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ANNUAL GENERAL MEETING.

WEDNESDAY, 28TH MARCH, 1951.

The Seventy-sixth Annual General Meeting was held in the Society's Rooms, Science House, Gloucester Street, Sydney, on Wednesday, 28th March, 1951.

Mr. D. J. Lee, B.Sc., President, occupied the chair.

The Minutes of the Annual General Meeting held on 29th March, 1950, were read and confirmed.

PRESIDENTIAL ADDRESS.

As is usual, the first part of my address is devoted to a brief review of the Society's activities during the past year.

Volume 75 of the Society's Proceedings was published during 1950. It consisted of 359 + xl pages, 12 plates and 442 text-figures, thus being a larger volume than the previous one. Financial assistance towards the cost of publication of three papers was received from Department of Anatomy, University of Sydney (£74 16s.), Commonwealth Scientific Publications Committee (£55) and University of Melbourne (£25). The annual grant from the State Government of £100 towards the cost of publication of the Proceedings was increased to £150 during the year.

Exchanges received from scientific societies and institutions totalled 1,414. Loans from the Library, particularly interstate inter-library loans, have been requested as in the previous year. Additional steel shelving has been installed in the Library and some duplicate books are still available for sale. New exchanges were commenced with: Academy of the Popular Republic of Roumania; California Zoological Club; Elisha Mitchell Scientific Society; Estacao de Melhoramento de Plantas, Elvas, Portugal; Société des Sciences Naturelles de Tunisie; University of Upsala ("Symbolae Botanicae Upsalienses"), and Victoria University College, Wellington, New Zealand. A number of books from the library of the late Dr. F. G. Hardwick were presented to the Library by his son, Mr. F. L. Hardwick.

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

June: A talk on "Coral Genera of Heron Island (Barrier Reef)", by Mr. K. E. W. Salter and Miss M. A. Besley.

July: The following members contributed items of interest: Miss M. Hindmarsh—a note on "Mitotic Poisons"; Mr. A. Musgrave—exhibition of specimens of *Stephanitis queenslandensis* Hacker, 1927, a member of the family Tingidae (Lace Bugs); Mr. A. K. O'Gower—exhibition of the eggs, larvae and pupae of cat fleas.

August—A series of talks was given by members of the New South Wales Department of Agriculture, the speakers being: Mr. Grahame Edgar, Director of Veterinary Research (investigations on problems of animal industry in the State); Dr. S. L. Macindoe, Principal Research Agronomist (an account of the organization, progress and results of plant research conducted primarily on the ten Experiment Farms and two Agricultural Colleges of New South Wales); Dr. F. T. Bowman, Special Fruit Research Officer (outline of the research work of the Division of Horticulture); Mr. S. L. Allman, Senior Entomologist (description of the Entomological Branch and its work with insect pest problems); and Dr. C. J. Magee, Chief Biologist (research in the Biological Branch which is directed mainly at preventing losses from plant diseases).

September: Talks on "Recent Changes in the Vegetation of North-western New South Wales", by Dr. N. C. W. Beadle and Professor N. A. Burges.

October: Short talks by Professor P. D. F. Murray on "The Fusion of Long Bones" and by Mr. B. R. A. O'Brien on "Some Aspects of Regeneration in Earthworms".

November: Talks on various aspects of Northern Australia were given by: Professor J. Macdonald Holmes—"The Geographical Background to the Problems of North

Australia"; Dr. W. Kirkland—"Medical Problems of North Australia"; and Dr. N. W. G. Macintosh—"Comments on the Physical Types of the Aborigines of Arnhem Land". A talk prepared by Mr. W. Poggendorf on "Problems in Agriculture" was given by Mr. E. B. Furby.

We thank all who have contributed to these programmes.

Since the last Annual Meeting the names of fourteen members have been added to the list, three members have been lost by death, and eighteen have resigned. The number of members as at 1st March, 1951, is: Ordinary Members, 206; Life Members, 22; Honorary Member, 1; and Corresponding Members, 3—total 232.

As Dr. Dorothy Carroll tendered her resignation as Secretary to the Society as from 22nd January, 1951, it was found necessary to make interim arrangements for the successful prosecution of the business of the Society. To this end Council appointed Dr. W. R. Browne as Honorary Secretary and Dr. A. B. Walkom as Honorary Editor for the time being. It is hoped that Council will be able to decide on some more permanent arrangement in the near future. Council's intention at present is to employ a part-time editor, if one can be found suitable and willing to undertake this responsibility, and carry on the secretarial work with an honorary secretary and have the assistant secretary in charge of the Society's rooms and library. In view of a further 50% increase in the basic cost of publication of the Society's Proceedings, Council has felt that some economy in the cost of the secretarial activities of the Society may be necessary in order to maintain the level of publication at one approximating that of previous years.

Two Special General Meetings were held on 25th October and 29th November, 1950, respectively, to make an addition to Rule VI as follows: "An Ordinary Member who has paid the Annual Subscription for forty years shall be exempt from payment of further subscriptions." Council's object was to relieve long-standing members of the burden of their subscriptions, particularly in their years of retirement.

Dr. Ida A. Browne resigned as a member of Council in April, 1950. Council expressed appreciation of her service on the Council during the past ten years.

Professor P. D. F. Murray was elected to fill the vacancy on the Council caused by the resignation of Dr. Ida Browne.

Dr. G. D. Osborne was granted leave of absence from the Council for six months from 1st January, 1951.

Dr. A. B. Walkom attended the Pan-Indian Ocean Science Congress at Bangalore in January, 1951, as one of the Australian delegates.

