Species, p. 375.

Biology, p. 393.

References, p. 394.

INTRODUCTION.

The genus *Culicoides*, the dominant blood-sucking "sandfly" genus in Australia, has long been neglected. Two species were described by Skuse (1889), two by Taylor (1911 and 1918) and one by Kieffer (1917). Both of Skuse's species (*C. molestus* and *C. marmoratus*) are now well known in eastern Australia, one of Taylor's (*C. ornatus*) is well known in North Australia whereas the second (*C. multimaculatus*) has not since been collected although it is an obviously distinctive species, and the Kieffer species (*C. brevitarsis*) still remains shrouded in mystery since nothing which could be referred to this species, on the basis of the original description, has yet been recovered.

The genus occurs in all States, including Tasmania, but is apparently absent from New Zealand. It is known to occur in New Guinea but with one exception the species seen in the limited collections from New Guinea are distinct from any known to occur on the mainland of Australia. No discussion of New Guinea species is presented herein since further material is needed to clarify the characters of the few species already described from that area.

The present paper considers twenty-one species of *Culicoides*, fifteen of which are described as new. Other new species are known to occur in Australia, but there has not been sufficient material of these available to characterize them adequately and they must await further collecting.

Collections have been made in various ways, by the finger moistened with 70% alcohol for specimens actually biting or on vegetation, by suction tube, by net sweeping and by light traps. Specimens have also been recovered from animal baits and the breeding of adults from larvae or pupae has yielded others. Many have contributed to these collections but particular acknowledgement should be made of the contributions of Mr. B. McMillan, Mr. J. R. Henry, Drs. I. M. and M. J. Mackerras, Dr. F. H. S. Roberts, Mr. R. F. Riek, Dr. Elizabeth Marks and Mr. A. Dyce.

¹Continued from Vol. 73, page 70 (1948) of these PROCEEDINGS.

²The work of the junior author has been made possible by a research grant jointly contributed by the Commonwealth Science and Industry Endowment Fund and the Commonwealth Scientific and Industrial Research Organization.

It will be obvious that most collections have been made in New South Wales and Queensland and it is by no means unlikely, if similarly intensive collecting were undertaken in other States, that considerably more species would be disclosed.

METHOD OF DESCRIPTION.

The basic characters used in the description of species are discussed in Part I of this series (Lee, 1948). An even more recent discussion will be found in Wirth (1952).

New species have only been described when sufficient material has been available to detail those characters regarded as definitive, not only in relation to other known species, but as far as possible to furnish, in addition, sufficient detail for the ready differentiation from such other new species as may be found from time to time.

Female specimens have been selected as holotypes in all cases, this being the sex of practical importance, and as many paratypes as possible have been included in the type series. Such paratypes have almost invariably been collected with the holotype and have in part provided details which are not clear in the holotype. When male specimens have been available one of these has been selected as allotype and others as paratypes but only when the specimens concerned have some close association with the holotype or occasionally when they have come from a similar ecological environment. Otherwise male characters are given from stated specimens but these have not been included in the type series.

In all but one case the majority of the type series will be found on mounted slide specimens since this appears most practicable for subsequent checking of details not precisely discernible in pinned material. Wherever pinned specimens have been available to provide characters of coloration these have been given.

Mounted specimens have usually been prepared by clearing in phenol (saturated solution in absolute alcohol) for from one to five hours, washing in absolute alcohol and mounting in fairly thin xylol-balsam. Separation of head and one wing from the body of the specimen has often been resorted to for purposes of illustration.

Illustrations have been made with the aid of a camera lucida with the exception of those of scutal patterns where a graticule and squared paper have been used.

Primary types are all lodged in the collection of the School of Public Health and Tropical Medicine, University of Sydney (abbreviated to SPHTM in text). Where possible paratypes have also been lodged in other museums, the British Museum, London (BM in text), the United States National Museum, Washington (USNM in text), the Division of Entomology, Commonwealth Scientific and Industrial Research Organization, Canberra (CSIRO in text) and Queensland Institute of Medical Research, Brisbane (QIMR in text).

Since this is the first occasion on which reasonably detailed information on the Australian species of *Culicoides* has been presented, full distribution lists are included. These are subdivided into States and as far as possible are arranged in an approximately north to south order.

Measurements considered to be significant are included for all species. These are presented together in Table 1. In nearly all cases the holotype has been measured (except when unsuitable for reasonably accurate measurement) and as far as possible average measurements are given from a series of ten paratype specimens. If these have not been available the material measured will be found detailed in the text for each individual species.

GENUS *CULICOIDES*: SYNONYMY AND GENERIC CHARACTERS.

Genus *CULICOIDES* Latreille.

Latreille, P. A., 1809.—Genera Crust. et Insect., 4: 251.

See also:

Carter, H. F., Ingram, A., and Macfie, J. W. S., 1920.—*Ann. Trop. Med. and Parasit.*, 14: 211.

Edwards, F. W., 1926.—*Trans. ent. Soc. Lond.*, 1926: 403.

Goetghebuer, M., 1920.—*Mem. Mus. Hist. Nat. Belg.*, 8, fasc. 3: 48.

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Synonymy.—Macfie (1940) lists as synonyms the following generic names: *Oecacta* Poey 1851, *Psychophaena* Philippi 1865, *Haematomyidium* Goeldi 1905, *Cotocripus* Brethes 1912, *Haemophoructus* Macfie 1925, *Synhelea* Kieffer 1925 and *Prosapelma* Kieffer 1925. To these is added *Hoffmania* Fox in Wirth 1952.

None of these concern the Australasian region, but it should be remembered that Skuse put almost all the species he described into *Ceratopogon* and some of these are strictly species of *Culicoides*.

Genotype: *C. pulicaris* (Linné) (*Culex*) 1758. *Syst. Nat.*, Ed. 10., No. 3: 603.

Generic Characters.

Most species of this genus are easily recognized by their spotted wings, but there are some in which the wing markings are faint or even absent and a few species in other genera with rather similar markings. However, the generally small size, the small simple claws, the lack of any pronounced modifications of the legs or of dense scale-like macrotrichia will differentiate members of *Culicoides* from species in other genera with variegated wings. Recourse to the key characters may be necessary to establish the generic identity of species lacking pronounced wing pattern.

In the head the eyes are bare and in the majority of species separated dorsally by a narrow space in the female and a rather broader one in the male. In both sexes a single long strong bristle arises between the eyes (absent when eyes are contiguous). The mouthparts are prominent and approximately as long as the height of the head in the female (relatively shorter in the male). The female palpi are five-segmented with the first, fourth and fifth segments considerably shorter than the subequal second and third segments. The latter is usually expanded with a sensory cup towards the distal end. The male palpi are similar but smaller. The female antennae have segment 1 distinct but smaller than 2 which is considerably expanded as usual; segments 3-10 are small and subequal and 11-15 are elongated; segment 15 has no terminal stylet. There are verticils of short hairs on all the flagellar segments. In the male, segment 2 is larger than in the female and only segments 13-15 are elongate. There are verticils of long hairs on segments 3-12.

The thorax has the scutum dull, sometimes mottled, with short hairs and few or no bristles. Humeral pits are always present and distinct. The legs are slender with no strong spines on femora or tarsi and no modified segments beyond a cordiform fourth tarsal segment in occasional species. The first hind tarsal segment is approximately twice or more the length of the second and the fourth tarsal segment is shorter than the fifth. The claws are small and equal in both sexes and the empodium minute.

The wings are clothed with microtrichia over the whole surface and macrotrichia are present but variable in extent. Spotting is usually but not always obvious. The branches of the radius form two cells, often rather similar to a figure eight, and the costa and R_{4+5} terminate together beyond the middle of the wing. M_2 arises distal to r-m, although its base may be obsolete. The intercalary fork is usually distinct.

The abdomen is of only moderate length in the female but rather longer and more slender in the male. The spermathecae are usually two in number and the lamellae small and rounded.

The genitalia of the male are rather complex, the ninth tergite being large and arched over the coxites and the structures between these, and with both distal and internal processes. The highly chitinized paired harpes are often specifically variable in shape and the phallosome is in the shape of an inverted Y.

GROUPING OF SPECIES.

For the practical convenience of identification the species of *Culicoides* dealt with herein are arranged in an order which follows as closely as possible increasing complexity of wing ornamentation, this being the most readily observable character

TABLE 1.

		<i>ducei</i> .	<i>palpalis</i> .	<i>robertsi</i> .	<i>ornatus</i> . ¹	<i>molestus</i> . ²	<i>immaculatus</i> .	<i>marksi</i> .	<i>subimmaculatus</i> .	
♀♀	Wing length	Holotype	1.02 mm.	0.92 mm.	0.90 mm.	1.09 mm.	1.35 mm.	1.11 mm.	1.25 mm.	1.22 mm.
		Average of selected series (see text)	0.92 mm.	0.97 mm.	1.00 mm.	1.04 mm.	1.10 mm.	1.18 mm.	1.21 mm.	1.22 mm.
		Range in above	0.87-0.96 mm.	0.90-1.05 mm.	0.90-1.08 mm.	0.96-1.11 mm.	1.02-1.24 mm.	1.15-1.22 mm.	1.09-1.32 mm.	1.13-1.23 mm.
Antenna	Holotype 3-10	210 μ	165 μ	190 μ	245 μ	270 μ	285 μ	255 μ	235 μ	
	" 11-15	180 μ	185 μ	180 μ	295 μ	280 μ	275 μ	265 μ	255 μ	
		Average of selected series (see text)—								
		3-10	190 μ	175 μ	200 μ	240 μ	215 μ	275 μ	255 μ	235 μ
Palp	Holotype, segment 2	50 μ	35 μ	50 μ	60 μ	65 μ	85 μ	65 μ	75 μ	
	" " 3	45 μ	50 μ	35 μ	65 μ	85 μ	95 μ	60 μ	75 μ	
	" " 4	25 μ	15 μ	20 μ	30 μ	35 μ	35 μ	25 μ	25 μ	
	" " 5	30 μ	20 μ	20 μ	25 μ	35 μ	25 μ	35 μ	20 μ	
Hind leg	Holotype, femur	315 μ	305 μ	295 μ	370 μ	450 μ	435 μ	385 μ	395 μ	
	" tibia	295 μ	270 μ	285 μ	345 μ	450 μ	420 μ	385 μ	410 μ	
	" tarsus I	140 μ	130 μ	130 μ	165 μ	230 μ	210 μ	190 μ	200 μ	
	" " II	75 μ	75 μ	85 μ	90 μ	120 μ	110 μ	100 μ	100 μ	
	" " III	55 μ	50 μ	55 μ	55 μ	75 μ	75 μ	70 μ	75 μ	
	" " IV	45 μ	40 μ	40 μ	40 μ	45 μ	50 μ	55 μ	45 μ	
	" " V	50 μ	45 μ	45 μ	50 μ	65 μ	60 μ	65 μ	55 μ	
	Average of selected series (see text)—									
Spermathecae	Tarsus I	125 μ	140 μ	145 μ	175 μ	180 μ	230 μ	180 μ	190 μ	
	" II	65 μ	75 μ	90 μ	95 μ	100 μ	125 μ	95 μ	100 μ	
	Holotype (a)		45 × 35 μ	35 × 30 μ	65 × 35 μ	40 × 35 μ	35 × 30 μ	35 × 30 μ	35 × 35 μ	
	" (b)		45 × 35 μ	40 × 35 μ	55 × 35 μ	45 × 30 μ	35 × 30 μ	30 × 25 μ	35 × 25 μ	
" (c)		10 × 10 μ	15 × 5 μ	—	duct 20 × 5 μ	—	25 × 25 μ	—		
♂♂	Wing length	0.78 mm.	0.83 mm.	1.01 mm.	—	—	—	1.07 mm.	1.43 mm.	
	Average of selected series	Antennal segments { 3-12	250 μ	280 μ	360 μ	—	—	380 μ	395 μ	
		{ 13-15	135 μ	180 μ	220 μ	—	—	200 μ	280 μ	

¹ Individual measurements from neoparatype.

² Individual measurements from specimen from Mosman, 26:1:1947.

³ Individual measurements from specimen from Burraneer Bay, 25:xi:1950.

under most conditions of observation. Basic groupings might be proposed on a number of different aspects of the wing pattern, e.g., number of pale spots in the intercalary fork, but the one used is the one which appears to follow most closely the order of increasing complexity. This is whether or not the apical portion of cell R_2 is included in the pale spot which lies immediately adjacent to the termination of R_{4+5} .

All species described fall into one or other of two groups on this character although one, *C. robertsi*, does present some difficulty and different specimens may result in differing decisions. With this one exception which should be otherwise easily recognizable, the basic grouping appears sound. It is not proposed that this grouping is a natural one but it does serve an essentially practical purpose.

(a) Species in which the distal portion of the second radial cell is dark, i.e., the pale spot adjacent to the termination of R_{4+5} does not include the second radial cell. Ten species are included in this group, namely, *immaculatus*, *subimmaculatus*, *palpalis*, *ornatus*, *molestus*, *marmoratus*, *mackayensis*, *rabaulti*, *angularis* and *magnesianus* (Group I).

TABLE 1.

<i>parvi-maculatus.</i>	<i>cuniculus.</i>	<i>mackay-ensis.</i>	<i>mcmillani.</i>	<i>rabaulti.</i>	<i>magni-maculatus.</i>	<i>mar-moratus.</i> ³	<i>mag-nesianus.</i> ⁴	<i>anten-nalis.</i>	<i>multi-maculatus.</i>	<i>angularis.</i> ⁵	<i>bancrofti.</i>
1.15 mm.	1.28 mm.	1.41 mm.	1.66 mm.	1.49 mm.	1.58 mm.	1.54 mm.	1.54 mm.	1.50 mm.	1.73 mm.	1.63 mm.	2.15 mm.
1.24 mm.	1.31 mm.	1.38 mm.	1.41 mm.	—	1.51 mm.	1.52 mm.	1.55 mm.	1.56 mm.	—	1.77 mm.	2.02 mm.
1.09—	1.23—	1.33—	1.28—	—	1.34—	1.47—	1.50—	1.46—	—	1.60—	1.92—
1.32 mm.	1.37 mm.	1.45 mm.	1.54 mm.	—	1.60 mm.	1.62 mm.	1.64 mm.	1.66 mm.	—	2.09 mm.	2.18 mm.
250 μ	305 μ	265 μ	320 μ	280 μ	340 μ	305 μ	270 μ	435 μ	—	270 μ	640 μ
250 μ	280 μ	355 μ	345 μ	395 μ	340 μ	360 μ	475 μ	385 μ	346 μ	500 μ	525 μ
265 μ	295 μ	285 μ	295 μ	—	325 μ	325 μ	255 μ	470 μ	—	265 μ	650 μ
265 μ	295 μ	355 μ	305 μ	—	335 μ	355 μ	470 μ	385 μ	—	505 μ	445 μ
65 μ	85 μ	85 μ	130 μ	100 μ	125 μ	65 μ	75 μ ⁷	110 μ	—	90 μ	100 μ
50 μ	70 μ	85 μ	100 μ	90 μ	75 μ	80 μ	75 μ	125 μ	—	100 μ	165 μ
25 μ	25 μ	25 μ	35 μ	25 μ	35 μ	35 μ	30 μ	50 μ	—	35 μ	40 μ
25 μ	30 μ	25 μ	35 μ	25 μ	35 μ	35 μ	40 μ	35 μ	—	25 μ	35 μ
360 μ	420 μ	460 μ	510 μ	—	500 μ	510 μ	525 μ	540 μ	—	540 μ	745 μ
345 μ	420 μ	435 μ	510 μ	—	500 μ	485 μ	510 μ	525 μ	—	525 μ	745 μ
170 μ	205 μ	220 μ	265 μ	280 μ	230 μ	230 μ	270 μ	225 μ	—	270 μ	360 μ
85 μ	115 μ	120 μ	130 μ	140 μ	130 μ	130 μ	140 μ	140 μ	—	140 μ	205 μ
60 μ	80 μ	75 μ	100 μ	90 μ	90 μ	90 μ	75 μ	90 μ	—	90 μ	130 μ
45 μ	55 μ	55 μ	65 μ	65 μ	65 μ	60 μ	55 μ	65 μ	—	60 μ	90 μ
55 μ	65 μ	60 μ	65 μ	65 μ	65 μ	60 μ	65 μ	65 μ	—	55 μ	90 μ
185 μ	215 μ	230 μ	225 μ	—	225 μ	235 μ	265 μ	270 μ	—	280 μ	370 μ
85 μ	120 μ	115 μ	105 μ	—	130 μ	135 μ	140 μ	145 μ	—	145 μ	210 μ
35 \times 25 μ	85 \times 65 μ	95 \times 50 μ	60 \times 45 μ ⁶	—	55 \times 45 μ	55 \times 45 μ	65 \times 50 μ	65 \times 50 μ	—	55 \times 45 μ	90 \times 50 μ ⁷
duct 15 μ	—	with duct	—	—	—	—	—	—	—	—	—
25 \times 25 μ	—	20 \times 10 μ	—	—	50 \times 40 μ	50 \times 50 μ	65 \times 40 μ	55 \times 45 μ	—	55 \times 45 μ	85 \times 55 μ
duct 15 μ	75 \times 60 μ	—	55 \times 45 μ	—	—	—	—	—	—	—	—
25 \times 20 μ	15 \times 5 μ	—	—	—	—	—	—	—	—	—	—
duct 20 μ	(duct)	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—

⁴ Individual measurements from paratype.⁵ Individual measurements from specimen from Cooranbong, 24:ix:1949.⁶ Specimen from Woodford, x:1950.⁷ Slightly collapsed.

(b) Species in which the distal portion of the second radial cell is pale, i.e., the pale spot adjacent to the termination of R_{4+5} includes the second radial cell, at least in part. Ten species are included in this group, namely *robertsi*,¹ *antennalis*, *bancrofti*, *magni-maculatus*, *cuniculus*, *dycei*, *multimaculatus*, *mcmillani*, *parvimaculatus* and *marksii* (Group II).

Key to Australian Species of Culicoides.