Miss Mary Tindale was appointed the Society's representative at the VIIth International Botanical Congress in Stockholm, 1950, and accredited observer at the International Union for the Protection of Nature Conference. Miss Tindale has informed the Society of a number of points dealt with by the Nomenclature Committee and offered to answer questions concerning special points in changes of the Rules.

The total net return from Science House for the year was £597. In future half-yearly meetings and half-yearly accounts and audits of the Science House Management Committee will be abandoned and only annual meetings will take place. A survey of the libraries of the owner-bodies of Science House has been made by the State Library Board of New South Wales at the request of the Societies' Library Committee, and a report thereon was received.

Following a request from the Information Service, Commonwealth Scientific and Industrial Research Organization, which had resulted from one of the recommendations of the Royal Society Scientific Information Conference (July, 1948), the Council decided that a synopsis of each paper published in the Proceedings would appear below the title of the paper. Such a synopsis will not interfere in any way with the arrangement of the paper but will facilitate the reading of the papers in the Proceedings. These authors' synopses will be introduced in Volume 76 for 1951.

Preservation of Natural Areas.—The Joint Committee of the Royal Zoological Society and Linnean Society considered another survey, in this case at the Spencer's Creek Dam site. The Snowy Mountains Hydro-electric Authority offered to supply

transport and accommodation for a field party for the projected Natural History survey of this area. Under the leadership of Dr. W. R. Browne, and with the help of a grant of £75 from Mr. E. J. Hallstrom, a party of eight geologists and biologists visited the Spencer's Creek area during the period 17th to 30th January, 1951. A report on this survey is now in course of preparation. It is considered that an initial survey of this kind in any area shortly to be changed completely by the construction of a large dam will provide valuable basic data for continued observation of the changes in the natural history of the area which must inevitably take place during and after the construction of the dam. It is hoped that further observations will be possible every year until the new environment has reached a state of stability in relation to a changed fauna and flora.

The Society again supported a request to renew the proclamation protecting certain wild flowers and native plants for three years from 1st July, 1950, and this has been done.

The Society has also supported appeals against the possible resumption of land within the Muogamarra Sanctuary. Similar action has been taken in a number of other cases wherein it appeared that natural areas within reserves were to be thrown open for development.

Commonwealth of Australia Jubilee Celebrations.—The Society is co-operating with the Royal Society of New South Wales and other scientific bodies in the planning of a conversazione in the Great Hall of the University of Sydney on 18th April, 1951. An exhibit dealing with the early natural history in the State will be our contribution.

We offer congratulations to: Dr. I. M. Mackerras, on the award of the Clarke Memorial Medal of the Royal Society of New South Wales for 1950 for his work on Diptera; Dr. T. B. Kiely, on obtaining the degree of D.Sc.Agr., and the award of the Royal Society's Medal for his work on the Black Spot of Citrus; Mr. Robert Endean, Miss Janet Harker and Miss Jean Liddell, on obtaining the M.Sc. degree of the University of Sydney; Miss Adele Millerd, on the award of a research fellowship which would enable her to study at the California Institute of Technology; and Miss Muriel Morris, on obtaining the degree of M.Sc. of the University of Sydney and receiving the award of an International Federation of University Women Fellowship to study at the University of Oxford.

Linnean Macleay Fellowships.

In 1949 the Council reappointed three Fellows for 1950, viz.: Miss M. Hindmarsh (Botany), Miss A. Millerd (Biochemistry) and Miss M. Morris (Zoology).

Miss Hindmarsh continued her investigation of mitotic poisons during 1950. In particular the effects of phosphates and nitrophenols were studied. Investigation of an unexpected result obtained when using phosphate buffers to control pH showed that phosphate inhibited mitosis in a manner similar to sulphanilamide inhibition. A similar result had been reported recently by I. Galinsky in the *Journal of Heredity*. Further work on this inhibition indicated that, although phosphate had a specific effect on cell division, other salts in an unbalanced solution may show a similar effect. 2,4-dinitrophenol upsets cell division by delaying or inhibiting spindle formation and by inducing stickiness in the chromosomes. It has been found, however, that dinitrophenol acts as a slow fixative, gradually killing the cells, and not as a specific mitotic poison. The action of mononitrophenols which have been reported to have a "colchicine-like" action on cell division is being investigated, since it is not known whether they too kill the cells.

Miss Millerd continued her investigation of the succinoxidase and carboxylase of the potato tuber. The investigation of the carboxylase activity of the potato tuber was carried along various lines: (i) the preparation of the enzyme, (ii) the splitting and reconstitution of the enzyme, and (iii) isolation of the product of reaction. Study of the succinoxidase system had almost reached finality when Miss Millerd was awarded a research fellowship which would enable her to study at the California Institute of Technology, and resigned her Fellowship as from 30th September, 1950.

Miss Morris completed a study of the life-history of one of our commercial prawns, a new species of *Metapenaeus*. The interesting point about this work is the fact that it demonstrates conclusively that there is a commercial prawn species breeding in our coastal lakes. All other well-known species of commercial value definitely go to sea to breed. It is hoped that this work will be published shortly. Miss Morris was awarded an International Federation of University Women Fellowship and resigned her Fellowship as from 14th July, 1950, to continue her studies on plankton at the University of Oxford.

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.

Miss Hindmarsh proposes to continue with the investigation of mitotic poisons on plant cells. The work on the effects of phosphate and dinitrophenol on cell division will be completed. Levan's results will be checked by testing the cytological action of nitrophenols and other related compounds, especially those which are not inhibitors of phosphate transfer. A further study of mitotic poisons of the spindle inhibitor type will be made, to look for any similarity in action or true colchicine effects. Work on the inhibition of cell division by sulphanilamide and its reversal by p-aminobenzoic acid will be continued as suitable material becomes available.

The subject of Mr. Stevens' studies will be the Geology and Petrology of Bathylithic Intrusions in the Cowra-Gunning Region.

Mr. Vallance proposes geological investigations in the Ordovician Metamorphic Belt of Central-western New South Wales.

We wish all three every success in their year's work.

Macleay Bacteriologist.

Dr. Yao-tseng Tchan arrived from Paris and commenced his work as Macleay Bacteriologist on 1st August, 1950. An opportunity to meet Dr. Tchan was given to members of Council and others at afternoon tea on 2nd August.

Dr. Tchan's work on the Gilgai and red-brown earth soils has made some progress. Generally speaking there is no N-fixation, but the addition of wheat straw modifies the general microflora and as the result less N is lost as ammonia and the humus content is increased. Experiments with wheat are not yet finished because the vegetative cycle of the plants being used has not run its full course. Also, during the work, estimation techniques for the N-fixation bacteria and the total soil flora have had to be modified. Dr. Tchan gained some knowledge of Australian ecological conditions as the result of an excursion with members of the Faculty of Agriculture. Dr. Tchan proposes to continue work on the two soils mentioned above, as well as certain soils of the Sydney area.

Obituaries.

It is recorded with regret that the following members died during the year: Professor W. J. Dakin, Dr. B. L. Middleton and Dr. G. A. Waterhouse.

William John Dakin, Emeritus Professor of Zoology in the University of Sydney, died on 2nd April, 1950. Before coming to Sydney as Professor of Zoology in 1929 Professor Dakin had wide experience of research and teaching in Liverpool, Kiel, Heligoland, Norway, Naples and Perth. Throughout his life he had a profound interest in the problems of marine biology, which he pursued with far more than normal vigour wherever he happened to be. He introduced this field of research to his department at Sydney University and from humble beginnings gradually developed a pattern of investigation which culminated in the foundation of the Commonwealth Scientific and Industrial Research Organization Fisheries Laboratory at Cronulla. During World War II Professor Dakin transferred his attention to problems of camouflage and was appointed Technical Director of Camouflage for the Commonwealth of Australia, an activity he continued until the end of the war. Throughout his life Professor Dakin not only produced a considerable volume of research papers, but also wrote several books, both text and documentary, and gained a widespread popularity

as a radio speaker, expounding in understandable terms to a very wide audience the problems of science he loved so dearly. Professor Dakin joined the Society in 1929, was a member of Council from 1930 to 1943, and was our President for the 1934–35 session.

Bertram Lindsay Middleton died on 16th October, 1950. Dr. Middleton was a graduate in Arts and Medicine of Trinity College, Dublin, who came to Australia following a world tour many years ago. In 1912 he commenced practice in Murrurundi, New South Wales, which he continued until the time of his death. Dr. Middleton had a lifelong interest in Lepidoptera and amassed a most extensive collection of Australian moths and butterflies amounting to some 10,000 specimens, which he bequeathed to the Australian Museum. Dr. Middleton had been a member of this Society since 1937.

Gustavus Athol Waterhouse died on 29th July, 1950. Dr. Waterhouse was a graduate in both engineering and science from the University of Sydney. He was Assistant Assayer at the Sydney branch of the Royal Mint from 1900 until it closed in 1926. His scientific work is best known from his long study of the Lepidoptera, which culminated in the production of the books "The Butterflies of Australia" (in collaboration with Mr. G. Lyell) and "What Butterfly is That?". Many other contributions to our knowledge of Australasian Lepidoptera have been published in various journals, and the collection of Australian Hesperiidae he assembled in the Australian Museum is undoubtedly one of the world's finest. Dr. Waterhouse was keenly interested in the affairs and management of a number of scientific societies, and it was in this field that he made outstanding contributions to the organization of scientific work in Australia. He first joined the Society in 1897 and was our President for the period 1921–23. The Society is particularly indebted to him for his supervision of our finances during the period 1926–43, when he acted (except during 1928–29) as our Honorary Treasurer. In 1943 ill health forced him to resign from the Council and he was elected a Corresponding Member. The sound management of the Society's finances carried out by Dr. Waterhouse has become increasingly obvious since his retirement from active participation in the Society's affairs, and we are indeed grateful for the foresight he displayed in building our finances to a level which makes it still possible to carry on without obvious retrenchment despite ever-rising costs for all our activities.

The Problems of Insect Quarantine.

1. Definition and Introduction.
2. Insect Pests in Australia: (*a*) Exotic species now present in Australia; (*b*) Australian insects of importance in other countries.
3. Recent Instances of the Spread of Exotic Pests within Australia.
4. Evidence of the Introduction of Insects into other Countries.
5. Exotic Insect Pests not yet introduced into Australia.
6. The Reality of the Economic Consequences of Pest Insect Introductions.
7. Recapitulation of the General Problem.
8. Can Quarantine Procedures be Justified?
9. The Development of Insect Quarantine Legislation.
10. The Broader Aspects of Insect Quarantine.

1. *Definition and Introduction.*

The concept which lately has been described as insect quarantine simply implies considerations of the prevention of entry of noxious insects into areas where they are not known to occur, whether such areas be geographically or politically limited. Initially of course the emphasis is on the prevention of such entry into countries whether they be continents, major geographical units of continents, or islands large or small. Despite this initial emphasis, problems of prevention of spread of noxious insects within geographically or politically limited areas also arise and are generally considered within the field of insect quarantine.