1. Wing without any pale area over the second radial cell; usually this area appears quite dark 2
Wing with the second radial cell pale distally (i.e., the pale spot adjacent to the termination of R_{4+5} includes portion of the second radial cell) 13
2. (1) Legs with fourth tarsal segments cordiform 3
Legs with fourth tarsal segments subcylindrical 5
3. (2) Wings without any pale area in the intercalary fork *C. subimmaculatus*.
Wings with one or two pale areas in the intercalary fork 4

¹ *C. robertsi* is a very small species and the character on which this basic segregation is made is difficult to determine. Nevertheless, most mounted specimens will disclose that it properly belongs in Group II.

4. (3) Wings with one large pale area in the intercalary fork; wing spotting comprising very large pale areas rather weakly contrasting with the interspersed darker parts; distal antennal segments 11-15 very markedly longer than the basal flagellar segments 3-10 *C. magnesianus*.
Wings with two pale areas in the intercalary fork; distal antennal segments 11-15 not showing marked contrast to basal segments 3-10 *C. molestus*.
5. (2) Wing without pale area in the intercalary fork 6
Wing with obvious pale area in the intercalary fork 7
6. (5) No pale spotting on any part of wing; macrotrichia abundant *C. immaculatus*.
Pale spotting apparent on wing, macrotrichia only moderately developed
..... *C. palpalis* (in part).
7. (5) Cell M_4 of wing with irregularly shaped, recurved or angular pale spot 8
Cell M_4 of wing with pale spot rounded or approximately so, but always without any partially enclosed dark area 9
8. (7) Wing with pale spot in cell M_4 often divided into two; larger species with wing length greater than 1.5 mm. *C. angularis*.
Wing with pale spot in cell M_4 undivided, smaller species with wing length less than 1.5 mm. *C. rabaulti*.
9. (7) Third segment of palp grossly swollen, ovoid, with single round sensory pit
..... *C. palpalis* (in part). 10
Third segment of palp not as above, with one or more sensory pits 10
10. (9) Wing with many small pale spots; spot over r-m narrow and straight-sided, expanding towards costa; small round pale spot almost at extremity of intercalary fork, pale spot adjacent to R_{4+5} including basal portion of intercalary fork but with a broad dark area between it and the distal spot; a single elongate tapering spermatheca *C. mackayensis*
Wing with fewer pale spots; separation of spots at base and apex of intercalary fork not so pronounced; spermathecae otherwise 11
11. (10) A small species with distinctive wing pattern; spot adjacent to R_{4+5} squarish and large, spot distally over intercalary fork large, triangular with longest side reaching wing margin; macrotrichia very sparse, restricted to wing tip *C. robertsi* (in part).
Larger species with wing pattern not as above, macrotrichia fairly dense 12
12. (11) Third segment of palp with single round sensory pit *C. ornatus*.
Third segment of palp with multiple sensory pits *C. marmoratus*.
13. (1) Wings with only one pale area in the intercalary fork (excluding any intrusion of the spot adjacent to R_{4+5} over the base of the intercalary fork area) 14
Wings with two or more pale spots in the intercalary fork area 17
14. (13) Antennae with basal flagellar segments 3-10 long and vasiform 15
Antennae with basal flagellar segments 3-10 shorter and subcylindrical 16
15. (14) Third segment of palp elongate, with single flask-shaped sensory pit .. *C. antennalis*.
Third segment of palp elongate, with many small round sensory pits *C. bancrofti*.
16. (14) Small species; wing almost devoid of macrotrichia, pale area over end of second radial cell not easily seen *C. robertsi* (in part).
Larger species; wing with dense macrotrichia, pale spots large and obvious, spot over the end of the second radial cell quite distinct *C. magnimaculatus*.
17. (13) Wing with two spots in distal part of intercalary fork, one more or less above the other *C. cuciculus*.
Wing with three spots in the intercalary fork 18
18. (17) Wing with only one pale spot in cell M_4 19
Wing with two pale spots in cell M_4 21
19. (18) Third segment of palp with three irregular sensory pits *C. multimaculatus*.
Third segment of palp with only one sensory pit 20
20. (19) Antennae short, distal flagellar segments 11-15 scarcely longer than basal ones. Third segment of palp short and wide, not as long as the fourth and fifth together
..... *C. dycei*.
Antennae longer, distal segments 11-15 distinctly longer than the basal ones. Third segment of palp long and narrow, longer than the fourth and fifth together
..... *C. mcmillani*.
21. (15) Wings with pale spots moderately large; spermathecae three in number with ducts and basal portions of body unchitinized *C. marksii*.
Wings with pale spots quite small; spermathecae three in number with ducts heavily chitinized, bodies very weakly so *C. parvimaeculatus*.

DESCRIPTION OF SPECIES.

GROUP I.

CULICOIDES IMMACULATUS, n. sp.

Types: Holotype ♀ and two ♀♀ paratypes mounted on slides in SPHTM.

Type Locality.—Holotype from Yam I., near Cape York, 22:viii:1949 (I. M. Mackerras, in well, biting); one paratype from Red I. Point, Cape York, North Queensland, 25:viii:1949 (I. M. Mackerras, biting); the other from Thursday I., 18:viii:1949 (I. M. Mackerras, biting in mangrove swamp).

Distinctive Characters.—This species has no obvious wing spots. It is only likely to be confused with *C. subimmaculatus*, but the absence of a pale spot over r-m, the greater abundance of macrotrichia and the subcylindrical tarsus IV (as compared with the cordate tarsus IV of *C. subimmaculatus*) should readily distinguish it. See also under *C. palpatis* for characters differentiating it and *C. immaculatus*.

Description.—As no dry unmounted material is available it is not possible to give details of coloration. Measurements are given for the holotype, average measurements are from the two paratypes only (Table 1).

Female.

Head: Eyes only moderately separated (Text-fig. 1), antennae with basal flagellar segments subcylindrical, wider near base than distally, distal segments normally elongate and no unusual contrast between the two (Text-fig. 19). Mouth parts equal in length to the height of the head, palpi with moderately enlarged third segment with single round sensory pit distally (Text-fig. 38).

Thorax: Legs in mounted specimens showing no trace of the bands on femora or tibiae which can be seen in most species. Tarsus IV is unmodified, the tibial comb is composed of four long spines.

The wings have the area enclosed by C and R darker than the rest of the wing, no evidence of wing spotting, and macrotrichiae moderately dense over all the wing surface (see Plate xvi, fig 1).

Abdomen: There are two subequal subspherical spermathecae each with a very short chitinized duct.

Male: This sex has not been taken.

Distribution.—QUEENSLAND: Cape York area, North Queensland (type series); Fantome I. near Townsville, v:1949 (E. J. Reye); Goat I., Moreton Bay, 24:x:1950 (E. J. Reye, biting).

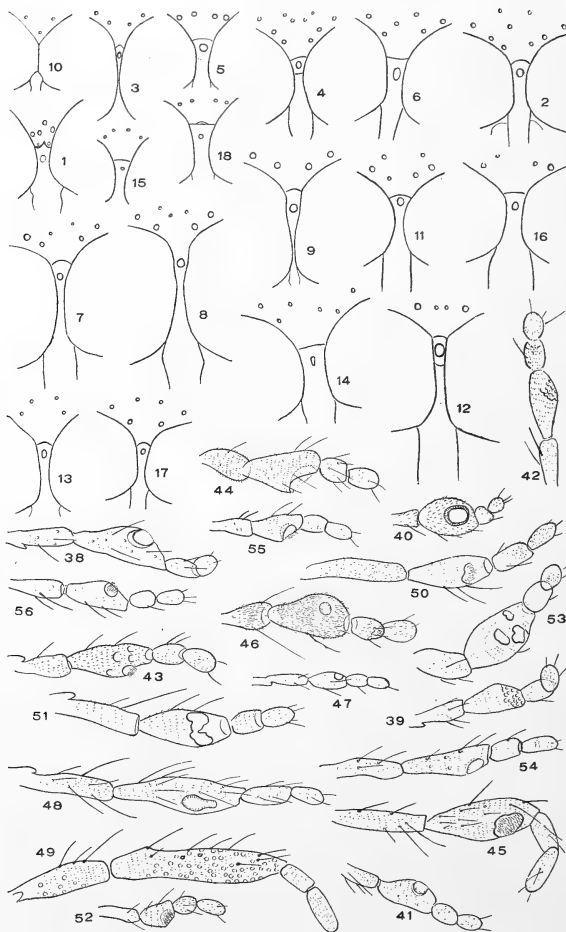
CULICOIDES SUBIMMACULATUS, n. sp.

Types: Holotype ♀ and 26 ♀♀ paratypes, all slide mounts. Holotype and paratype series in SPHTM, other paratypes in BM, USNM, QIMR, and CSIRO.

Type Locality.—All of type series from Palm Beach, New South Wales, 2:iii:1946 (D. J. Lee). They were taken biting man in considerable numbers in the late afternoon in bush about 300 feet above sea level.

Distinctive Characters.—*C. subimmaculatus* is distinguishable from *C. immaculatus* on the characters outlined under the latter species. Confusion might also arise with *C. palpatis* in which some spotting can usually be detected in cell M_4 and the anal cell (no spots in these areas in *C. subimmaculatus*). It lacks the excessively swollen third palpal segment of *C. palpatis* and tarsus IV is cordate, a character only found elsewhere in *C. molestus* and *C. magnesianus*.

Description.—Essentially from the type series, coloration characters from pinned specimens from Mosman, New South Wales, 19:xi:1923 (Mackerras) and male characters from specimens from Coff's Harbour, New South Wales, 17:viii:1952 (E. J. Reye, in net, 1600 hours). Measurements are given for the holotype, average measurements from ten paratypes and for the male sex a series of eight specimens from Coff's Harbour has been used (see Table 1).



Text-figures 1-18. Interorbital space of various species. ($\times 190$ approx.)

1, *C. immaculatus*; 2, *C. subimmaculatus*; 3, *C. palpalis*; 4, *C. ornatus*; 5, *C. molestus*; 6, *C. marmoratus*; 7, *C. mackayensis*; 8, *C. angularis*; 9, *C. magnesianus*; 10, *C. robertsi*; 11, *C. antennalis*; 12, *C. bancrofti*; 13, *C. magnimaculatus*; 14, *C. cuniculus*; 15, *C. dycei*; 16, *C. mcmillani*; 17, *C. parvimaculatus*; 18, *C. marksi*.

Text-figures 1, 2, 10, 11, 13, 14, 16, 17 and 18 drawn from holotype specimens; 3, 4, 7, 9 and 15 from paratypes; 5 and 6 from specimens in the selected series mentioned in the description; 8, a specimen from Cooranbong and 12, a specimen from Hornsby.

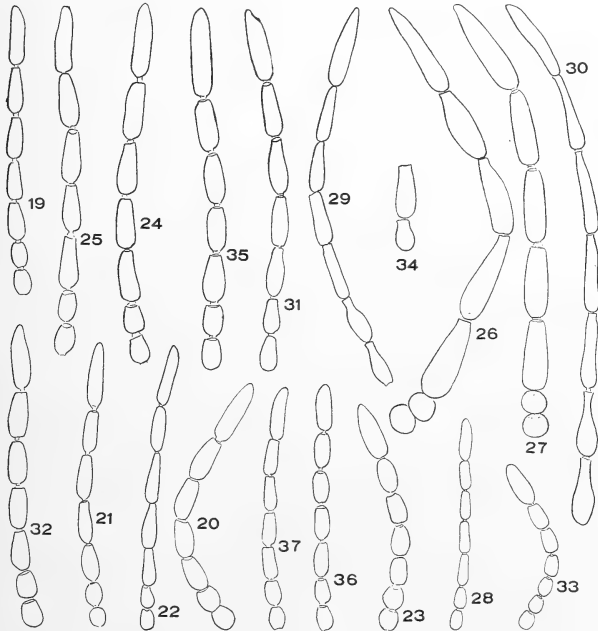
Text-figures 38-56. Palp of various species. ($\times 190$ approx.)

38, *C. immaculatus*; 39, *C. subimmaculatus*; 40, *C. palpalis*; 41, *C. ornatus*; 42, *C. molestus*; 43, *C. marmoratus*; 44, *C. mackayensis*; 45, *C. angularis*; 46, *C. magnesianus*; 47, *C. robertsi*; 48, *C. antennalis*; 49, *C. bancrofti*; 50, *C. magnimaculatus*; 51, *C. cuniculus*; 52, *C. dycei*; 53, *C. multimaculatus*; 54, *C. mcmillani*; 55, *C. parvimaculatus*; 56, *C. marksi*.

Text-figures 38, 47, 48, 53 drawn from holotypes; 39, 40, 41, 44, 45, 46, 49, 50, 51, 52, 55 and 56 from paratypes; 42 and 43 from specimens in the selected series mentioned in the text; 54, a specimen from Woodford.

Female.

The head is dark brown with lighter brownish bloom dorsally, the antennae and palpi are dark brown. The scutum has no pattern of spots or bands and is almost entirely covered by a dull yellowish-brown bloom similar to that on the head and also on the scutellum. The pleura are dark brown, the legs brown with no trace of banding. Halteres yellowish. Abdomen dark brown.



Text-figures 19-37. Segments 9-15 of the antenna of various species.

(Figs. 19-33, $\times 150$; 34-37, $\times 190$ approx.)

19, *C. immaculatus*; 20, *C. subimmaculatus*; 21, *C. palpalis*; 22, *C. ornatus*; 23, *C. molestus*; 24, *C. marmoratus*; 25, *C. mackayensis*; 26, *C. angularis*; 27, *C. magnesianus*; 28, *C. robertsi*; 29, *C. antennalis*; 30, *C. bancrofti*; 31, *C. magnimaculatus*; 32, *C. cuniculus*; 33, *C. dycei*; 34, *C. multimaculatus* (segments 10 and 11 only); 35, *C. mcmillani*; 36, *C. parvimaculatus*; 37, *C. marksi*.

Text-figures 19, 20, 27, 29, 31, 34, 35 and 36 drawn from holotypes; 21, 22, 25, 26, 28, 30, 32, 33 and 37 from paratypes; 23 and 24 from the selected series mentioned in the description.

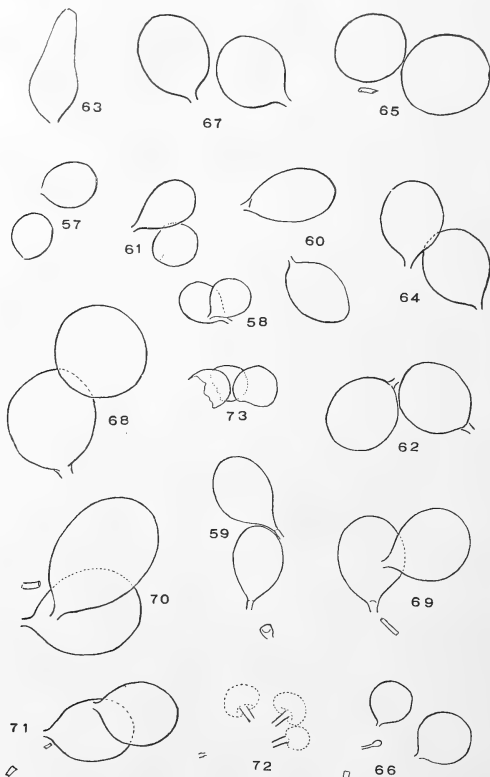
Head: The eyes are well divided (Text-fig. 2), the antennae (Text-fig 20) short with the basal flagellar segments subspherical and the distal five normally elongate. The third segment of the palpus is moderately enlarged with a series of many very small sensory pits on the distal half (Text-fig. 39). Length of mouth parts less than height of head.

Thorax: Tarsus IV of all legs cordate (Text-fig. 77); tibial comb comprising four spines. The wings are greyish with no strongly contrasting pattern but only two small pale areas, one over r-m, the other adjacent to the termination of R_{3+4+5} . Macrotrichia sparse (see Plate xvi, fig. 4).

Abdomen: Two subequal subspherical spermathecae with short chitinous ducts, one narrow elongate duct and a short broad duct (Text-fig. 58).

Male.

Apart from the usual sexual differences, essentially similar to the female. Genitalia with harpes as in Text-fig. 77.



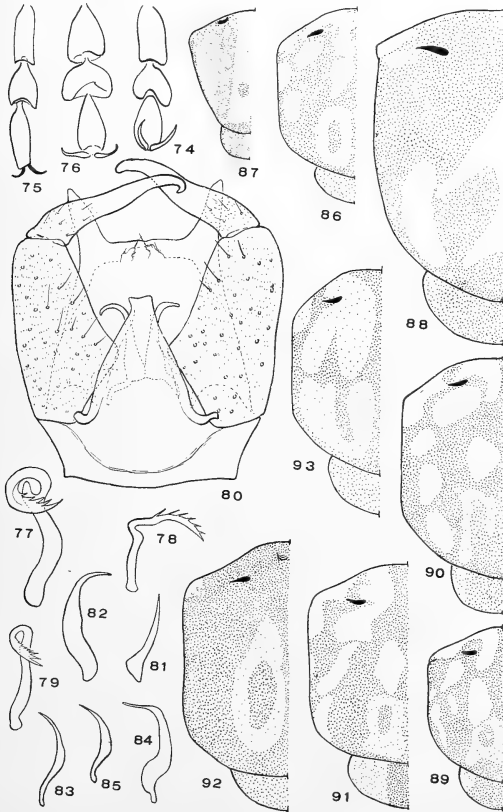
Text-figures 57-73. Spermathecae of various species. ($\times 250$.)

57, *C. immaculatus*; 58, *C. subimmaculatus*; 59, *C. palpalis*; 60, *C. ornatus*; 61, *C. molestus*; 62, *C. marmoratus*; 63, *C. mackayensis*; 64, *C. angularis*; 65, *C. magnesianus*; 66, *C. robertsi*; 67, *C. antennalis*; 68, *C. bancrofti*; 69, *C. magnimaculatus*; 70, *C. cuciculus*; 71, *C. mcmillani*; 72, *C. parvimaculatus*; 73, *C. marksi*.

Text-figures 66, 67, 69, 70 and 73 drawn from holotypes; 57, 58, 59, 60, 63, 65 and 72 from paratypes; 61 and 62 from specimens in the selected series mentioned in the text; 64, a specimen from Cooranbong; 68, one from N. of Coff's Harbour, 71 a specimen from Woodford.