The basic problems are further complicated by the fact that certain of the harmless or relatively harmless insects of one country may prove to be pests or even serious hazards to the economy or health of another country, simply because a different set of environmental conditions may make an enormous difference in the level of population

attained and in the ecological relationships of the insect and the plant or animal life of the new environment. Furthermore, the insects themselves may not be intrinsically noxious but may act as vectors of human, animal or plant diseases and, for this reason, may be regarded as undesirable immigrants.

In actual fact there are natural ecological barriers of varying magnitude which, in themselves, offer considerable opposition to the spread of insects from one country to another, the most effective of these being the various oceans of the world. Deserts and mountain ranges operate in the same way, and tracts of country ecologically unsuitable to or otherwise uninhabited by the host plant or animal may also form barriers.

Such natural barriers have not proved adequate to prevent the spread of insect pests from country to country, even when separated by wide oceans, since the artificial methods of transfer by ships or aircraft are readily available. The tempo of such exchanges does seem to have increased very markedly with each increase in the speed of transport. For instance, Deputy (1948) claims that few field insects of any importance, other than the Hessian Fly and the Codling Moth, had established themselves in the United States of America prior to 1850. In his opinion, few insects other than stored product pests were able to survive the lengthy journeys of the old sailing vessels, and it was not until the advent of steam vessels that the majority of exotic pest species now present in America were able to reach there. The story of recent introductions of insects into Hawaii, particularly by aircraft, is one to be told at a later stage, but, when unfolded, it does disclose an infinitely greater rate of exchange of insect species than obtained up till a few years ago, when extensive intercontinental air traffic was not in operation.

It is contended, then, that we are now, even more than previously, faced with the necessity of devising artificial protective measures, and some, but not all, of these must have a legislative content.

Most countries have varying enactments governing the entry of insect pests, and such legislation is usually embodied in Plant Protection Acts or Quarantine Regulations for Animal and Plant Diseases and Pests. Further, such legislation may be under the administrative control of various authorities such as departments of health or of agriculture.

As sometimes happens with a principle or activity which has undergone gradual development over a period of years, the arguments for and against these become obscure and it may be found that the underlying reasons for certain actions appear to have been accepted without being adequately stated. Such a position may arise particularly when a system of legislation is built up item by item on specific issues, rather than being the result of a full investigation of a general problem at any particular time. Furthermore, when we are dealing with precautionary measures to prevent the entry of undesirable insects, or in the closely related field, plant diseases, it is particularly difficult, when such measures are successful, to establish that any real danger was imminent. Perhaps the most important evidence we can offer is the result of lapsed quarantine precautions due to the exigencies of World War II.

It is for these reasons that it has been felt worth while to review the activities of insect quarantine measures and precautions, particularly as they affect Australia, and endeavour to establish whether or not we have a great deal to gain by the continuance of such activities.

Australia, with its distinctive fauna and flora, and complete lack of agriculture and animal husbandry prior to the advent of the white man, and with her relatively brief period of colonization, should be a very favourable area for the investigation of the economic consequences of the introduction of noxious insects. Many of its insect pests are obvious introductions; some are indigenous and, moreover, the results of the emigration of some of its indigenous insects to other countries are well known. Its disadvantages are its size and the complexity of its insect fauna, which remains inadequately studied in most groups as compared with Hawaii, with a small island area and relatively small and better known insect fauna. However, the diversity of the

environments presented within Australia, as well as the diversity of its primary industries, may in some measure compensate for these disadvantages.

Finally, I should remark that in presenting this address I have in mind not the entomologists or even biologists who may happen to hear it, but rather those whose studies have followed different disciplines and yet who may feel that some elucidation of this problem is worthy of a few minutes of their attention.

2. *Insect Pests in Australia.*

(*a*) Exotic species now present in Australia.

The noxious insects of Australia are partly indigenous species which have transferred themselves from native hosts, either animal or plant, to introduced animals or to plants of agricultural or horticultural significance, and partly exotic species of insects which have entered the Commonwealth since 1788. There is no question concerning the relative importance of the two, the introduced pest species being far more numerous and damaging.

It is difficult to learn much about those pests which became established during the first hundred years or so of our history, and it is even difficult to pinpoint the entry of those which have appeared within the last twenty years. On the other hand, there is some information available concerning those pests which have been intercepted at the occasion of entry, but here we find a regrettable tendency to believe that such abortive introductions could not have established themselves in any case. That such a belief has no basis in fact is evidenced by a selection of cases cited at a later stage of this address.

However, let us consider those pests which may safely be considered to have entered Australia within the past 180 odd years. In the case of those which have been recorded from Australia over a long period, the evidence that they are exotic is simply that they have been known at least as long, if not longer, elsewhere and that they are associated with, particularly, plants which are themselves definite introductions to Australia.

One of the earliest Aphids to arrive in Australia was the Woolly Aphis of Apple, which was recorded as early as 1846 in Victoria. The Aphididae generally are of special interest since no native species are known and yet some 15 or more introduced species are established pests of a variety of plants. This is a remarkable record for one family, but when we consider that most Aphids over-winter in the egg stage one realizes how easily they might enter a new country on imported plants. Much the same applies to the scale insects, which have a long period of attachment to the plant host and hence considerable opportunity for transfer, with their hosts, from country to country. Among the more important scale pests are the Red Scale, the San José Scale, the Mussel Scale, and the White Wax Scale. All of these are definite introductions.

The Green Vegetable Bug has only been known in New South Wales since about 1911, but has become a widespread pest in the intervening years. Similarly the Peach Tip Moth first appeared in the Sydney district about 1909 and has since spread throughout most coastal districts.