Distribution.—QUEENSLAND: Magnetic I., 9:vii:1952 (E. J. Reye, biting man, 1600 hrs.); South Townsville, 11:vii:1952 (E. J. Reye, biting man, 1630 hrs.); Bowen, (S. J. Crighton), 14:vii:1952 (E. J. Reye, biting in bush, 1000 hrs); Bucasia, iii:1951 (H. A. Edmonds); Fraser I., 14:ii:1949 (biting fiercely), 9:xii:1952 (biting in daylight, seashore mangroves); Tin Can Bay, 17:iv:1938 (R. V. Smythe, biting); Noosa, 7:v:1949 (M. J. Mackerras, resting in tent); Maroochydhore, 31:x:1951 (M. A. Reye); Redcliffe, 10:ix:1938 (F. A. Perkins); Fisherman I., 12:i:1951, 9:xii:1951 (E. J. Reye, biting, 1800 hrs.); Lota, 7:i:1952 (E. J. Reye, biting); Peel I., 30:x:1950 (E. J. Reye),

6:ix:1951 (E. J. Reye, biting, 1530 hrs.); Goat I., 3:x:1950, 24:x:1950 (E. J. Reye); Southport, 3:ii:1952 (E. J. Reye, biting); Texas, 22:xii:1951 (E. J. Reye, light trap, 2000 hrs.). NEW SOUTH WALES: Boonoo Boonoo Falls, 1:v:1938; Tweed Heads, xii:1948; Evans Head, 26:ix:1950 (M. J. Mackerras); Moonee Beach, 18:x:1950 (M. J. Mackerras, biting at dusk); Mooni, Coff's Harbour, 14:ii:1925; Coff's Harbour, 17:viii:1952 (E. J. Reye, 1630 hrs., net in creek flat mangroves); Bob's Farm, 25:i:1942 (0600-0700,



Text-figures 74-76. Tarsal segments III-V. ($\times 250$)
74, *C. subimmaculatus*; 75, *C. ornatus*; 76, *C. molestus*.

Text-figures 77-85. Harpes. ($\times 250$)

77, *C. subimmaculatus*; 78, *C. palpalis*; 79, *C. marmoratus*; 80, *C. angularis* (complete male genitalia); 81, *C. robertsi*; 82, *C. magnimaculatus*; 83, *C. dycei*; 84, *C. parvimaculatus*; 85, *C. marksi*.

Text-figures 86-93. Scutal patterns. ($\times 70$)

86, *C. palpalis*; 87, *C. robertsi*; 88, *C. bancrofti*; 89, *C. dycei*; 90, *C. parvimaculatus*; 91, *C. marksi*; 92, *C. antennalis*; 93, *C. marmoratus*.

Text-figure 74 drawn from holotype; 75 from a paratype; 76 from a specimen in the selected series mentioned in the description; 81 and 85 from allotypes; the rest as mentioned in the descriptions of the individual species.

(biting); Palm Beach, 2:iii:1946 (D. J. Lee); Careel Bay, 3:ii:1949 (biting), 16:ii:1949 (D. J. Lee, biting, 12 noon); Avalon, 25:i:1949 (K. O'Gower); Narrabeen, 29:ix:1948 (B. McMillan); Cowan Cr., 29:x:1949 (B. McMillan); Hornsby, 6:x:1951 (D. J. Lee and B. McMillan); McCarr's Cr., 17:xi:1947 (biting, mangrove flat, 5.30 p.m.); Castle-crag, 13:xi:1951 (Dr. Hedburg); Roseville, 13:x:1923 (Nicholson); Mosman, 19:xi:1923 (Mackerras); Walsh L., 29:i:1949 (B. McMillan); Oyster Bay, 1:i:1950, 8:i:1950, ii:1950, xi:1950 (Brown-Deverell), 29:i:1951 (Mrs. Amos); Oatley Park, 27:ix:1952 (E. J. Reye, net, 1415 hrs.); Woolooware Bay, 27:ix:1952 (E. J. Reye, net, 1645 hrs.); Quibray Bay, 14:xii:1948, 28:x:1952 (E. J. Reye, net, 1000 hrs.); Burraneer Bay, 25:xi:1950 (Kinsella); Cronulla, 25:ii:1942 (in car headlights); Woronora, 11:x:1952 (E. J. Reye, 1630 hrs., net among mangroves); Port Kembla, 20:x:1949; Merimbula, 17:xi:1948 (E. Pratt).

CULICOIDES PALPALIS, n. sp.

Types: Holotype ♀, allotype ♂, together with 17 ♀♀ and 15 ♂♂ paratype slides. Holotype, allotype and paratype series in SPHTM. Other paratypes in BM, USNM, QIMR and CSIRO.

Type Locality.—Texas, Queensland (on New South Wales border). All specimens in type series taken in light trap, 20:i:1952 (A. L. Dyce).

Distinctive Characters.—This species is particularly characterized by the grossly swollen third segment of the palpi. The wing has a faint but definite pattern which, in contrast to *C. immaculatus* and *C. subimmaculatus*, includes the posterior part of the wing.

Description.—From the type series except for coloration characters which are taken from pinned specimens from Bundy, via Moree, v:1952 (E. J. Reye). Measurements are given for the holotype and a series of ten paratypes of each sex (Table 1).

Female.

Generally dark brown in colour, including antennae, palpi, thorax and abdomen. Scutum with complex greyish pattern (see Text-fig. 86). Legs rather lighter brown than rest of body, with the bases of all tibiae pale, the apices of fore and mid femora also pale, but not quite so obviously, and the bases of fore and mid femora also pale. Wings with pattern of fair but not strong contrast (Plate xvi, figs. 2 and 3), macrotrichiae moderate in density, radial cells dark brown except at base of first. Halteres pale yellowish.

Head: Antennae with basal segments of flagellum globular, distal segments elongate, each approximately twice as long as the individual basal segments, except 15 which is about half as long again as the penultimate (Text-fig. 21). Palpi with second segment elongate and expanded apically, third segment ovoid, grossly enlarged, longer than wide with maximum width at middle, sensory organ as in Text-figure 40. Fourth segment very small and globular, fifth also small but ovoid in shape. The eyes are narrowly separated in the inter-orbital area (Text-fig. 3). Mouth-parts rather less in length than height of the head.

Thorax: The pattern of the scutum is of the form shown in Text-figure 86. The legs are as described above, the tibial comb comprises four spines, the first rather longer than the other three. Tarsus IV is subcylindrical.

Abdomen: The spermathecae are as in Text-figure 59.

Male.

This sex possesses a similar wing pattern to that of the female although the spotting tends to be less intense and the macrotrichia are rather more sparse. The palpi are similar in form except that the third segment is smaller although the same proportions are maintained. The harpes are as in Text-figure 78.

Distribution.—QUEENSLAND: Blue Mts. Goldfield, Cape York Pen., 14:xi:1947 (J. L. Wassell, light trap); Magnetic I., 9:xii:1952 (E. J. Reye, in net, 1000 hrs. and 1530 hrs.); Bowen, 14:vii:1952 (E. J. Reye, in net, 1200 hrs.); Mirani, 15:vii:1952 (E. J. Reye, in net, 1200 hrs.); Longreach, 1951 (R. F. Riek, light trap); Gootchie, 20:vii:1952

(E. J. Reye, in net, 1600 hrs.); Dayboro, 7:viii:1951 (E. J. Reye, culture from pond edge); Roma, 11:v:1948 (J. L. Wassell, 2100-2200 hrs.); Yeerongpilly, 15:iv:1952 (R. F. Riek, light trap); Noondoo, iii:1951; Texas, 20:i:1952 (A. L. Dyce). NEW SOUTH WALES: Gravesend, 12:vi:1952 (E. J. Reye, 1600-1700 hrs., in net); Yagobie, 3:xii:1951 (A. L. Dyce, 1925-0500 hrs., light trap); Biniguy, 19:x:1951 (A. L. Dyce); Moree, 10:xi:1951 (A. L. Dyce, 1830-2130 hrs., Mercury vapour light trap), 11:xi:1951 (A. L. Dyce, dusk to 2130 hrs., M.V. light trap), 22:xi:1951 (A. L. Dyce, M.V. light trap); 23-24:xi:1951 (A. L. Dyce, 1830-0500, M.V. light trap), 25:xi:1951 (A. L. Dyce, M.V. light trap); Bundy, via Moree, 30:x:1951 (A. L. Dyce, light trap), 7:xi:1951 (A. L. Dyce, rabbit modified trap, 9.30-11.30 a.m.), 6:xii:1951 (A. L. Dyce, 6-9 p.m., M.V. trap), 6-7:xii:1951 (A. L. Dyce, live rabbit trap, suction, 5 p.m.-10 a.m.), 2:v:1952 (E. J. Reye), 24:v:1952 (E. J. Reye, 2300 hrs., Mercury vapour light trap in caravan), 29:v:1952 (E. J. Reye, 1730-1950 hrs., light trap), 7:vi:1952 (E. J. Reye, 1600 hrs., net); Castle Hill, 29:x:1952 (D. J. Lee, light trap), 31:x:1952 (D. J. Lee, light trap).

CULICOIDES ORNATUS Taylor.

Taylor, F. H., 1911.—*Rept. Aust. Inst. Trop. Med.*: 73.

Types: I have been unable to trace the type of this species (or, indeed, any specimens identified by Taylor) and must assume that it is no longer in existence. This assumption is corroborated by correspondence on file in the School of Public Health and Tropical Medicine, Sydney, wherein it is disclosed that the author of the species was himself unable to locate the type (correspondence with J. W. S. Macfie, 1939). In view of this evidence it has been considered advisable to set up a new type series comprising a neotype ♀ and 26 ♀♀ neoparatypes. Neotype and neoparatype series in SPHTM, other neoparatypes in BM, USNM, CSIRO and QIMR.

Type Locality.—All the above from Magnetic I., Queensland, 9:vii:1952 (E. J. Reye, 1600 hrs.). This locality is less than five miles from the original type locality of Townsville.

Distinctive Characters.—This species most resembles *C. molestus*, from which it differs in having the pale spot on the costa immediately adjacent to R_{4+5} returning backward below the radial cells and in having only one spot within the intercalary fork instead of two. Tarsus IV is not cordate as in *C. molestus* and there is a single sensory pit on the third segment of the palpi.

Description.—From the neotype series except for coloration characters which are taken from specimens from Gladstone and Darwin. Measurements of a single specimen are given from a neoparatype, average measurements from a series of ten neoparatypes (Table 1).

Female.

A small brown species with brown antennae and palpi, darker brown thorax and abdomen. Scutum with complex grey pattern anteriorly and laterally. Scutellum dark brown. Femora dark brown, tibiae light brown with dark brown tips, tarsi mainly light brown, rather darker on basal portion of Tarsus I. Wings with fair but not strong contrast, macrotrichia moderately dense over most of wing. Halteres creamy-white.

Head: Antennae with basal segments of flagellum subcylindrical, distal segments normally elongate (Text-fig. 22). Third segment of palpi expanded distally with a single round sensory pit (Text-fig. 41). Eyes moderately separated (Text-fig. 4). Mouth-parts almost equal in length to height of head.

Thorax: Legs without any obvious modifications, Tarsus IV not cordate but rather bell-shaped (Text-fig. 75). Tibial comb of four spines. Wings as illustrated in Plate xvi, fig. 5.

Abdomen: Two subequal round to ovoid spermathecae, each with short chitinized duct (Text-fig. 60).

Male: This sex has not so far been taken.

Distribution.—WESTERN AUSTRALIA: Wyndham, ii:1931 (H. J. Willings); Port Hedland, 6:i:1948 (Dept. Agric.). NORTHERN TERRITORY: Bathurst I., Reichart's Cr., near

Darwin, 18:xi:1942 (A. R. Woodhill); Berry's Springs, near Darwin, 18:xi:1942 (A. R. Woodhill). QUEENSLAND: Yam I., Cape York, 23:viii:1949 (I. M. Mackerras, in well); Cairns, 27:xii:1942 (A. R. McCulloch); Palm I., 2:vi:1948 (J. L. Wassell, edge of scrub, in light trap, 8-9 p.m.); Townsville, xi:1945 (A. J. Bearup); Magnetic I., 9:vii:1952 (E. J. Reye, in net and biting, 1530 hrs.); South Townsville, 11:vii:1952 (E. J. Reye, in net and biting, 1630 hrs.); Gladstone, 23:i:1947 (E. N. Marks, biting in hospital); Fraser I., 9:xii:1938 (biting in daylight, seashore mangroves); Comslie, 19:xi:1951 (R. F. Riek, biting horse).

CULICOIDES MOLESTUS (Skuse).

Skuse, F. A., 1889. PROC. LINN. SOC. N.S.W., 4 (2nd series): 305 (*Ceratopogon*).

Kieffer, J. J., 1906. Chironomidae in Wytzman's Genera Insectorum, fasc 42: 54 (*Culicoides*).

Macfie, J. W. S., 1939. PROC. LINN. SOC. N.S.W., 64: 556.

Type: Holotype ♀ in Macleay Museum, University of Sydney.

Type Locality.—Berowra, New South Wales (January).

Synonymy: *Ceratopogon molestus* Skuse, 1889, *loc. cit.*—*Nec Culicoides molestus* Kieffer, J. J., 1910, *Mem. Ind. Mus.*, 2, No. 4: 192.

Distinctive Characters.—Two pale spots in the intercalary fork area, no pale area immediately below the second radial cell and the cordate Tarsus IV separate this from its closest ally, *C. ornatus*. The sensory pits on the third palpal segment are multiple.

Female.

Additional data on this species (including average measurements of ten specimens) have been provided by mounted specimens taken at Berowra, 6:iii:1946 (R. H. Wharton). Individual measurements are from a specimen from Mosman, 26:i:1947 (Table 1). Details of the antennae are figured in Text-figure 23, of the palpi in Text-figure 42, of the wing in Plate xvi, fig. 6, of the tarsi in Text-figure 76, and the spermathecae in Text-figure 61. There is no distinct scutal pattern although there is a covering of yellowish-grey bloom indistinctly differentiated into a median and two lateral bands separated by two lighter submedian bands.

Male: No specimens of this sex are available for description.

Distribution.—QUEENSLAND: Cockle Bay, Magnetic I., 9:vii:1952 (E. J. Reye, biting, 1600 hrs.); South Townsville, 11:vii:1952 (E. J. Reye, biting, 1630 hrs.); Mackay, ix-x:1950; Fisherman I., 11:xii:1950 (1600 hrs.). NEW SOUTH WALES: Tilligerry Cr., 18:ii:1949 (B. McMillan); Berowra, 6:iii:1946 (D. J. Lee and R. H. Wharton); Mt. Kuring-gai, 29:x:1949 (B. McMillan); Cowan Cr., 29:x:1949 (B. McMillan); 30:xii:1951 (B. McMillan, biting, 4 p.m.), 2:iv:1952 (B. McMillan, biting 4.30 p.m.); Bobbin Head, 17:iii:1948 (B. McMillan); Kuring-gai Chase, 28:xii:1929 (L. M. Willings); Palm Beach, 2:iii:1946 (D. J. Lee); Hornsby, 14:v:1949 (biting); French's Forest, 6:iv:1949 (biting); McCarr's Cr., 29:iv:1949 (D. J. Lee, mangrove area); Killara, 11:ii:1946 (Miss Kent, biting, 6 p.m.); Mosman, 19:xi:1923 (Mackerras), 2:iv:1943 (biting), 20:i:1947 (D. J. Lee, biting at dusk), 6:iv:1947 (D. J. Lee, biting, 6 p.m.); 8:xi:1947 (D. J. Lee, biting in garden); Hunter's Hill, 14:xi:1940 (A. R. Woodhill, biting 5-7 p.m., 400 yards from salt water); Lillipilli, 9:iii:1946 (A. J. Bearup); Oyster Bay, 29:i:1951 (Mrs. Amos); Gundamaian, 19:xi:1923 (Mackerras); National Park, 12:iv:1924 (Mackerras), 25:iv:1925 (Mackerras), 30:iii:1947 (B. McMillan).

CULICOIDES MARMORATUS (Skuse).

Skuse, F. A., 1889. PROC. LINN. SOC. N.S.W., 4 (2nd series): 304-5 (*Ceratopogon*).

Macfie, J. W. S., 1939. PROC. LINN. SOC. N.S.W., 64: 556.

Type: Holotype ♀ in Macleay Museum, University of Sydney.

Type Locality.—Sydney, New South Wales.

Synonymy.—*Ceratopogon marmoratus* Skuse, 1889, *loc. cit.*

Distinctive Characters.—Characters serving to differentiate this species are the form of the pale spot adjoining the distal end of the second radial cell, this spot being bilobed,

with one lobe beside the termination of the cell, the other beneath it; the single pale spot in the intercalary area which at times is indented distally, the general strength of the spotting which has a greater degree of contrast than in the preceding species; the sensory organ of the palpi which consists of one large irregular pit and a number of smaller subsidiary ones. No single character is specifically diagnostic but there should be agreement with the essential characters listed above and the wing spot distribution as figured in Plate xvi, figs. 7 and 8. Two types of wing spotting are illustrated, the difference being in the intercalary fork area. Other specimens show this pale spot considerably reduced.

Additional details of the head are provided in Text-figures 6, 24 and 43, and of the spermathecae in Text-figure 62. These are all drawn from a series of specimens from Burraneer Bay (near Sydney), New South Wales, 25:xi:1950 (Kinsella, 6 p.m.). All measurements in Table 1 are from this same series.

A male specimen from Hornsby, New South Wales, 11:xi:1950 (D. J. Lee, light trap), has been used for illustrating the harpes of the male genitalia (Text-fig. 79).

Distribution.—QUEENSLAND: Magnetic I., 9:vii:1952 (E. J. Reye, Mangroves, 1000 hrs.); Mackay, ix-x:1950; Noosa, 1:v:1949 (M. J. Mackerras, biting); Tin Can Bay Rd., 17:iv:1949 (biting in tent); Dayboro, 13:xi:1949 (ex horse); Auchenflower, 10:ix:1950 (J. Pope, scrub); Mt. Coot-tha, 21:xi:1949; Yeerongpilly, 5:v:1938 (F. H. S. Roberts), 3-4:i:1952 (R. F. Riek, light trap), 7:iv:1952 (R. F. Riek, light trap); Sunnybank, 19:viii:1950 (M. J. Mackerras, biting); Corinda, 18:iv:1948; Peel I., 30:x:1950 (E. J. Reye); Mt. Tambourine, 17:xi:1949; Little Nerang R., 25:ix:1949 (biting). NEW SOUTH WALES: Nelson's Bay, 4:vi:1950 (B. McMillan, 500'); Anna Bay, 21:viii:1948 (B. McMillan, biting); Newcastle, 1:1948 (B. McMillan); Mt. Kuring-gai, 29:x:1949 (B. McMillan); Cowan Cr., 29:x:1949 (B. McMillan); Hornsby Gully, 29:x:1950 (D. J. Lee and B. McMillan, 5 p.m.); Hornsby, xi:1950 (D. J. Lee, light trap), 11:xi:1950 (D. J. Lee, light trap); Palm Beach, 2:iii:1946 (D. J. Lee, biting at dusk); Narrabeen, 26:vii:1948 (B. McMillan); French's Forest, 6:iv:1949 (biting); Hunter's Hill, 14:xi:1946 (A. R. Woodhill); Mosman, 30:iii:1947 (D. J. Lee); Oatley Bay, 27:ix:1952 (E. J. Reye, 1540 hrs.); Oyster Bay, 5:xi:1950 (D. J. Lee); Woollooware Bay, 27:ix:1952 (E. J. Reye, 1645 hrs.); Burraneer Bay, 25:xi:1950 (Kinsella, 6 p.m.); Gundamain, iv:1950 (A. J. Bearup, near waterfall); National Park, Uloola Falls, 23:x:1949 (B. McMillan); National Park, 12:xi:1949 (B. McMillan); Heathcote, 13:iv:1946, 12:v:1946, 5:viii:1946, 21:ix:1946 (all J. R. Henry); Engadine, 20:ii:1947 (J. R. Henry, biting); Merimbula, 17:xi:1948 (E. Pratt).

CULICOIDES MACKAYENSIS, n. sp.

Types: Holotype ♀ and 14 ♀♀ paratype slides. Holotype and paratype series in SPHTM, paratypes in each of BM, USNM, QIMR and CSIRO.

Type Locality.—All the above from Mackay, Queensland, 15:vii:1952 (E. J. Reye, 1620 hrs., net in mangroves).

Distinctive Characters.—This species has an unusual wing spot distribution with a small pale area in the base of the intercalary fork (this spot may be confluent with the pale area surrounding the distal extremity of the second radial cell) together with a marginal pale spot near the termination of the lower branch of the intercalary fork. Another feature seen in the wing is the narrow pale area running over M_{3+4} and Cu, (this is also seen in *C. multimaculatus*), and the pale area over r-m is a band rather than a rounded spot as in most species. The single spermatheca is also of characteristic shape (see Text-fig. 63).

Description.—Only the type series has been available for description. Individual measurements are from the holotype, average measurements from a series of ten paratypes (Table 1).

Female.

The slide specimens reveal that the legs have distinct preapical pale spots on the femora and even more obvious pale spots adjacent to the bases of the tibiae. The wings

have a complex pattern of moderately strong contrast and the halteres are obviously dark in colour.

Head: Eyes rather closely approximated (Text-fig. 7), antennae with basal flagellar segments not much longer than broad, distal segments elongate with rather strong contrast between the two (Text-fig. 25). The third segment of the palpi with greatest expansion near middle and a single very large sensory pit (Text-fig. 44). The mouth parts are equal in length to the height of the head.

Thorax: Legs with no obvious modifications, Tarsus IV subcylindrical, tibial comb of four spines. Wings with moderately dense macrotrichia, spotting as in Plate xvi, fig. 12.

Abdomen: A single spermatheca of unusual shape as in Text-fig. 63.

Male: This sex has not yet been taken.

Distribution.—QUEENSLAND: Only known from the type locality.

CULICOIDES RABAUli Macfie.

Macfie, J. W. S., 1939. PROC. LINN. SOC. N.S.W. 64: 367.

Type: Holotype ♀ on slide in SPHTM.

Type Locality.—Rabaul, New Britain.

Distinctive Characters.—Despite access to the unique type which is unfortunately in a distorted condition, it has not been possible to characterize this species adequately. *C. rabauli* is one of the species with a curved or inverted V-shaped pale area inside cell M₁. It is distinct from *C. marksi* since it has only one pale spot in the intercalary fork area, *C. marksi* having three.

The closest species to *C. rabauli* is *C. angularis* and it is not possible to differentiate the two adequately, although in our opinion they are distinct species. It has been thought better to describe as new *C. angularis* realizing that it may fall into synonymy when *C. rabauli* is better known rather than to risk an erroneous recording of *C. rabauli* from southern Australia. Of the characters which can be fully observed in the type of *C. rabauli* there is only one which offers a point of distinction from *C. angularis*. In cell M₁ the pale spot is undivided in *C. rabauli* whereas it is usually divided into a large and a small section in *C. angularis*. Details of the antennae and palpi are not sufficiently clear in the *C. rabauli* type to determine exact differences although it is considered possible that other differences may be found in these characters. A photograph of the wing of the type is included (Plate xv, fig. 10) for comparison with that of *C. angularis*. These are indicative of the difference in size which appears to be associated with the two species. Such measurements as are possible on the holotype are included in Table 1.

Distribution.—NEW GUINEA: Rabaul. QUEENSLAND: A small series of specimens from Heron I. has been placed tentatively as *C. rabauli* since they show the undivided pale spot in cell M₁. Heron I., 24:v:1947 (J. L. Wassell, tree hole and *Pisonia* tree hole).

CULICOIDES ANGULARIS, n. sp.

Types: Holotype ♀ and 8 ♀♀ paratypes, all pinned specimens with the exception of one paratype mounted on a slide. All in SPHTM.

Type Locality.—Mittagong, New South Wales, 27:xi:1936 (D. J. Lee, bred from larvae found in rock pool).

Distinctive Characters.—See under *C. rabauli*.

Description.—From the type series, some additional data being provided from the specimens from Cooranbong listed below. Individual measurements are from a specimen from Cooranbong, 24:ix:1949, average from two specimens, one a paratype, the other from Cooranbong as above (Table 1).

Female.

A large brown species. Head dark brown including antennae and palpi. Thorax dark brown, scutum dark brown for the anterior fourth, rest covered by a golden-brown

bloom, except the prescutellar area, which is greyish. Scutellum with middle third dark brown, sides greyish. The legs are brown with a slightly paler indefinite band just before the apex of each femora and somewhat more pronounced pale band at the base of the tibiae. Wings with pattern of quite strong contrast, halteres with creamy white knobs. Abdomen dark brown.

Head: Eyes narrowly separated (Text-fig. 8), antenna long with short globular basal flagellar segments, and very elongated distal ones (Text-fig. 26). Palp with elongate third segment moderately swollen near middle and with a single large sensory pit (Text-fig. 45). Mouth-parts as long as height of head.

Thorax: Legs unmodified, Tarsus IV cylindrical. Wings with moderately dense macrotrichia, pattern as in Plate xvi, fig. 11. The pale area in cell M_1 is usually divided but occasionally both sections are fused.

Abdomen: Two subequal, subspherical spermathecae, each with short duct (Text-fig. 64).

Male.

A specimen from Cooranbong has been used for the figure of the male terminalia (Text-fig. 80).

Distribution.—QUEENSLAND: Mt. Glorious: 4:x:1952 (E. N. Marks, water-filled groove in log in rain forest). NEW SOUTH WALES: Cooranbong, 24:ix:1949 (B. McMillan, bred from tree hole); Mittagong, 27:ix:1936 (D. J. Lee, bred from rock pool).

CULICOIDES MAGNESIANUS, n. sp.

Types: Holotype ♀ and .15 ♀♀ paratypes, mounted on slides. Holotype and paratype series in SPHTM, paratypes in BM, USNM, QIMR, and CSIRO.

Type Locality.—Magnetic I., Queensland, 8:vii:1952 (E. J. Reye, 1700 hrs., net in mangrove).

Distinctive Characters.—The wing pattern of this large species is characteristic though very weak. It comprises many large pale areas separated by darker areas as shown in Plate xvi, fig. 9. Although the third segment of the palp is large and distally swollen, it is distinct from the shorter and broader segment of *C. palpalis* and the sensory organ is no more than one-third the width of the segment as compared with fully one-half in *C. palpalis*. From *C. molestus* and *C. subimmaculatus*, the other two species with Tarsus IV cordate, *C. magnesianus* is readily distinguished by its single palpal sensory organ, the other two having numerous small pits.

Description.—From the type series of slides, no pinned material available for coloration characters. Individual measurements are from a paratype, averages from a series of ten paratypes (Table I).

Female.

Head: Eyes narrowly separated (Text-fig. 9). Antennae with basal flagellar segments almost spherical, distal segments very elongate with very strong contrast between the two (Text-fig. 27). The mounted specimens appear to show that the pedicel and first flagellar segment and segments 10-15 are distinctly darker than the intermediate flagellar segments. The palp has a larger third segment, narrow at base and distally expanded with a single sensory pit, the diameter of which is about one-third that of the greatest width of the segment (Text-fig. 46).

Thorax: The femora and tibiae are dark brown, the tarsi lighter in colour. There is a distinct pale band basally on each tibia and Tarsus IV is strongly cordiform. Wings (see Plate xvi, fig. 9). The halteres are dark in colour.

Abdomen: There are two subequal spherical spermathecae, together with a small isolated duct which in some specimens exhibits a slight terminal expansion.

Male: This sex has not been taken.

Distribution.—Only known from the type locality.

GROUP II.

CULICOIDES ROBERTSI, n. sp.

Types: Holotype ♀ and 32 ♀♀ paratypes, allotype ♂ and five ♂♂ paratypes. Holotype, allotype and paratype series in SPHTM. Paratypes in BM, USNM, CSIRO and QIMR. All on slides.

Type Locality.—Yeerongpilly, Queensland, 15:iv:1952, R. F. Riek (in light trap). All ♂♂ same data except date which is April, 1952.

Distinctive Characters.—A small dark species with characteristic wing markings unlikely to be confused with any other known Australian species. This is also the only species in which the eye margins are fused below the frons.

Description.—From the type series except for coloration characters which are from pinned specimens taken with the ♂♂ of the type series. The holotype provided the individual measurements, a series of ten paratypes the average measurements. Measurements of the male sex are from the six male specimens in the type series (Table 1).

Female.

The head is almost black, with brown antennae. Scutum with simple pattern (Text-fig. 87) consisting of a median greyish longitudinal band about one-third the width of the scutum, flanked on either side by a dark brown longitudinal band and laterally to these a longitudinal brownish-grey area changing to dark brown at the lateral and anterior margins. At about two-thirds from the anterior margin, within the median grey band are two rounded black spots which in some specimens are also produced longitudinally as bands. The scutellum is dark brown, the pleura and coxae black. Legs brown, lighter distally. Wings with spotting of moderate strength anteriorly, weaker on posterior half of wing. Halteres light yellowish-brown. Abdomen black.

Head: Eyes contiguous (Text-fig. 10) and hence no inter-orbital hair. Antennae (Text-fig. 28) with basal flagellar segments a little longer than wide, subcylindrical, distal five normally elongate. Palpi (Text-fig. 47) with segments II-V not grossly varying in size, segment III very slightly swollen with single round sensory pit. Length of mouth-parts slightly less than height of head.

Thorax: Legs without any obvious modifications, tibial comb of hind leg of five equal spines. Wing pattern as in Plate xvi, fig. 13.

Abdomen: Spermathecae (Text-fig. 66) comprising two spherical normal organs with short chitinous ducts, one rudimentary spermatheca with very small knob and longer duct and an additional short chitinized duct.

Male.

Similar to female in essential characters. Genitalia: The ninth tergite lacks the usual horns at the distal corner and the harpes are very simple structures (Text-fig. 81).

Distribution.—QUEENSLAND: Eidsvold, 25:iv:1924 (Bancroft); Chinchilla, 13:xii:1949 (from horse); Texas, 24:iii:1952 (Reye, biting man); Yeerongpilly, 5:v:1938 (Roberts), 1:ii:1950 (Riek, in light trap), 3:i:1952 (Riek, in light trap), 15:iv:1952 (Riek, in light trap). NEW SOUTH WALES: Ballina, 2:ii:1952 (Reye, biting man and in rabbit-baited trap in mangrove zone); Clarence R., i:1950 (from horse).

CULICOIDES ANTENNALIS, n. sp.

Types: Holotype ♀ and 20 ♀♀ paratypes, all on slides. Holotype and paratype series in SPHTM, paratypes in BM, USNM, QIMR and CSIRO.

Type Locality.—Hornsby, New South Wales, 6:x:1951 (D. J. Lee) for holotypes, same data but different dates (27:ix:1951, 4:x:1951 and 6:x:1951) for paratypes.

Distinctive Characters.—A large species, only likely to be confused with *C. bancrofti*. The distribution of wing spots is rather similar in the two, but the spot over r-m is often smaller in *C. antennalis*. The antennae with unusually long vasiform basal flagellar segments are similar in both species, but the sensory organs of the third segment of the palp are quite distinct. A single pit of moderate size is present in

C. antennalis, whereas there is a multiplicity of small pits over this segment in *C. bancrofti*.

Description.—Based on the type series and pinned specimens from Hornsby, 29:x:1951 (B. McMillan). Measurements are from the holotype and a series of ten paratypes (Table 1).

Female.

A large very dark species. The head, including antennae and palpi, is almost black. The scutum is very dark brown with a limited lighter pattern in the prescutellar area only. Scutellum and sides of thorax very dark brown. The legs, including the tarsi, are dark brown, but Tarsus I is a little paler at the base. The wings are rather dark with definite but not outstanding pattern of yellowish spots and the halteres have brown stems with the knobs whitish or creamy except near the junction with the stem where they are dark. The abdomen is very dark brown.

Head: Eyes moderately separated (Text-fig. 11), mouth-parts at least equal in length to height of head. Basal flagellar segments of antennae elongate and vasiform in shape, distal segments more elongated, contrast between the two not great but antennae obviously long (Text-fig. 29). Third segment of palp long with single sensory pit of unusual shape (Text-fig. 48).

Thorax: Legs unmodified, Tarsus IV cylindrical, tibial comb of four spines. Wings (Plate xvi, fig. 14) with moderately dense macrotrichia over most of surface. The pale spot over r-m is variable in size.

Abdomen: Two almost equal spherical spermathecae, each with a short chitinized duct (Text-fig. 67).

Male: No specimens of this sex have been taken.

Distribution.—NEW SOUTH WALES: Palm Beach, 2:iii:1946 (D. J. Lee); Hornsby, 29:x:1950 (D. J. Lee, 5 p.m.), (B. McMillan), xi:1950 (D. J. Lee, light trap), 2:xi:1950 (D. J. Lee, biting on ridge, 5.45–6.15 p.m.), 27:ix:1951 (D. J. Lee, light trap), 4:x:1951 (D. J. Lee, light trap), 6:x:1951 (D. J. Lee, light trap), 9:x:1951 (D. J. Lee); Heathcote, 5:viii:1946 (J. Henry, caught on rise and biting in gorge).

CULICOIDES BANCROFTI, n. sp.

Types: Holotype ♀ and one ♀ paratype, mounted on slides, and four pinned ♀♀ paratypes, all in SPHTM.

Type Locality.—Hornsby, New South Wales, 29:x:1950 for holotype, 2:xi:1950 for all paratypes (D. J. Lee, in gully and on ridge, some biting).

Distinctive Characters.—Only to be confused with *C. antennalis* under which species the distinctive features are discussed.

Description.—From the type series. Measurements are of the holotype and of a series of three specimens, one a paratype, another from Hornsby and a third from north of Coff's Harbour (Table 1).

Female.

A large very dark species with brownish wings. The head is black with very dark brown antennae and palpi. Thorax very dark brown, almost black, with greyish pattern on scutum restricted to posterior half (see Text-fig. 88). The legs including the tarsi are very dark, with a pre-apical paler brown band on all femora and a lighter band at the base of each tibia. Wings with membrane brownish, this coloration being particularly noticeable along the anterior third; the pale spots rather yellowish in colour. Halteres yellowish, abdomen dull black.

Head: Eyes narrowly separated (Text-fig. 12). Antennae with basal flagellar segments elongate and vasiform, distal segments a little more elongate and cylindrical, total length of antennae obviously long (Text-fig. 30). Third segment of palpi very much lengthened but not expanded, many small sensory pits present, diffusely arranged over most of the segment, a few also present on the second segment (Text-fig. 49).

Thorax: Legs unmodified, Tarsus IV cylindrical, wings with moderately dense macrotrichia over most of membrane, pattern as in Plate xvi, fig. 16.

Abdomen: Two almost equal spherical spermathecae each with short duct (Text-fig. 68).

Male: This sex is unknown.

Distribution.—QUEENSLAND: Jimna, 9:x:1948 (J. L. Wassell, 7 p.m., at light). NEW SOUTH WALES: North of Coff's Harbour, 27:ix:1950 (M. J. Mackerras, biting midday, raining, in forest); Hornsby Gully, 29:x:1950 (D. J. Lee, 1700 hrs.), (B. McMillan), 2:xi:1950 (D. J. Lee, biting, on ridge, 5.45-6.15 p.m.); Fitzroy Falls, 22-27:xi:1937 (A. L. Tonnoir).

CULICOIDES MAGNIMACULATUS, n. sp.

Types: Holotype ♀ and 12 ♀♀ paratypes mounted on slides. Holotype and paratype series in SPHTM, paratypes in BM, USNM, QIMR and CSIRO.

Type Locality.—All of type series from Cooranbong, New South Wales, 24:ix:1949 (B. McMillan).

Distinctive Characters.—A species with a very obvious pattern of large pale spots, with only one such spot in each of the intercalary fork and cell M, and a particularly extensive pale area over the basal portion of the wing. The extent of the pale areas is somewhat similar to that found in *C. magnesianus*, but the degree of contrast is markedly stronger and much of the second radial cell is pale instead of entirely dark as in *C. magnesianus*.