The Mediterranean Fruit Fly was first discovered in Western Australia in 1896 and the Brown Vegetable Weevil in Victoria in 1905. An earlier introduction was the Maize and Tomato Caterpillar, the first record of which dates back to 1858.

Our domestic fleas are introductions despite the fact that there are many native species. Most of our mosquitoes are indigenous, but the two most noteworthy domestic species, *Culex fatigans* and *Aëdes aegypti* are undoubtedly introduced and have been here for many years.

It is safe to say that most, if not all, pests of stored products, grains and fabrics have been introduced with certain of the materials they commonly infest. The same applies in large measure to pests of stock and other domestic animals. Taken together with the pests associated with the introduced plants of agriculture and horticulture, the sum total of insect pest species which have entered the Commonwealth from elsewhere is a very formidable one.

(*b*) Australian insects of importance in other countries.

The earliest and most often quoted case of an indigenous Australian insect becoming a pest elsewhere is that of the Cottony Cushion Scale. In Australia this scale appears to be restricted to the members of the large genera, *Acacia*, *Pittosporum*, *Casuarina*, *Grevillea*, *Hakea* and possibly other native Australian plants. When introduced into other parts of the world it almost immediately extended its host range to include *Citrus*, *Prunus*, *Pyrus*, *Robinia*, *Vitis*, *Laurus*, *Magnolia*, *Quercus*, *Buxus* and many other surprisingly different food plants (Essig, 1948).

The introduction of the Cottony Cushion Scale to California took place about 1868, and it soon became one of the most serious pests of Citrus and later appeared on many other fruit crops and ornamentals. By 1890 it had killed hundreds of thousands of orange trees.*

Not so widely known are the cases cited by Miller (1948). "The Blue-gum Chalcid (*Rhicnopeltella eucalypti*)" is "a Tasmanian insect established in New Zealand, where it is actually destroying, throughout the country, over a period of years, the Tasmanian blue gum (*Eucalyptus globulus*) but does not attack any other species of eucalypt. On the other hand the various species of *Eucalyptus* are attacked by the scale, *Eriococcus coriaceus*, the Chrysomelid beetle, *Paropsis dilatata*, and the weevil, *Gonipterus scutellatus*—all Australian species normal to the hosts. The scale actually kills the trees, especially the more susceptible *Eucalyptus globulus*, but little harm is caused by the beetles except that the weevil may produce a pronounced stunting of growth". Certain Australian termites, *Coptotermes acinaciformes* and a species of *Porotermes*, have also been introduced to New Zealand within the last twenty years, and the eucalypt weevil, *Gonipterus*, has also caused severe damage to eucalypts in South Africa following its introduction there from Australia.

3. *Recent Instances of the Spread of Exotic Pests within Australia.*

The time of introduction of most exotic insect pests cannot be established for many of our major pests, either because their early establishment passed unnoticed some time during the last century, or because their importance as pests did not coincide with their early distribution in the Commonwealth. In regard to the latter it is possible that the Sheep Blowfly (*Lucilia cuprina*) did not achieve pest status until long after its arrival, such status being conditional on changes in the type of sheep developed in the country.

Recent introductions are few in number, and this may be a chance occurrence or a tribute to the quarantines which have operated for the past forty odd years. Evidence derived from elsewhere would almost conclusively establish the validity of the latter viewpoint.

We must look particularly to these more recent cases for evidence of what actually happens following a new pest introduction, and one of the most illuminating is the case of the Buffalo Fly.

In one respect the Buffalo Fly is falsely entered in this class, since it seems most probable that it entered Australia as far back as 1825, when buffaloes came to the Northern Territory from Timor. However, the pest remained confined to the Darwin area for many years, and it was not until 1912 that Gilruth was the first to suggest that this fly might eventually prove a major one of cattle. Extensive movements of cattle in the north, which took place in succeeding years, distributed the fly over a much wider area. In 1927 it extended from Broome in Western Australia to the western border of Queensland, and in the following year it entered Queensland south of Camooweal. The range of distribution of Buffalo Fly in Queensland advanced and receded from time to time in the ensuing years in concert with cattle movements and seasonal conditions. A series of wet seasons from 1939 to 1941 resulted in the fly

* Fortunately for our international reputation this pest was eventually brought under complete control in California and in the other countries to which it had been introduced, by the introduction from Australia of a predatory ladybird beetle.

crossing the low rainfall hinterland of the Gulf of Carpentaria, and once across this climatic, but intermittent, barrier its progress to the coast and southward down the eastern coast of Queensland, almost continuously populated with cattle, has been unimpeded (Belschner, 1946).

The history of Buffalo Fly in Australia provides a number of most interesting lessons, although of course we have only gained our wisdom after the event. The adult fly itself has an almost continuous association with cattle and only survives away from its host for a matter of 24 hours. Hence it is most unlikely that adults could be introduced unless cattle were being imported at the same time. The larval stages could survive and develop in cattle dung, but again it is most unlikely that such material would reach Australia without the importation of cattle. Given this knowledge, prevention of its entry would have been quite a simple matter.

Again, for almost 90 years the pest had a restricted distribution in the Northern Territory. At any time during this period an eradication programme might have been attempted, although it must be admitted that this would have had greater chances of success had modern insecticides then been available.

Further, the crossing of the intermittent climatic barrier south of the Gulf of Carpentaria took place in spite of fairly vigorous quarantine precautions in north-west Queensland, assisted, at least in part, by the lack of co-operation of those responsible for cattle movements.

Finally, it is interesting to note that once across this barrier the fly quickly extended its distribution to the hypothetical limits postulated for its distribution by Handschin (1932).

Compared with the Buffalo Fly, the spread of the Cabbage White Butterfly following its introduction, perhaps from New Zealand, was extremely rapid. It was first recorded in a restricted area of Victoria in 1939, following which it was found at Albury in 1940 and in Sydney in 1941, and thence spread rapidly to Queensland. A case of this nature emphasizes the urgent necessity for rapid decisions as to whether any attempts should be made at eradication following the first discovery of such a pest. Delay may mean the loss of all opportunity of eradication and leave us with just one more perennial pest species to be subjected to measures of control year after year. Further, the rapid spread through a number of States also emphasizes the fact that States distant from the site of introduction may really be equally concerned in the arrival, or in the eradication, of the pest within the area of early establishment in the country.

The Argentine Ant is again a recent introduction. It was first recognized in a Melbourne suburb in 1939 and in Perth in 1941. The first Sydney findings were in 1950, but it seems likely that it has been present here for at least three years. It is possible that three separate introductions were involved, but it is equally feasible that this pest has been unknowingly transferred from place to place, perhaps in potplants. There is no doubt, however, that this aggressive insect will continue to spread as opportunity offers (it rarely flies), unless eradicated or most carefully controlled.

In these cases at least we have very tangible evidence of introduction and subsequent spread within Australia. Similar events have taken place many times in the past; others are perhaps still going on. But it is such cases of rapid dispersion that make it clear that widespread distribution following an introduction is possible and, indeed, is almost inevitable, although in many cases the time necessary for obvious dispersion may be a very variable factor.

4. *Evidence of the Introduction of Insects into other Countries.*

In the field of medical entomology clear evidence is available of the transfer of pest insects between the continents of Africa and America across the formidable barrier presented by the Atlantic Ocean.

The chigoe flea, *Tunga penetrans*, which occurs in the tropical and subtropical areas of North and South America, including the West Indies, has been established in Africa for less than eighty years. It is not difficult to envisage how such an insect

with a semi-permanent attachment to the body of man or pigs should effect its transfer from America to Africa.

On the other hand, it is a far more difficult matter for a mosquito to traverse the same ocean, yet this has been accomplished by at least one non-domestic* species, *Anopheles gambiae*. This potent African vector of malaria reached Natal in Brazil about 1930 and in the ensuing years was responsible for epidemics of malaria of the greatest importance.

We may say that these cases all come from the past and that all that is likely to happen has already happened. A counter to this view comes from our knowledge of what has happened in Hawaii in very recent years.

Swezey (1948) discusses 31 species of insects which became established in Hawaii during and since World War II. Included are a variety of moths, wasps, beetles, bugs and flies, and a grasshopper and a cricket. Some of these have already been shown to be devastating pests, others are potentially dangerous, and some, on the other hand, are beneficial. It is revealed that some of these must have come from U.S.A. and others from various parts of the Western Pacific Zone.† A significant number of these introduced insects were first found in the vicinity of Pearl Harbour, "which could be accounted for by reason of the excessive increase in shipping and airplane arrivals at this military centre, and the consequent great difficulty of carrying on quarantine inspections". No attempt is made to include the large number of interceptions of migrant insects made by entomologists in their quarantine inspections. Another point of interest is the fact that many of the first records of these introduced insects came from light traps which have been operated in the Pearl Harbour area with the express purpose of gaining prompt knowledge of the establishment of any anopheline mosquitoes, an event which has not so far taken place.

It is perhaps of interest to mention two of these introductions which are not known to be detrimental. One is the introduction of the wasp *Eumenes latreillei petiolaris* (Schulz) from New Guinea. This wasp has effected a considerable measure of control on the moth *Anacamptodes fragilaria* (Grossbeck), which itself reached Pearl Harbour from California only two years prior to the wasp which has proved such a valuable addition to the fauna of Hawaii. Such a happy set of circumstances is unlikely to occur with any frequency, but it is interesting to record that a chance introduction from the east of a potentially destructive pest is brought under control, at least in part, by an equally chance introduction from the west.

The other of special interest is the introduction of an apparently harmless wingless grasshopper, *Paraidemona mimica* Scudder, from U.S.A., probably Texas. This is one of those cases where it is difficult to imagine how a wingless insect, in the absence of any host animal or plant or other material with which it might be closely associated, should manage to join a ship or an aircraft in order to accomplish such a journey.

In an address to the Entomological Society of Queensland in September, 1950, a guest speaker, Mr. C. Pemberton, stated that a total of 219 species of insects were introduced into Hawaii during the years of World War II. The most important among these was undoubtedly the Oriental Fruit Fly, *Dacus dorsalis* (Hendel), which appeared first in 1945 and rapidly became established throughout the entire group. Its attacks on avocardos and mangoes virtually ruined these industries until 1950, when the work of a team of 40 men on a half-million dollar budget started to show results, principally from the introduction of 15 different parasites gathered from various countries of the Western Pacific Zone. The Oriental Fruit Fly is one of those particularly devastating pests when divorced from its natural controls, and is capable of breeding in all sorts of different fruits and nuts (more than a hundred different host plants

* Certain domestic species, e.g. *Aëdes aegypti*, have become tropicopolitan or, *Culex fatigans*, almost cosmopolitan. Such species which are likely to breed in drinking water might easily have been distributed in water barrels in the days of sailing vessels.

† Of the 31 species discussed, 11 have come from the U.S.A., 6 from Guam, 5 from the Philippines, 5 from other Pacific islands or the Orient, while the origin of the remaining 4 species is uncertain.

were recorded in Hawaii—Cooley, 1950) and should by no means be considered as just another fruit fly.