Description.—From the type series, additional characters of coloration from pinned specimens from Woy Woy, 22:ix:1923 (Mackerras). Measurements are from the holotype and a series of ten paratypes (Table 1).

Female.

Head, antennae and palpi dark brown. Scutum dark brown along the anterior margin to just beyond humeral pits, elsewhere with a greyish or yellowish brown pattern, the most prominent feature of which is a broad median longitudinal greyish band. Scutellum dark brown at the centre, greyish-brown at the sides. Legs brown with lighter bands just before apices of the femora and at bases of the tibiae. Wing pattern of strong contrast. Halteres creamy, abdomen dark brown.

Head: Eyes moderately separated (Text-fig. 13). Antennae with basal flagellar segments approximately twice as long as broad, widest near base and tapering slightly distally, distal segments normally elongate, the contrast between the two not particularly marked (Text-fig. 31). The third segment of the palpi slightly swollen, with a single irregularly oval sensory pit (Text-fig. 50). Mouthparts not quite as long as height of head.

Thorax: Legs unmodified, tibial comb of four spines. Wings with moderately dense macrotrichiae, pattern as in Plate xvi, fig. 15.

Abdomen: Two subequal subspherical spermathecae, each with a short chitinized duct together with a third longer chitinized duct (Text-fig. 69).

Male.

A specimen from Oatley Park, 27:ix:1952 (E. J. Reye) has been used for the illustration of the harpes (Text-fig. 82).

Distribution.—QUEENSLAND: COOFOY, 2:v:1949 (M. J. Mackerras, biting); Mountain Cr., Buderim Mt., 24:viii:1947 (J. L. Wassell, biting, 1600 hrs.); Burpengary (E. J. Reye); Maroon, 18:ix:1948 (E. N. Marks, biting in forest country about 4 p.m.); Deception Bay, 7:viii:1951 (E. J. Reye, emergence trap on dam); Brisbane, 20:xi:1949 (from horse); Yeerongpilly, 9:viii:1951 (E. J. Reye, light trap); Dunwich (M. J. Mackerras, biting); Tambourine, 17:xi:1949; Mudgeraba Cr., 26:viii:1950 (M.J.M.); Lamington National Park, 24:ix:1950 (M. Crust). NEW SOUTH WALES: Noonameene, via Bingara, 20-24:x:1952 (A. L. Dyce, dusk to 10.30 p.m.); N. of Coff's Harbour, 27:ix:1950 (M. J. Mackerras, biting midday); Nyngan, viii:1948 (J. Armstrong,

biting); Molong Cr., Mt. Canoblas, 8:x:1950 (M. J. Mackerras); Ben Buckley, via Mudgee, 16:v:1952 (B. V. Fennessy, on human); Gummi Plain, 3:iii:1951 (B. McMillan, aspirated 5 p.m., 3800'); Barrington, Rocky Crossing, 6:iii:1951 (B. McMillan); Nelson's Bay, 14:viii:1949 (B. McMillan), 4:vi:1950 (B. McMillan, 500'); Anna Bay, 21:viii:1949 (B. McMillan, biting); Cooranbong, 28:v:1949 (B. McMillan), 4:vii:1949 (B. McMillan, 1400'); 24:ix:1949 (B. McMillan), 1:vi:1951 (B. McMillan); Woy Woy, 22:ix:1923 (Mackerras); Camp, Lett R., Hartley, 13:x:1950 (M. J. Mackerras, biting); Mt. Solitary, 23:ix:1951 (B. McMillan, some biting 9 a.m.); Blue Gum Forest, Blue Mts., 1:iv:1950 (B. McMillan, biting); Springwood, 16:iv:1950 (B. McMillan, biting); Woodford, x:1950 (K. J. Clinton); Little Mackeral Beach, Pittwater, 9:ix:1951 (B. McMillan, biting); Hornsby Gully, 28:x:1950 (D. J. Lee, 5.30-6 p.m.); Hornsby, 14:v:1949 (B. McMillan), 9:x:1950 (D. J. Lee), xi:1950 (D. J. Lee, light trap), 6:xii:1950 (D. J. Lee, light trap), 15:xii:1950 (D. J. Lee, light trap), 16:xii:1950 (D. J. Lee, light trap), 22:ix:1951 (D. J. Lee, some biting), 27:ix:1951 (D. J. Lee), 1:x:1951 (D. J. Lee), 4:x:1951 (D. J. Lee), 10:x:1951 (D. J. Lee); McCarr's Cr., 29:iv:1949 (D. J. Lee, sea level, mangroves); Narrabeen, 29:ix:1948 (B. McMillan); Oatley Bay, 27:ix:1952 (E. J. Reye, net); Sutherland, 17:viii:1920 (Mackerras); Burraneer Bay, 25:xi:1950 (Kinsela); National Park, 1:i:1926 (Mackerras), 12:xi:1949 (B. McMillan); Uloola Falls, National Park, 23:x:1949 (B. McMillan); Woronora Gorge, 11:x:1952 (E. J. Reye, net, 1200-1600 hrs.); Heathcote, 12:v:1946 (J. R. Henry), 5:viii:1946 (J. R. Henry, caught on rise and biting in gorge), 5:iv:1947 (J. R. Henry), 3:iv:1949 (J. R. Henry), 21:ix:1949 (J. R. Henry); Leumeah, 20:x:1951 (B. McMillan); Mittagang, 17:x:1945 (D. J. Lee); Upper Shoalhaven R., 30:iv:1950 (B. McMillan, biting); Milton, 20:x:1947 (biting man); Merimbula, 17:xi:1948 (E. Pratt); Parklea (N.S.W. Dept. Agric.). VICTORIA: Mt. Cobberas, 1:i:1952 (K. Harper, biting). SOUTH AUSTRALIA: Winkie, near Berri, x:1947 (H. J. Davis, biting man). TASMANIA: Strahan, 6:ii:1923 (A. Tonnoir); Queenstown (F. Worsnop).

CULICOIDES CUNICULUS, n. sp.

Types: Holotype ♀ and 4 ♀♀ paratypes, all slide specimens, in SPHTM.

Type Locality.—Noondoo, Queensland, 30:iii:1952 (E. J. Reye, in rabbit burrow, 1400 hrs). (All specimens.)

Distinctive Characters.—This is not a striking species, but the inclusion of the distal portion of the second radial cell within a pale area will distinguish it from *C. ornatus*, to which species there is most superficial resemblance. A distinctive character is the presence of two pale areas in the intercalary fork associated with short antennae with no marked contrast between the basal and distal flagellar segments and palpi with a large, very irregularly shaped sensory pit.

Description.—From the type series only, no unmounted material available for details of coloration. Measurements are from the holotype and the series of four paratypes (Table 1).

Female.

Head: Eyes widely separated (Text-fig. 14). Antennae (Text-fig. 32) with basal flagellar segments subcylindrical, slightly wider near base, distal segments elongate but no marked contrast between the two. Third segment of palpi with greatest expansion at middle and a large irregularly-shaped sensory pit (Text-fig. 51). Mouth-parts rather less in length than height of head.

Thorax: Legs unmodified, Tarsus IV cylindrical, pale markings just before end of femora on first and second pairs of legs and basally on all tibiae. Tibial comb usually of five, occasionally of six spines. Wings with pattern of only moderate contrast, macrotrichia rather sparse. (See Plate xvi, fig. 17.) Halteres pale.

Abdomen: Two subequal ovoid spermathecae each with a short chitinized duct together with a third chitinized duct (Text-fig. 70).

Male: This sex is not yet known.

Distribution.—Queensland: Only known from the type locality.

CULICOIDES DYCEI, n. sp.

Types: Holotype ♀, allotype ♀♀ and 3 ♂♂ paratypes, all slide specimens. Holotype, allotype and paratype series in SPHTM, paratypes in BM, USNM, QIMR and CSIRO.

Type Locality.—Entire type series from Moree, New South Wales (A. L. Dyce).

Distinctive Characters.—*C. dycei* and *C. mcmillani* both have three distinct spots in the intercalary fork associated with a single pale spot in cell M₁. The most obvious differences between the two are the short, rather wide third palpal segments of *C. dycei* as compared with the elongated third palpal segment of *C. mcmillani* and the short antennae of the former in marked contrast to the elongated antennae of the latter.

Description.—From the type series and for coloration characters pinned specimens from Bundy, via Moree, v:1952 (E. J. Reye). Measurements have been taken from the holotype, a series of ten paratypes and for the male sex a series of six specimens comprising allotype, three paratypes and two specimens from Texas, 20:i:1952 (Table 1).

Female.

A small brownish species with distinctly mottled wings. Head, antenna and palpi dark brown. Thorax dark brown, scutum with distinct pattern of grey spots (Text-fig. 89). Scutellum dark brown. Legs brown with preapical pale spots on all femora and basal pale spots on all tibiae. Halteres pale yellowish. Abdomen dark brown.

Head.—Eyes moderately separated (Text-fig. 15). Antennae (Text-fig. 33) with basal flagellar segments cylindrical, distal segments a little more elongate with no striking differentiation between the two. Third segment of the palpi short but expanded, a single large sensory pit (Text-fig. 52). Mouthparts not as long as height of head.

Thorax: Legs unmodified, Tarsus IV subcylindrical, tibial comb of four spines. Wings with rather sparse macrotrichia, pattern as in Plate xvi, fig. 18.

Abdomen: There are no chitinized spermathecae.

Male: Similar, apart from sexual differences, to the female; harpes as in Text-figure 83.

Distribution.—QUEENSLAND: Gootchie, 20:vii:1952 (E. J. Reye, 1600 hrs., net); Texas, 20:i:1952 (A. L. Dyce), 22:ii:1951 (E. J. Reye, light trap 1930–0545 hrs.). NEW SOUTH WALES: Gravesend, 12:vi:1952 (E. J. Reye, net, 1630 hrs.); Yagobie, 12:vi:1952 (E. J. Reye, net, 0815 hrs.), 3:xii:1951 (A. L. Dyce, light trap); Moree (A. L. Dyce), 22:xi:1951 (A. L. Dyce, mercury vapour light trap, 8.30–10 p.m.), 25:xi:1951 (A. L. Dyce, M.V. trap, 6.30–8.30 p.m.); Bundy, x:1951 (A. L. Dyce, light trap), 7:xi:1951 (A. L. Dyce, rabbit modified trap 9.30–11.30 a.m.), 6:xii:1951 (A. L. Dyce, M.V. trap, 6–9 p.m.), 6–7:xii:1951 (A. L. Dyce, 5 p.m. to 10 a.m., live rabbit trap, suction), iv:1952 (E. J. Reye, net), 24:v:1952 (E. J. Reye, light trap, 2345 hrs.), 10:vi:1952 (E. J. Reye, net, 1600 hrs.).

CULICOIDES MULTIMACULATUS Taylor.

Taylor, F. H., 1918. *Aust. Zoologist*, 1: 169.

Macfie, J. W. S., 1939. *Proc. Linn. Soc. N.S.W.*, 64: 556.

Type: Holotype ♀ in SPHTM (on three slides).

Type Locality.—Portsea, Victoria.

Distinctive Characters.—The type of this species remains unique. It is a large species with a strongly patterned wing. The three pale spots in the intercalary fork together with a single spot in cell M₁ may cause confusion of this species with either *C. dycei* or *C. mcmillani*. The former is a considerably smaller species and there is only a single sensory pit on the third segment of the palp as compared with three irregular pits in *C. multimaculatus*; *C. mcmillani* is about as large as *C. multimaculatus*, but again there is only a single sensory pit on the third palpal segment. In *C. mcmillani* the latter segment is elongate and only slightly expanded at about two-thirds from the base, whereas in *C. multimaculatus* it is decidedly swollen with maximum breadth at about the middle.

Certain details are added to the previous descriptions, comprising a figure of the palp (Text-fig. 53) and a figure of segment 10 and 11 of the antennae (Text-fig. 34) to show the contrast between the basal and first distal flagellar segments. The wing pattern is reproduced in Plate xvi, fig. 19. Certain measurements from the holotype are given in Table 1.

Distribution.—The species is still only known from the type locality.

CULICOIDES MCMILLANI, n. sp.

Type: Holotype ♀ on slide in SPHTM.

Type Locality.—Bull's Swamp, Barrington Tops, New South Wales (B. McMillan, flying, 6 p.m., 4800 feet).

Distinctive Characters.—See under *C. dycei*.

Description.—From holotype and specimens listed below. No unmounted material available. Measurements are from the holotype and a series of three other specimens from Hartley, Woodford and Hornsby (Table 1).

Female.

Head: Eyes distinctly separated (Text-fig. 16), antennae with basal flagellar segments subcylindrical, distal ones elongate giving a definite but not exaggerated contrast (Text-fig. 35). The third segment of the palp is distinctly lengthened, slightly expanded, at about three-quarters from the base with a single large oval sensory pit (Text-fig. 54).

Thorax: The legs are unmodified, with Tarsus IV subcylindrical. There is a pale preapical band on the fore and mid femora and on all legs a pale band near the base of the tibia. Tibial comb of four spines. Wings with moderate macrotrichia, pattern as in Plate xvi, fig. 20. The halteres appear brownish on the basal half, lighter above.

Abdomen: Two subequal ovate spermathecae, each with a short duct together with two additional separate short chitinated ducts (Text-fig. 71, specimen from Woodford).

Male: This sex has not been taken.

Distribution.—NEW SOUTH WALES: Bull's Swamp, Barrington Tops, 4800 feet (B. McMillan, flying, 6 p.m.); Nelson's Bay (B. McMillan); Camp, Lett R., Hartley, 13:x:1950 (M. J. Mackerras, biting at dusk); Woodford, x:1950 (K. J. Clinton); Hornsby, 1:x:1951 (D. J. Lee).

CULICOIDES PARVIMACULATUS, n. sp.

Types: Holotype ♀ and 14 ♀♀ paratypes. Holotype and paratype series in SPHTM, paratypes in BM, USNM, QIMR and CSIRO.

Type Locality.—Leumeah, New South Wales, 20:x:1951 (B. McMillan).

Distinctive Characters.—This species is particularly distinctive because of the smallness of the individual pale spots of the wing. The arrangement is much the same as that in *C. marksi*, there being three spots in the intercalary fork associated with two in cell M_4 , but all spots in *C. parvimaculatus* are small whereas all are large in *C. marksi*. There is also a considerable difference in form of the spermathecae of the two species.

Description.—From the type series, coloration characters from pinned material from Eidsvold, Queensland, 24:iv:1924 (Bancroft). Measurements are from the holotype and a series of ten paratypes (Table 1).

Female.

A small species, the head dark brown with narrow longitudinal greyish band on the vertex, pedicels of antennae dark brown, rest of antennae and palpi brown. Thorax dark brown, scutum with a distinct pattern of greyish spots (Text-fig. 90). Scutellum dark brown. Legs brown with a paler preapical band on the fore and mid femora and a similar basal pale band on all tibiae. Wings with strongly contrasting pattern, halteres light brown. Abdomen lighter brown than the thorax.

Head: Eyes rather narrowly separated (Text-fig. 17). Antennae with basal flagellar segments subcylindrical, distal segments elongate, the contrast between the two not

marked (Text-fig. 36). Palpi with a short expanded third segment, the greatest width being a little beyond the middle and with a single large sensory pit (Text-fig. 55). The mouth-parts rather less in length than height of head.

Thorax: Legs unmodified, Tarsus IV subcylindrical, tibial comb of four spines. Wings with moderate development of macrotrichia, pattern as in Plate xvi, fig. 22.

Abdomen: Three mushroom-like spermathecae, each with a duct approximately equal to height of knob, together with a fourth short isolated duct. Body of spermathecae variable in form, sometimes rounded, sometimes tapering to a blunt point.

Male.

A specimen from Hornsby, 11:i:1950 (D. J. Lee) has been used to provide a figure of the harpes (Text-fig. 84).

Distribution.—QUEENSLAND: Eidsvold, 24:iv:1924 (Bancroft); Tin Can Bay Rd., 17:iv:1949 (M. J. Mackerras, biting in tent). NEW SOUTH WALES: Springwood, 16:iv:1950 (B. McMillan); Hornsby, 14:v:1949, 11:xi:1950 (D. J. Lee, light trap), 4:x:1951 (D. J. Lee); Sutherland, 7:viii:1926 (I. M. Mackerras); Heathcote, 12:v:1946 (J. R. Henry), 21:ix:1949 (J. R. Henry); Leumeah, 20:x:1951 (B. McMillan).

CULICOIDES MARKSI, n. sp.

Types: Holotype ♀, allotype ♂, 12 ♀♀ and two ♂♂ paratypes. Holotype, allotype and paratype series in SPHTM, paratypes in BM, USNM, CSIRO and QIMR.

Type Locality.—All of type series from Yagobie, New South Wales, 3:xii:1951 (A. L. Dyce, light trap).

Distinctive Characters.—See *C. parvimaclatus*. *C. marksi* is another species with characteristic spermathecae. Three are developed, but only the distal half to two-thirds of each subequal sphere is chitinized.

Description.—From the type series, coloration characters from pinned specimen from Bundy, via Moree, v:1952 (E. J. Reye). Measurements are from the holotype, a series of ten paratypes and, for the male sex, the three specimens in the type series (Table 1).

Female.

A medium-sized dark species with head including palpi and pedicels of antennae dark brown, flagellum brown. Thorax dark brown, scutum with extensive greyish pattern (Text-fig. 91) and scutellum brown with lateral greyish patches. Legs brown with distinct preapical pale bands on all femora and basal pale bands on all tibiae. Wing pattern of strong contrast, halteres brown basally becoming whitish apically; abdomen dark brown.

Head: Eyes widely separated (Text-fig. 18). Antennae with basal flagellar segments subcylindrical, distal segments elongate, contrast not pronounced (Text-fig. 37). Third segment of palp expanded about two-thirds from base with a large single sensory pit (Text-fig. 56).

Thorax: Legs unmodified, Tarsus IV rather bell-shaped; tibial comb of four spines. Wings with macrotrichia only moderately developed, pattern as in Plate xvi, fig. 21.

Abdomen: The spermathecae comprise three subequal incomplete spheres (Text-fig. 73).

Male: The male harpes are figured in Text-fig. 85.