We have mentioned before the claim that the tempo of insect transfers from country to country underwent a marked increase with the advent of steam navigation. Then, subsequent to the more or less general introduction of quarantine precautions in the first decade of this century, there did appear to be a slowing up of such transfers. For instance, only four major insect pests have become established in the U.S.A. in the quarantine period 1912 to 1948 (Deputy, 1948). Of these, one, the Mediterranean Fruit Fly, has been eradicated and two entered from Mexico, the Mexican Fruit Fly and the Pink Bollworm. The fourth, the White Fringed Beetle, appears to have entered from South America.

In contrast to this, some 30 major pests entered and became established in the U.S.A. during the fifty years prior to the introduction of quarantine precautions.

How, then, do we reconcile the Hawaiian experience with such a trend? Admittedly, quarantine services were in part disrupted during the war, but beyond this we saw for the first time the real effect of extensive air transport. There seems no question that the increased speed of air transport over all previous methods has again brought in its train another and even greater increase in the tempo of insect transference from country to country and has presented us with quite a new set of problems.

At this stage I feel it would be pertinent to review the role of aircraft in insect pest introductions. To those who travel by aircraft, particularly in the northern half of Australia, the frequency with which mosquitoes and house flies are encountered inside passenger cabins is well known, but the extent to which other insects travel inside aircraft is not generally appreciated.

A number of detailed surveys of the insect passengers in aircraft have been made by various workers in the U.S.A. Hughes (1949) gives in considerable detail the entomological findings from a large number of aircraft entering various airports in the U.S.A. from other countries for the 10-year period 1937–47. Out of a total of 80,716 planes inspected during this period, 28,752, or 35·6% of the total, harboured arthropods. From the same total 3,873 or 4·8% harboured mosquitoes. The total number of arthropods found in this period was 106,106, of which 16,846 were alive, and this in spite of the increasing use of disinsectization measures.

The same author records that 12,825 mosquitoes were found during this period, representing 10 genera with a total of 73 species. Of these, 48 were indigenous to one or more of the areas at which they were intercepted, but 25, or 34·2%, of the total number of species, were truly exotic. Some of these were, of course, South American, but a number must have travelled considerably further and nine of them undoubtedly embarked on their flight at some point in the Western Pacific Zone. The distances involved would necessarily be from 4,000 to 6,000 miles.

For one year (1945) the total arthropod records comprised "taxonomically determined categories consisting of 20 orders, 191 families, 680 genera and 524 species", and within the class Insecta, exclusive of biting mosquitoes, 17 orders, 188 families, 670 genera and 491 species were determined, not all catches being identified as far as the species.

Admittedly many of these insects arrived at their destinations dead, but approximately 15% were alive, despite, I must emphasize, the current disinsectization measures applied up till the time of disembarkation.

Another type of evidence of survival of insects in aircraft has been provided by Laird (1948), who transported mosquitoes in cages by aircraft from New Zealand to Japan and back. Of 75 female *Aëdes notoscriptus*, 60% survived the 18-day journey of more than 12,000 miles over a wide range of conditions, and the average life span of those which survived was 61 days. Other details are given, but the above is surely sufficient to establish the ability of mosquitoes to withstand successfully long journeys by air.

5. *Exotic Insect Pests not yet Introduced into Australia.*

A system of insect quarantine regulations and the precautions that go with these would not be justified if it could be shown that there were few, if any, major pests still occurring elsewhere which had not so far reached and successfully established themselves within the Commonwealth.

A little reflection on the part of entomologists will call to mind quite a formidable list of insect pests, well known elsewhere in the world, which have not yet appeared in Australia and yet would certainly occasion us serious trouble in the fields of agriculture, animal husbandry or health.

Among the more obvious plant pests are the European Corn Borer, the Hessian Fly, the Oriental Fruit Fly, the Mexican Fruit Fly, the Boll Weevil, a number of Vine Moths, certain Sugar Cane Borers, the Colorado Potato Beetle, the Apple Capsid, the Pineapple Mealy Bug, Chinch Bugs, the Japanese Beetle, the Gypsy Moth, certain Rice Borers, the European Red Mite, Sirex Wood Boring Wasps and Dry Wood Termites.

In the veterinary field obvious exotic pests, the exclusion of which is most important, are the Warble Flies, the Screw Worm and certain species of ticks other than those already in Australia.

From the viewpoint of human disease we would be most concerned in excluding such potent vectors of malaria as *Anopheles punctulatus punctulatus*, *Anopheles sundaicus* and *Anopheles gambiae*, although quite a number of other species would be considered dangerous. Other arthropods to be excluded would be Tse-tse flies, certain ticks (e.g., *Ornithodorus*) and blood-sucking bugs (Reduviidae).

Particularly in the agricultural field, closer study would reveal an infinitely greater list of pest species one would wish to see prevented from entering the country. However, in each field we have mentioned only the most obvious of the recognized undesirables, and it must be emphasized that other problems exist of an equally serious nature. These are worthy of specific citation.

(i) Phytophagous insects of little or no status as pests in their native environment may be particularly devastating in a new environment or new host-relationship.

(ii) The danger of a plant insect pest does not always lie in the direct damage caused, but such insects may introduce with them a new plant disease. On the other hand, the disease may be present without an adequate vector species, which may find an opportunity of entering at some later stage. Our major concerns here are with plant-sucking bugs and virus diseases.

(iii) Again, in the case of human diseases particularly, we may find the vector well established without the disease, as in the classic case of Yellow Fever. One method of introducing the disease is in infected vectors, a possibility which increases with faster means of transport and the diversification of transport routes. On the other hand we may have the disease and certain of its vectors, but would still find a far more serious problem developing from the introduction of more potent vectors of the same disease.