Distribution.—QUEENSLAND: Townsville, 12:vii:1952 (E. J. Reye, 1700 hrs., net); St. Lawrence, 16:vii:1952 (E. J. Reye, 1715 hrs., net); Roma, 11:v:1948 (J. L. Wassell, light trap, 9–10 p.m.); Dayboro, 7:viii:1951 (E. J. Reye, cultured from pond margin); Longreach (R. F. Riek); Yelarbon, 20:i:1944 (E. N. Marks); Texas, 22:xii:1951 (A. L. Dyce, light trap), 20:i:1952 (A. L. Dyce, light trap). NEW SOUTH WALES: Yagobie, 3:xii:1951 (A. L. Dyce, light trap); Moree, 30:x:1951 (A. L. Dyce), 22:xi:1951 (A. L. Dyce, mercury vapour light trap, 8.30–10 p.m.), 23:xi:1951 (A. L. Dyce, light trap), 25:xi:1951 (A. L. Dyce, M.V. trap, 6.30–8.30 p.m.), 4:v:1952 (A. L. Dyce, biting); Bundy, v:1952 (E. J. Reye), 24:v:1952 (E. J. Reye, 2300 hrs., light trap); 6:xii:1951

(A. L. Dyce, trap, 6-9 p.m.); Merrylands, ii:1952 (E. J. Reye, 1830 hrs.). VICTORIA: Murrayville, 20:ii:1952 (on human).

DOUBTFUL SPECIES.

There is only one previously described species which has not been recognized in any of the material seen by us. This is *C. brevitarsis* Kieffer, the description of which does not fit any of the species dealt with above and it seems that its identity must remain in doubt until such time as the type is re-examined.

We have not included this species in the key, and it may also be noted that the character from which it derives its specific name is common to most Australian species. However, in case anything resembling this species is taken a translation of the original description is included.

CULICOIDES BREVITARSIS Kieffer.

Kieffer, J. J., 1917. *Ann. Nat. Mus. Hung.*, 15: 187.

Type: Presumably in National Museum of Hungary, Budapest.

Type Locality.—Cited as Australia, no specific locality being mentioned.

Distinctive Characters.—It should be easy to recognize this species from the wing pattern which consists of no more than a smoky patch over the radial cells and a pale area over r-m which extends to the costa. Also we are not aware of any other Australasian species in which the M_{3+4} -Cu₁ fork is immediately below the distal extremity of R_{4+5} .

Translation of Original Description.

"♀. Reddish-brown, eyes glabrous, mouth-parts as long as the height of the head. Fifth segment of the palpi a little longer than the penultimate. Antennal segments 4-10 half as long again as wide, slightly thinner at the distal extremity, segments 11-15 elongated, 11-14 slightly thinner in their distal half, 11 almost half as long again as 10, scarcely shorter than 12, 13 a little longer than 12, a little shorter than 14, 15 the longest, obtuse distally, without stylet. Halteres yellowish. Wings hyaline, with a smoky patch on the two radial cells, surface with microscopic hairs resembling a fine dotting, distal extremity with some longer and sparse hairs, at the junction of R_{4+5} and r-m is found a transverse marginal space deprived of microscopic hairs and appearing whitish; R_{4+5} reaching the middle of the wing, at least half as long again as R₁, first radial cell a little longer than the second, both of them very narrow, r-m very long and oblique, as usual the bifurcation of M a little distal to r-m, that of the base of Cu₁ on M_{3+4} is situated under the termination of R_{4+5} , Cu₁ very oblique. Legs pale yellow, slender, without long hairs, first tarsal segments of the four anterior legs as long as the four following segments together, first tarsal segments of the two posterior legs shorter and thicker, scarcely as long as the two following segments together, fourth segment distinctly shorter than the fifth, empodium absent. Length 1 mm."

Distribution.—This species has not since been recovered.

BIOLOGY.

A great deal of observation is still required to give even reasonable information on the breeding habits, life histories and general adult habits of the various species of *Culicoides*.

What little is known is in part revealed in the distribution lists for individual species, particularly such information as concerns observed blood-sucking habits.

Those deserving of consideration as pest species are *C. subimmaculatus*, *C. ornatus*, *C. molestus*, *C. marmoratus* and *C. magnimaculatus*. The first two are the commonest plague species of coastal areas where they occur. *C. molestus* has usually been considered the dominant pest species but, although it is frequently taken biting man, it often plays only a minor role in outbreaks of intense sandfly activity. On the other hand when sandfly activity is not particularly noticeable, as in the harbourside suburbs of Sydney, *C. molestus* is the usual species taken. *C. marmoratus* is again a pest, especially of coastal areas, but it is not so closely restricted to the vicinity of mangrove

areas as are *C. ornatus* and *C. subimmaculatus*. *C. magnimaculatus* is a widespread species often taken in considerable numbers attacking man and, although most commonly taken along the coastal gullies, is by no means restricted to such areas.

Other species which are known to bite man are *C. immaculatus*, *C. robertsi*, *C. antennalis*, *C. bancrofti*, *C. mcmillani*, *C. parvimaculatus* and *C. marksii*, but so far no instances are known of these species qualifying as dominant biting species. *C. robertsi*, however, is well known as a night-biting species attacking horses.

Breeding habitats are known for some seven species. *C. subimmaculatus* breeds in the low-lying estuarine zone covered by spring tides in the area between mangroves and actual dry land, often delimited by the presence of *Salicornia* (see Lee, 1949). *C. marmoratus* has been found breeding in the same type of area but other evidence would suggest that it is not necessarily limited to such areas. *C. angularis* has been found breeding in small rockholes in sandstone gullies and also in treeholes. *C. rabauli* (specimens from Heron I.) has also been bred from treeholes. *C. magnimaculatus*, *C. marksii* and *C. palpalis* have been bred from soil taken from the margins of ponds.

References.

Systematic references are quoted in full in the text, other references as in Part I of this series (these PROCEEDINGS, 1948, Vol. 72 (for 1947), pp. 330-331) with the following additions:

LEE, D. J., 1949.—Sandfly Breeding Places. *Aust. J. Sci.*, 12: 74-75.

WIRTH, W. W., 1952.—The Heleidae of California. *Univ. Calif. Pub. in Entom.*, Vol. 9, No. 2: 95-266.

EXPLANATION OF PLATE XVI.

Wing photographs. (× 30.)

1, *C. immaculatus*; 2 and 3, the different types of spotting seen in *C. palpalis*; 4, *C. subimmaculatus*; 5, *C. ornatus*; 6, *C. molestus*; 7 and 8, two types of wing spotting seen in *C. marmoratus*; 9, *C. magnesianus*; 10, *C. rabauli*; 11, *C. angularis*; 12, *C. mackayensis*; 13, *C. robertsi*; 14, *C. antennalis*; 15, *C. magnimaculatus*; 16, *C. bancrofti*; 17, *C. cuniculus*; 18, *C. dycei*; 19, *C. multimaculatus*; 20, *C. mcmillani*; 21, *C. marksii*; 22, *C. parvimaculatus*.

BACTERIOLOGY ACCOUNT.
BALANCE SHEET at 29th February, 1952.

LIABILITIES.		ASSETS.	
£	s. d.	£	s. d.
Accumulated Funds.		Fixed Assets.	
Amount bequeathed by Sir William		Commonwealth Loans, at cost	15,320 0 0
Macleay	12,000 0 0	Debentures:	
Accumulated Income Capitalized	6,120 0 0	Metropolitan Water, Sewerage and	
		Drainage Board, at cost	800 0 0
Income Account at 29th February, 1952	993 2 6	Freehold Property, at cost	16,120 0 0
Commercial Banking Company of		Current Assets.	
Sydney, Ltd.	857 9 8	Commonwealth Savings Bank	3,850 0 0
Current Liabilities.			12 2
	1,850 12 2		
	£19,970 12 2		£19,970 12 2

INCOME ACCOUNT. Year Ended 29th February, 1952.

	£	s. d.	£	s. d.
To Salary	975	0 0	By Balance from 1950-51	1,171 12 6
" Equipment and Repairs	156	11 10	" Interest	543 1 7
" Insurance	16	11	" Donations	450 0 0
" Loss on sale of bonds	80	16 3	" Rent	151 13 4
" Ramsgate Property:				
Stamp Duty	39	0 0		
Legal Expenses	46	14 11		
Insurance	5	13 6		
Rates	5	3 4		
Repairs	13	8 2		
" Balance to 1952-53	109	19 11		
	993	2 6		
	£2,316	7 5		£2,316 7 5

AUDITOR'S REPORT TO MEMBERS.

I have examined the books of account and vouchers of the Linnean Society of New South Wales for the year ended 29th February, 1952, and certify that the above Balance Sheet and accompanying Income Account are correct and in accordance therewith, and in my opinion present the true state of the Society's affairs at 29th February, 1952, as shown by the books. Certificates of the investments have been inspected.

S. J. RAYMENT, Chartered Accountant (Aust.),
Auditor.
3rd March, 1952.

A. B. WALKOM,
Hon. Treasurer.

ABSTRACT OF PROCEEDINGS

ORDINARY MONTHLY MEETING.

26th MARCH, 1952.

Mr. S. J. Copland, President, in the Chair.

Library accessions amounting to 51 volumes, 375 parts or numbers, 10 bulletins, 6 reports and 12 pamphlets, total 454, had been received since the last meeting.

PAPERS READ (by title only).

1. A Check List of the Trombiculid Larvae of Asia and Australasia. By Carl E. M. Gunther.
2. Ecological Classification and Nomenclature. By N. C. W. Beadle and A. B. Costin. With a Note on Pasture Classification, by C. W. E. Moore.

ORDINARY MONTHLY MEETING.

30th APRIL, 1952.

Mr. S. J. Copland, President, occupied the Chair.

The President announced that the Council had elected the following Office-bearers for the 1952-53 session: Vice-Presidents: Dr. Lilian Fraser, Dr. A. R. Woodhill, Mr. D. J. Lee and Mr. A. N. Colefax; Honorary Treasurer: Dr. A. B. Walkom; Honorary Editor: Dr. A. B. Walkom; Honorary Secretary: Dr. W. R. Browne.

The following were elected Ordinary Members of the Society: Professor Charles Baehni, Dr.sc., Geneva, Switzerland; Mr. Alan L. Dyce, B.Sc.Agr., Canberra, A.C.T.; Mr. John M. Monro, Armidale, N.S.W.; Rev. Robert G. Palmer, Glen Davis, N.S.W.; Mr. Milton J. Slade, Cessnock, N.S.W.; and Mr. Owen B. Williams, B.Agr.Sc., Deniliquin, N.S.W.

Library accessions amounting to 10 volumes, 78 parts or numbers, 7 bulletins, 4 reports and 8 pamphlets, total 107, had been received since the last meeting.

The papers taken as read at the March Ordinary Monthly Meeting were discussed.

PAPERS READ.

1. Studies of Nitrogen-fixing Bacteria. I. A Note on the Estimation of *Azotobacter* in the Soil. By Y. T. Tchan, Macleay Bacteriologist.
2. Studies of Nitrogen-fixing Bacteria. II. The Presence of Aerobic Non-symbiotic Nitrogen-fixing Bacteria in Soils of the Sydney District. By Y. T. Tchan, Macleay Bacteriologist.
3. A Note on the Stratigraphy and Structure of the Wellington-Molong-Orange-Canowindra Region. By Germaine Joplin and others.

NOTES AND EXHIBITS.

Dr. Y. T. Tchan exhibited and demonstrated an arrangement by which the Siedentopf Phoku attachment for photomicrographic work could be adapted for taking 35 mm. black and white or colour film.

Dr. N. C. W. Beadle showed a series of kodasides to compare and contrast certain features of the Northern American and Australian vegetation, and some slides showing the features of the laterite profile and its use as a building material in Ceylon.

ORDINARY MONTHLY MEETING.

28th MAY, 1952.

Mr. S. J. Copland, President, occupied the Chair.

Mr. D. H. Ashton, B.Sc., Surrey Hills, Victoria, was elected an Ordinary Member of the Society.

The President offered congratulations to Miss Helen Lancaster on obtaining her M.Sc. degree of the University of Sydney.

Library accessions amounting to 20 volumes, 117 parts or numbers, 21 bulletins, 1 report and 2 pamphlets, total 161, had been received since the last meeting.

PAPERS READ.

1. Ordovician Stratigraphy at Cliefden Caves, near Mandurama, N.S.W. By N. C. Stevens.

2. Taxonomic Notes on the Genus *Ablepharus* (Sauria: Scincidae). III. A New Species from North-west Australia. By Stephen J. Copland.

3. Notes on Australasian Simuliidae (Diptera). III. By I. M. Mackerras and M. J. Mackerras.

NOTES AND EXHIBITS.

Dr. A. R. Woodhill exhibited a specimen of *Megarhinus speciosus*, one of the largest known mosquitoes, which is mainly tropical and sub-tropical but occurs in small numbers as far south as Sydney. The larvae are predaceous on other mosquito larvae but the adults are not blood-feeders.

Mr. S. J. Copland exhibited a specimen of the rare Scincid lizard, *Lygosoma truncatum*. It was one of three found in the Macpherson Ranges. Only two individuals were previously known—both from islands in Moreton Bay. This is the first mainland record.

A lecturette was given by Mr. D. P. Clark, entitled "Ecological Study of the Microfauna of the Soil".

ORDINARY MONTHLY MEETING.

25th JUNE, 1952.

Mr. S. J. Copland, President, occupied the Chair.

Miss Julia M. Langley, B.Sc., Gordon; Mr. B. D. H. Latter, B.Sc.Agr., Coogee; and Mr. D. F. McMichael, B.Sc., Australian Museum, Sydney, were elected Ordinary Members of the Society.

The President offered congratulations to Professor N. A. Burges, who has accepted an invitation to the Chair of Botany in the University of Liverpool; and to Dr. Daphne Elliot (*née* Davison) and Dr. Ian Fraser, on obtaining the degree of Ph.D., of the University of Cambridge.

The President announced that a Special General Meeting will be held at 7.15 p.m. on Wednesday, 30th July, 1952, to consider an alteration of the Rules of the Society recommended by Council.

Library accessions amounting to 10 volumes, 91 parts or numbers, 3 bulletins and 6 pamphlets, total 110, had been received since the last meeting.

PAPERS READ.

1. The Petrology of the Cowra Intrusion and Associated Xenoliths. By N. C. Stevens.

2. A Mainland Race of the Scincid Lizard, *Lygosoma truncatum* (Peters). By Stephen J. Copland.

Lecturettes on Mitochondria; Cytology and Function in Plants and Bacteria were given by Miss M. Hindmarsh, Dr. R. N. Robertson and Dr. Y. T. Tchan.

SPECIAL GENERAL MEETING.

30th JULY, 1952, at 7.15 p.m.

Mr. S. J. Copland, President, occupied the Chair.

BUSINESS.

To consider an alteration of the Rules of the Society recommended by the Council, by the addition of a rule xvii, reading as follows: The Council may decide that the duties of the Secretary as set out in Rule XLIX shall be carried out by one or more

Honorary Secretaries. In this event the Council shall consist of eighteen members, and the Honorary Secretaries shall be Office-bearers to be elected by the Council in terms of Rules xxviii and xvi.

The adoption of the Council's recommendation was passed unanimously.

ORDINARY MONTHLY MEETING.

30th JULY, 1952.

Mr. S. J. Copland, President, occupied the Chair.

Messrs. R. W. Jessup, M.Sc., Armidale, N.S.W.; G. R. Meyer, Ryde, N.S.W.; and G. E. Sullivan, M.Sc. (N.Z.), Sydney University, were elected Ordinary Members of the Society.

The Chairman made the following announcements:

1. On account of the Sydney Meeting of the Australian and New Zealand Association for the Advancement of Science, which will take place from 20th to 27th August, 1952, inclusive, and the University Centenary Celebrations, there will be no Ordinary Monthly Meeting of the Society in August.

2. A Special General Meeting will be held on 24th September, 1953, at 7.15 p.m., to confirm the alteration of the Rules, adopted at the Special General Meeting on 30th July, 1952.

3. Individual members who wish to subscribe to the memorial to be erected in the Transvaal to the late Dr. Robert Broom should send their contributions to the Hon. Treasurer of the Society.

4. By decision of the Deputy Commissioner of Taxation, the Linnean Society has been approved as a scientific research institute, donations to which for purposes of research are tax-free.

Library accessions amounting to 11 volumes, 182 parts or numbers, 4 bulletins, 6 reports and 2 pamphlets, total 205, had been received since last meeting.

PAPERS READ.

1. Revision of the Genus *Calotis* R.Br. By Gwenda L. Davis.
2. Ropy Smut of Liverpool Plains Grass. By Dorothy E. Shaw.
3. Notes on *Phlebotomus* from the Australasian Region (Diptera: Psychodidae). By G. B. Fairchild. (*Communicated by D. J. Lee.*)
4. Australian Rust Studies. IX. Physiologic Race Determinations and Surveys of Cereal Rusts. By W. L. Waterhouse.

NOTES AND EXHIBITS.

Dr. N. C. W. Beadle exhibited, on behalf of himself and Professor N. A. Burges, a series of test-tubes containing laboratory-prepared laterite and illustrating the formation of a laterite soil-profile with reduced and bleached zones and zones of deposited oxidized iron. The maintenance of a fluctuating water-level and a high rate of microbiological activity leads to anaerobic conditions and the formation of ferrous iron at depth. This is deposited in oxidized form at the surface. In the laboratory the process can be accelerated by providing the micro-organisms with an additional carbon source such as glucose.

Mr. A. J. Bearup exhibited a small water crustacean, *Mesocyclops obsoletus*, with a larval tapeworm in the body cavity. The adult worm is a species of *Spirometra* (Cestoda-Dibothriocephalidae), a parasite of dogs and cats. Larval stages have been followed through Cyclopoida to tadpoles, thence to pigs and other animals and back to cats. Recently, many wild pigs bred in western New South Wales have been found to harbour the larvae (spargana) of this worm.

LECTURETTE.

A lecturette, illustrated by a film and exhibits, on the Natural History of Heard Island, was given by Mr. K. G. Brown, B.Sc., Biologist to the Australian Antarctic Expedition, 1951.

SPECIAL GENERAL MEETING.

24th SEPTEMBER, 1952.

Mr. S. J. Copland, President, occupied the Chair.

BUSINESS.

To confirm the adoption of the alteration of the Rules of the Society passed at the Special General Meeting held on 30th July, 1952.

It was resolved unanimously that the adoption of the alteration of the Rules of the Society be confirmed.

ORDINARY MONTHLY MEETING.

24th SEPTEMBER, 1952.

Mr. S. J. Copland, President, occupied the Chair.

Mr. M. A. Bateman, Enfield, N.S.W.; Miss Nola J. Hannon, B.Sc., Penshurst, N.S.W.; and Mr. J. Walker, B.Sc.Agr., N.S.W. Department of Agriculture, Sydney, were elected Ordinary Members of the Society.

The President referred to the death on 17th August, 1952, of Sir William Dixon, who had been a Life Member of the Society since 1927.

The President offered congratulations to Dr. Marie E. Phillips, on obtaining the Ph.D. degree of the University of Manchester.

The President announced that the Council is prepared to receive applications for Linnean Macleay Fellowships tenable for one year from 1st January, 1953, from qualified candidates. Applications should be lodged with the Hon. Secretary not later than Wednesday, 5th November, 1952.

The attention of members was drawn to the claims of the Forestry Advisory Council of N.S.W., which would be grateful for contributions towards the increased costs of the Council in many directions, such contributions to be sent to Mrs. A. G. Hudson, Hon. Treasurer, Forestry Advisory Council of N.S.W., Yarrabung Road, St. Ives, N.S.W.

An opportunity was given for the discussion of two papers read at the July Monthly Meeting, namely, "Notes on *Phlebotomus* from the Australasian Region (Diptera: Psychodidae)", by G. B. Fairchild (*communicated by D. J. Lee*), and "Australian Rust Studies. IX. Physiologic Race Determinations and Surveys of Cereal Rusts", by W. L. Waterhouse.

Library accessions amounting to 47 volumes, 174 parts or numbers, 24 bulletins, 6 reports and 22 pamphlets, total 273, had been received since the last meeting.

PAPERS READ.

1. A Corallanid Isopod parasitic on Freshwater Prawns in Queensland. By E. F. Riek.
2. A Note on the Unusual Longevity of *Ciboria aestivatis* (Wint.) Rehm. By W. L. Waterhouse.
3. A Note on the Occurrence of an Undescribed Rust on *Cryptostemma calendulaceum* (L.) R.Br. By W. L. Waterhouse.
4. A Note on an Unusual Spore Form in *Puccinia malvacearum* Bert. By W. L. Waterhouse.
5. Study of Soil Algae. I. Fluorescence Microscopy for the Study of Soil Algae. By Y. T. Tchan, Macleay Bacteriologist to the Society.

LECTURETTE.

Professor T. G. B. Osborn, Sherardian Professor of Botany, University of Oxford, and formerly Professor of Botany in the University of Sydney, gave an illustrated talk on "The new Botany School in the University of Oxford".

ORDINARY MONTHLY MEETING.

29th OCTOBER, 1952.

Mr. S. J. Copland, President, occupied the Chair.

Messrs. J. S. Bunt, B.Sc.Agr., Sydney University, and J. D. McLean, B.Sc., Hurstville, N.S.W., were elected Ordinary Members of the Society.

The President announced that the Council is prepared to receive applications for Linnean Macleay Fellowships tenable for one year from 1st January, 1953, from qualified candidates. Applications should be lodged with the Hon. Secretary not later than Wednesday, 5th November, 1952.

Library accessions amounting to 11 volumes, 90 parts or numbers, 15 bulletins, 3 reports and 4 pamphlets, total 123, had been received since the last meeting.

PAPERS READ.

1. Revision of Australian and New Zealand Species of Theleporaceae and Hydnaceae in the Herbarium of the Royal Botanic Gardens, Kew. By G. H. Cunningham. (*Communicated by Professor N. A. Burges.*)

2. Notes on the Morphology and Biology of *Ectenopsis vulpecula* Wied. var. *angusta* Macq. (Diptera, Tabanidae, Pangoniinae). By Kathleen M. I. English.

LECTURETTE.

Professor C. E. Marshall, Professor of Geology in the University of Sydney, gave a lecturette on "Preservation of Plant-tissues in Coal".

ORDINARY MONTHLY MEETING.

26th NOVEMBER, 1952.

Mr. S. J. Copland, President, occupied the Chair.

Dr. C. G. Hansford, M.A., Sc.D. (Cantab.), F.L.S., Waite Agricultural Research Institute, Adelaide, South Australia, and Mr. P. G. Valder, B.Sc.Agr., Biological Branch, N.S.W. Department of Agriculture, Sydney, were elected Ordinary Members of the Society.

The President referred to the death, on 20th November, 1952, of Mr. Walter Mervyn Carne, who had been a member of the Society since 1905.

The President announced that Miss Mary Hindmarsh and Mr. T. G. Vallance had been reappointed to Linnean Macleay Fellowships in Botany and Geology respectively for the year 1953.

The President also announced that the Royal Society of New South Wales has called for nominations for the award of the Edgeworth David Medal.

Library accessions amounting to 9 volumes, 38 parts or numbers, 2 bulletins, 1 report and 5 pamphlets, total 55, had been received since the last meeting.

PAPERS READ.

1. The Effect of Colchicine on the Spindle of Root Tip Cells. By Mary M. Hindmarsh, Linnean Macleay Fellow in Botany.

2. Australian Rust Studies. X. Further Breeding Work with "Khapli" Emmer Wheat, an Outstanding Source of Stem Rust Resistance. By W. L. Waterhouse.

3. A Study of the Microflora of Wheat Grains in N.S.W. By Dorothy E. Shaw and P. G. Valder.

4. Yellow Spot Disease of Wheat in Australia. By P. G. Valder and Dorothy E. Shaw.

5. Australian Clover Rusts. By B. D. H. Latter.

6. A Compound *Eucalyptus* Hybrid. By L. D. Pryor.

7. Variable Resistance to Leaf-eating Insects in some Eucalypts. By L. D. Pryor.

8. The *Culex pipiens* Group in South-eastern Australia. I. By N. V. Dobrotworsky, M.Sc. (*Communicated by D. J. Lee.*)

9. Australasian Ceratopogonidae (Diptera, Nematocera). Part VI. Australian Species of *Culicoides*. By David J. Lee, B.Sc., and Eric J. Reye, M.B., B.S.

LECTURETTE.

A lecturette on the Australian Museum Expedition to North-west Australia, was given by Mr. H. O. Fletcher, Leader of the Expedition.

LIST OF MEMBERS.

(15th December, 1952.)

ORDINARY MEMBERS.

(An asterisk (*) denotes Life Member.)

- 1940 Abbie, Professor Andrew Arthur, M.D., B.S., B.Sc., Ph.D., c.o. University of Adelaide, Adelaide, South Australia.
- 1927 *Albert, Michel Francois, "Boomerang", 42 Billyard Avenue, Elizabeth Bay, Sydney.
- 1940 *Allman, Stuart Leo, B.Sc.Agr., M.Sc., Entomological Branch, Department of Agriculture, Farrer Place, Sydney.
- 1922 Anderson, Robert Henry, B.Sc.Agr., Botanic Gardens, Sydney.
- 1927 *Armstrong, Jack Walter Trench, "Callubri", Nyngan, N.S.W.
- 1952 Ashton, David Hungerford, B.Sc., 92 Warrigal Road, Surrey Hills, E.10, Victoria.
- 1912 Arousseau, Marcel, B.Sc., c.o. Mr. G. H. Arousseau, 229 Woodland Street, Balgowlah, N.S.W.
- 1952 Baas-Becking, Professor L. G. M., Ph.D., D.Sc., Botany School, Sydney University.
- 1951 Backhouse, Thomas Clive, M.B., B.S., D.P.H., D.T.M. & H., F.R.A.C.P., School of Public Health and Tropical Medicine, Sydney University.
- 1948 Baddams, Miss Greta, B.A., B.Sc., New England University College, Armidale, N.S.W.
- 1952 Baehni, Professor Charles, Dr.sc., Conservatoire botanique, Université de Genève, 192, rue de Lausanne, Genève, Switzerland.
- 1949 Baker, Eldred Percy, B.Sc.Agr., Ph.D., Faculty of Agriculture, Sydney University.
- 1950 *Barber, Professor Horace Newton, M.A., Ph.D., Department of Botany, University of Tasmania, Hobart, Tasmania.
- 1948 Barrett, Mrs. Judith Hope, M.Sc. (née Balmain), Dairy Research Institute, Shinfield, near Reading, Berks, England.
- 1935 *Beadle, Noel Charles William, D.Sc., Botany School, Sydney University.
- 1946 Bearup, Arthur Joseph, 66 Pacific Avenue, Penshurst, N.S.W.
- 1940 Beattie, Joan Marion, D.Sc. (née Crockford), c.o. Lake George Mine, Captain's Flat, N.S.W.
- 1952 Bennett, Miss Isobel Ida, Department of Zoology, Sydney University.
- 1907 Benson, Professor William Noel, B.A., D.Sc., F.G.S., University of Otago, Dunedin, New Zealand.
- 1948 Besly, Miss Mary Ann Catherine, B.A., 7 Myra Street, Wahroonga, N.S.W.
- 1948 Birch, Louis Charles, D.Ag.Sc., M.Sc., Department of Zoology, Sydney University.
- 1941 Blake, Stanley Thatcher, M.Sc., Botanic Gardens, Brisbane, Queensland.
- 1929 Boardman, William, M.Sc., Zoology Department, University of Melbourne, Carlton, N.3. Victoria.
- 1946 Brett, Robert Gordon Lindsay, B.Sc., 7 Petty Street, West Hobart, Tasmania.
- 1950 Brown, Kenneth George, 6 Dolphin Street, Randwick, N.S.W.
- 1924 Browne, Ida Alison, D.Sc. (née Brown), Department of Geology, Sydney University.
- 1949 Browne, Lindsay Blakeston Barton, Department of Zoology, Sydney University.
- 1911 Browne, William Rowan, D.Sc., Department of Geology, Sydney University.
- 1952 Bunt, John Stuart, B.Sc.Agr., Faculty of Agriculture, Sydney University.
- 1949 Burden, John Henry, 1 Havilah Street, Chatswood, N.S.W.
- 1931 *Burges, Professor Norman Alan, M.Sc., Ph.D., Professor of Botany, University of Liverpool, Liverpool, England.
- 1920 Burkitt, Professor Arthur Neville St. George Handcock, M.B., B.Sc., Medical School, Sydney University.
- 1927 Campbell, Thomas Graham, Division of Economic Entomology, C.S.I.R.O., P.O. Box 109, City, Canberra, A.C.T.
- 1934 *Carey, Professor Samuel Warren, D.Sc., Geology Department, University of Tasmania, Hobart, Tasmania.
- 1949 Carne, Phillip Broughton, B.Agr.Sci. (Melb.), 7 Thames Street, Sunbury-on-Thames, Middlesex, England.
- 1936 *Chadwick, Clarence Earl, B.Sc., Entomological Branch, Department of Agriculture, Farrer Place, Sydney.
- 1947 Christian, Stanley Hinton, Malaria Control, Department of Public Health, Banz, Western Highlands, via Lae, New Guinea.
- 1932 *Churchward, John Gordon, B.Sc.Agr., Ph.D., 1 Hunter Street, Woolwich, N.S.W.
- 1946 Clark, Laurance Ross, M.Sc., c.o. C.S.I.R.O., Division of Entomology, P.O. Box 109, City, Canberra, A.C.T.
- 1901 Cleland, Professor John Burton, M.D., Ch.M., 1 Dashwood Road, Beaumont, Adelaide, South Australia.

- 1942 Cleland, Kenneth Wollaston, M.B., Department of Anatomy, Sydney University.
 1931 Colefax, Allen Neville, B.Sc., Department of Zoology, Sydney University.
 1946 Colless, Donald Henry, Borneo Malaria Research, Labuan, British North Borneo.
 1942 Copland, Stephen John, M.Sc., Chilton Parade, Warrawee, N.S.W.
 1947 Costin, Alec Baillie, 12 Barambah Road, Roseville, N.S.W.
 1908 Cotton, Professor Leo Arthur, M.A., D.Sc., 113 Queen's Parade East, Newport Beach, N.S.W.
 1950 Crawford, Lindsay Dinham, B.Sc., Queen Victoria Museum and Art Gallery, Launceston, Tasmania.
 1945 Davis, Mrs. Gwenda Louise, B.Sc., New England University College, Armidale, N.S.W.
 1936 Day, Maxwell Frank, Ph.D., B.Sc., C.S.I.R.O., Box 109, Canberra, A.C.T.
 1934 Day, William Eric, 23 Gelling Avenue, Strathfield, N.S.W.
 1925 de Beuzeville, Wilfred Alexander Watt, J.P., "Melamere", Welham Street, Beecroft, N.S.W.
 1937 Deuquet, Camille, B.Com., 126 Hurstville Road, Oatley, N.S.W.
 1948 Drover, Donald P., Institute of Agriculture, University of Western Australia, Nedlands, W.A.
 1926 Dumigan, Edward Jarrett, 10 High Street, Toowoomba, Queensland.
 1946 Durie, Peter Harold, B.Sc., C.S.I.R.O., Veterinary Parasitology Laboratory, Yeerongpilly, Brisbane, Queensland.
 1952 Dyce, Alan Lindsay, B.Sc.Agr., 29 Edwards Street, Moree, 7N, N.S.W.
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LIST OF NEW GENUS, SPECIES, AND SUBSPECIES.

Vol. 77.

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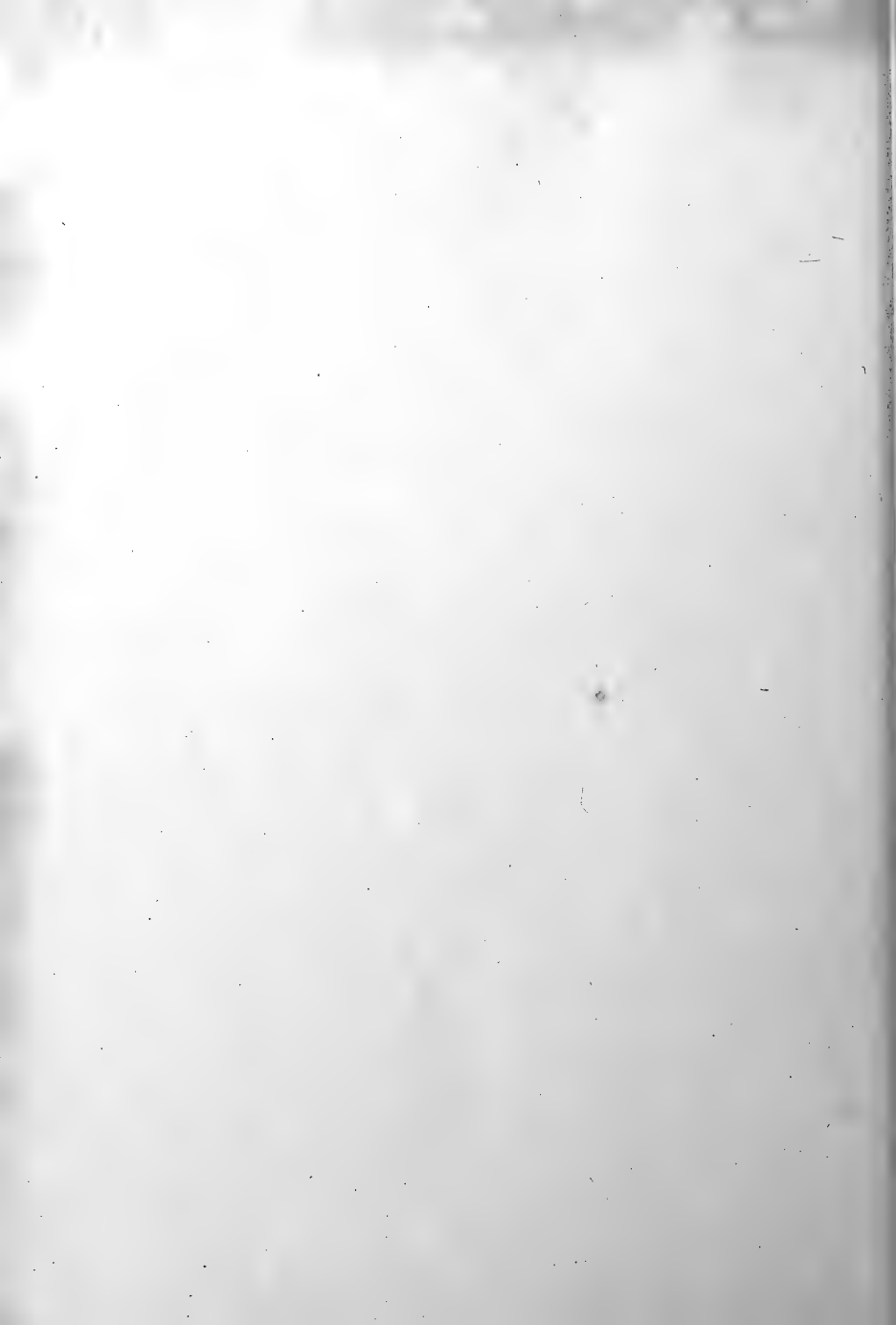
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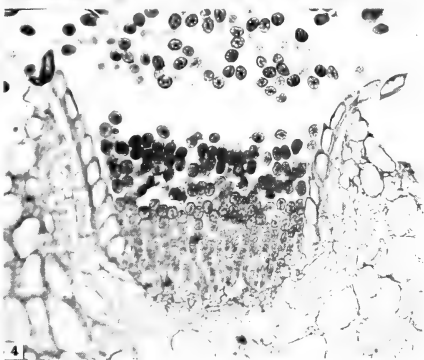
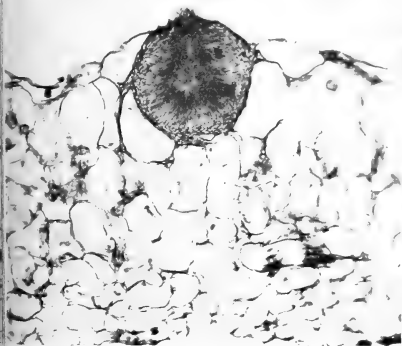
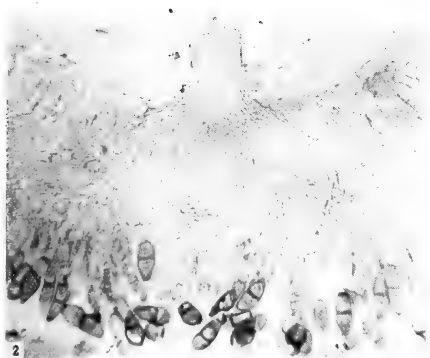
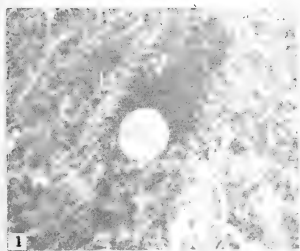
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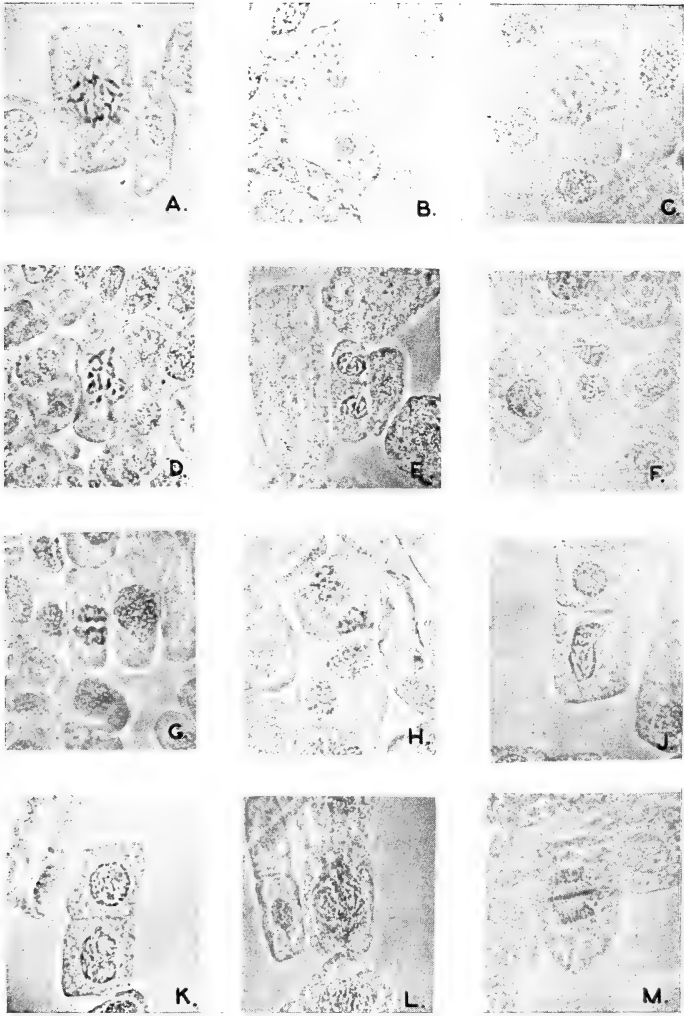
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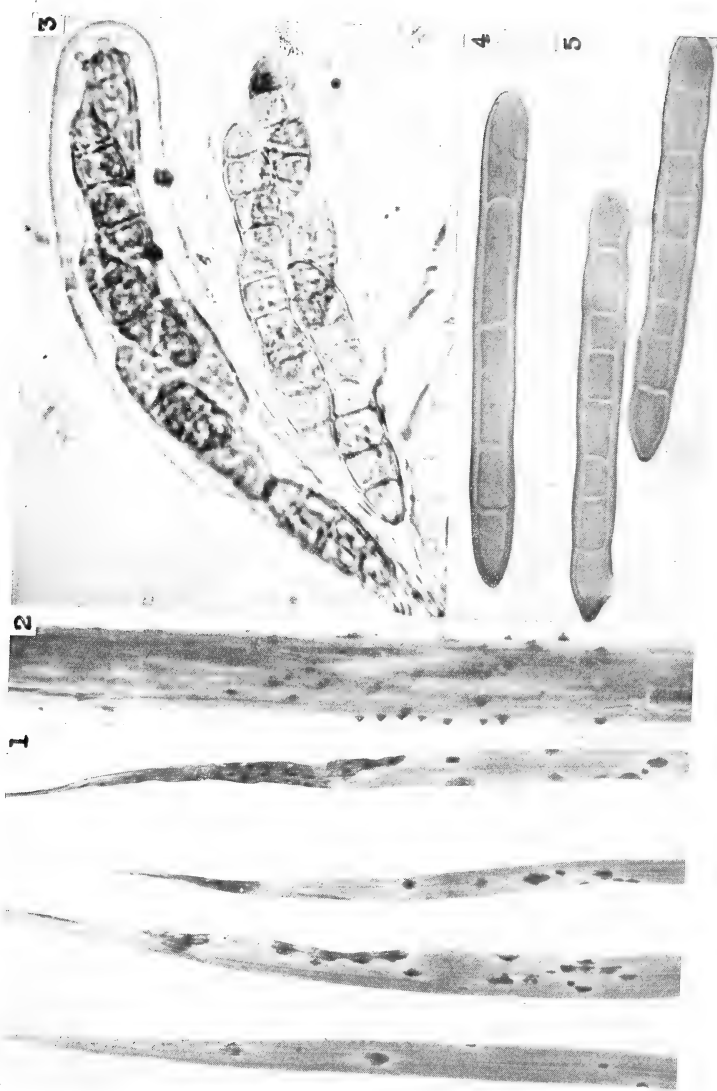




1, *Ciboria aestivalis*. 2, *Matva rotundifolia*.
3, 4, *Cryptostemma calendulaceum*.



Effect of colchicine on the spindle of root tip cells.



Yellow Spot Disease of Wheat.





Eucalyptus hybrid.





Eucalyptus hybrid.



1



2



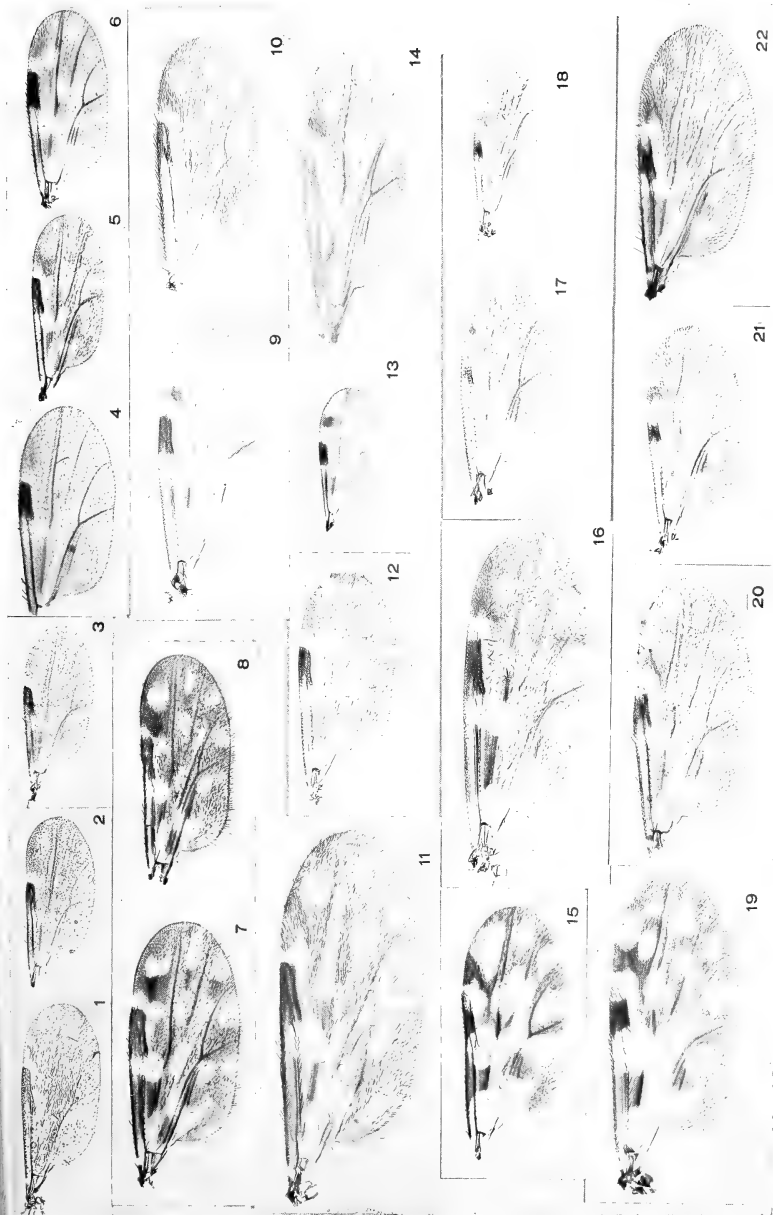
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1 (left to right). *E. rubida*, *E. rubida* × *E. maculosa*, *E. maculosa*, *E. rubida* × *E. Macarthuri* × *E. viminalis*, *E. Macarthuri*, *E. viminalis*.

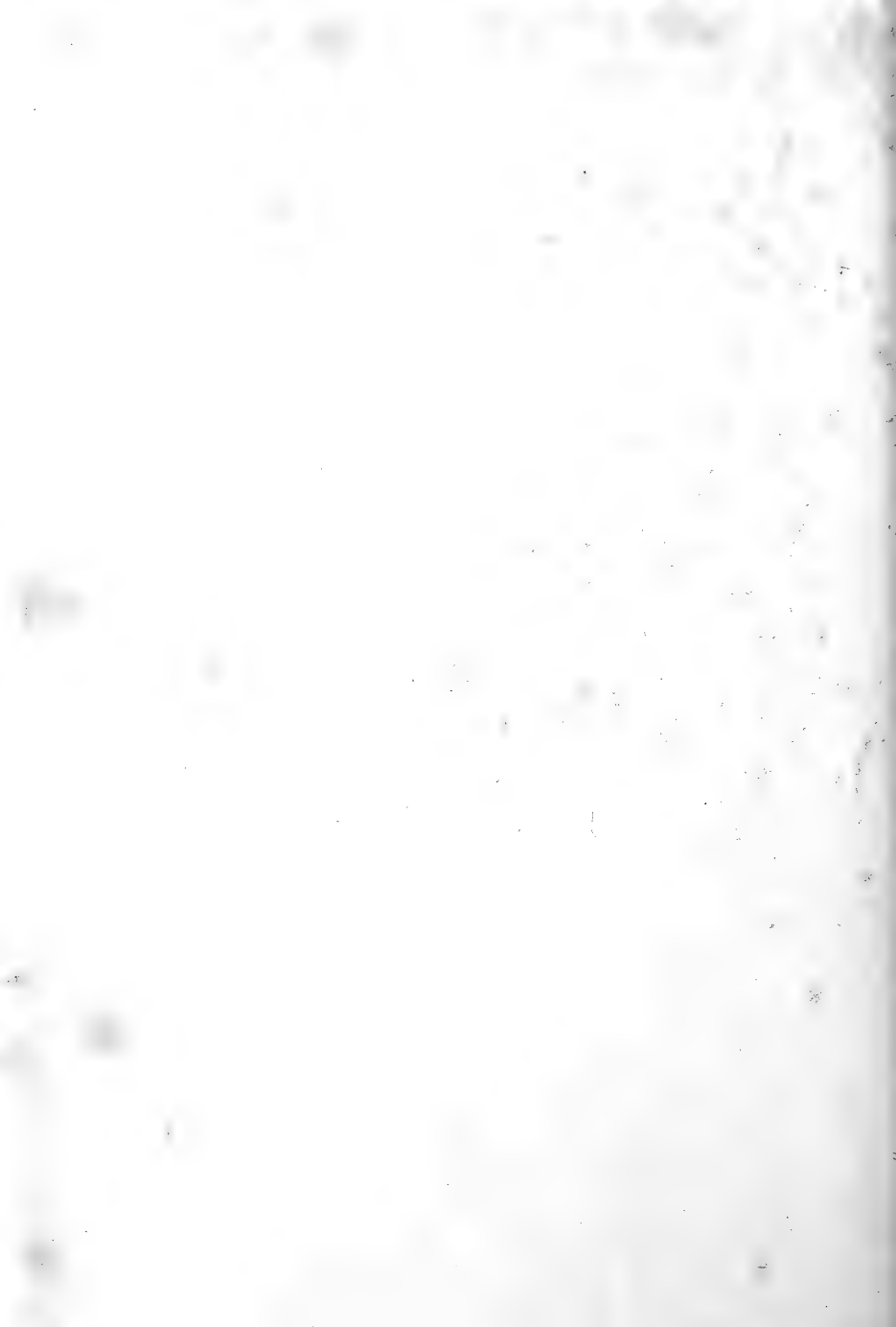
2. Progeny of supposed *E. rubida* × *E. maculosa*.

3. Progeny from hybrid presumably containing *E. rubida*, *E. Macarthuri* and *E. viminalis*.





Wings of species of *Cuticoides*.









(Issued July 3, 1952.)

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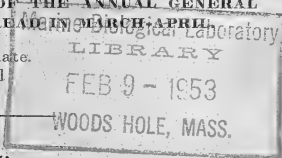
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MEETING AND THE PAPERS READ THEREAT, APRIL

With one plate.
[Plate i.]



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There is no obvious correlation between the humus content of the soil and the presence or absence of our organism. In the 11 samples of soils giving a positive test the humus content ranges from nil to 96 mg. per g. Chalaust (1948) in France has pointed out that the numbers of *Azotobacter* vary with the humus content of the soil. Our results show no such relationship but they include only a small number of soils.

Other aspects of the problem may be raised. It seems possible that our organism lives mainly in sandy soils, but here, too, the number of samples is too small to give a definite conclusion. Our organism is found in soils whose pH ranges from 5.5 to 7.0.

These preliminary investigations show that acid tolerant N-fixing organisms are present in Australia, especially in the Sydney district. Their general ecology in Australia is still unknown except that the pH and humus content of soils seem to be without effect. It will be interesting to investigate the physiology of this group of organisms in relation to their ecology.

Acknowledgements.

The author is indebted to Professor N. A. Burges, Hon. Professor Baas-Becking, Dr. N. C. W. Beadle and Dr. H. S. McKee for their criticism and help. Also to all the staff of the University of Sydney who collected soil samples for this work.

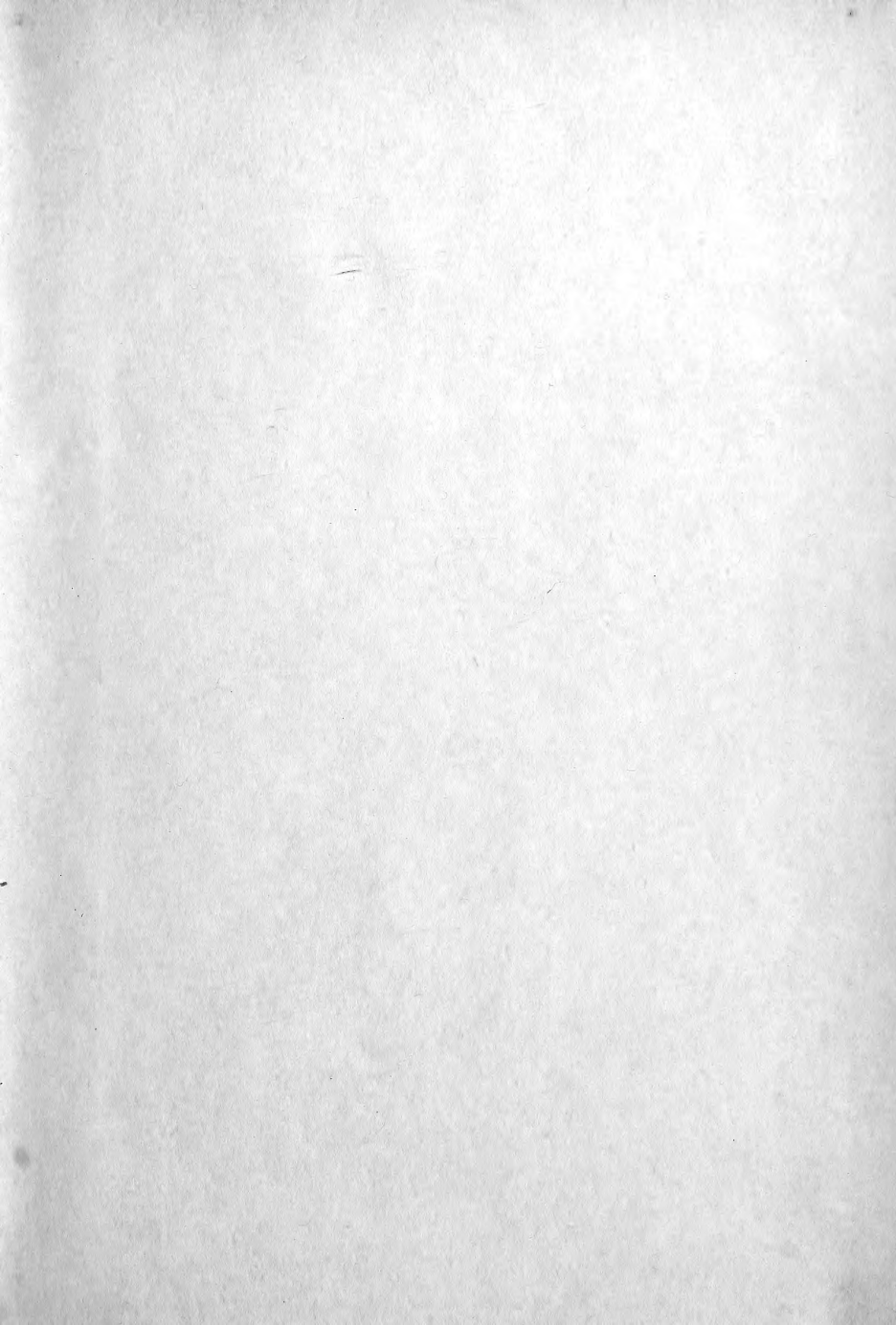
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