(iv) Further, it is worth emphasizing that species differences are often of the greatest importance. The fact that we have present in the country certain ticks or certain mosquitoes is no reason for complacency concerning the possibility of the introduction of other species of these groups, and this applies time and time again in a wide variety of groups and genera.

(v) Finally, even though a pest is already present in the country, it may not necessarily be widely distributed and its reintroduction at other points may be just as damaging as a *de novo* introduction. Such circumstances can readily be visualized in the case of a pest of the nature of the Argentine Ant.

6. *The Reality of the Consequences of Pest Insect Introductions.*

Following the introduction of *Anopheles gambiae* into Brazil in 1930 the loss in human lives directly attributable to this introduction was considerable, reaching an estimated total of 14,000 to 20,000 people. For the State of Rio Grande do Norte the estimated deaths exceeded 5,000 out of a population of 243,000 odd. (This State is only a portion of the total area invaded by *A. gambiae* and the estimates were made in

1938, a year before the intensive anti-gambiae campaign commenced). In the same area more than 51,000 cases of malaria were estimated to occur and the economic losses occasioned by the debilitated population were considerable. To these consequences must be added the actual 3,000,000 dollar cost of the eradication of this species from the invaded area.*

Again in 1944 *Anopheles gambiae* caused more than 32,000 primary cases of malaria, of which almost 1,800 were fatal, after its introduction to Upper Egypt was first noticed in 1942. Here also a successful eradication campaign cost a total of £1,000,000 sterling.

Estimates of the economic losses due to insect pests have been made from time to time, but as they are usually based on reductions of yield for various crops they are not necessarily convincing. Estimates of the losses due to Sheep Blowfly were estimated to amount to £3,000,000 in this country during 1942, and this is rather more tangible than a loss of a percentage of a crop before its actual maturity. Even more convincing are figures given for control or eradication programmes. For instance, the Cattle Tick eradication programme on the North Coast of New South Wales had cost £3,000,000 up to the end of 1940.

Unequivocal evidence is also presented by those cases of almost complete annihilation of particular primary industries as was occasioned by the Cottony Cushion Scale on Citrus in California (see above) and more recently the ruin of the avocardo and mango industries in Hawaii by the Oriental Fruit Fly. In the latter case a sum of 500,000 dollars was allocated for the investigation of control measures.

Apart from such tangible cases there is no doubt that considerable losses are occasioned by most insect pests, even though they may be difficult to estimate convincingly. On the other hand, the actual cost of having insect pests, apart from such losses, is clearly indicated by the money spent on their control, and a partial estimate of this (exclusive of labour costs) is presented by the value of insecticides used. No accurate Australian estimates are available for insecticide consumption, but from the limited data of production of certain basic insecticides, and the market has by no means reached saturation for chlorine-containing insecticides at least, it would appear that, at a conservative estimate, two to three million pounds worth of insecticides are annually consumed in this country, and the real figure may be even higher.

Other figures on expenditure for individual pest control or eradication in American cases are quoted by Annand (1950). For example, one fairly recently established pest, the White Fringed Beetle, has occasioned the expenditure of about 1,200,000 dollars during 1950, to which we can add a total of some 9,000,000 dollars spent prior to 1949.

Generally, a perusal of appropriate sources of information does give more and more confirmation of the actual costs of insect pest introductions as being far in excess of the costs of administering quarantine precautions. Up to a point increases in appropriations for such work do increase its efficiency, but beyond this it is a matter of training and knowledge.

7. *Recapitulation of the General Problem.*

In reviewing the evidence presented above it is clear that the following points have been established:

(i) That a very considerable transfer of insect pests has gone on in the past from country to country, even between those separated by wide oceans; and this has been largely accomplished through the agency of modern methods of transport.

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* Soper and Wilson (1943) discount the theory that *A. gambiae* arrived by aircraft. One of the reasons (there are others) is that the first discovery, which had all the appearances of revealing a very recent introduction, was made at a distance of seven kilometres from the airfield with no foci of infestation closer to it. In this connection it is interesting to record that Mr. Hegener, a Dutch colleague, captured a live specimen of *Anopheles bancroftii* on the sixth floor of the Hotel Metropole, Sydney, in April, 1945. This species has not been found south of Queensland and is certainly not known to occur in the Sydney district. It is interesting to speculate just how this insect could have arrived at this location, a distance of more than three miles from the flying boat terminal and considerably more from the land plane airport.

(ii) That, once introduced, insect pest species have proved themselves capable of rapid or delayed spread throughout large tracts of the invaded country.

(iii) That insects of little or no importance in one country may become major pests in another, or, in other words, it is not always possible to prejudge the importance of a particular species should it appear outside its native environment.

(iv) That the possibilities of insect transfers have increased with each marked improvement in methods of transportation, and that recent increases in the volume and diversity of routes of air transport have enormously increased the possibilities of further transfers.

(v) That serious economic losses are involved following the introduction of important pest species which may also be accompanied by serious losses of human life in the case of species of medical importance.

(vi) Finally, that even the reintroduction of existing species may have undesirable consequences either by extending the existing range of distribution of the pest or by the introduction of plant or animal diseases.

It seems obvious, then, that consideration should be given to the possibilities of preventing the entry of insect pests into countries new to them, and we do, indeed, find that insect pest quarantines have been in force in most countries for approximately the last forty years.

8. *Can Insect Quarantine Precautions be Justified?*

Wardle (1929) is prepared to contend that "it is doubtful whether any pest which is at present to the fore would have been prevented by quarantine Acts from gaining admittance to the country" had U.S.A. instituted Plant Quarantine legislation fifty years earlier than it did. He considers that "the possibility of legislative barriers really fulfilling their intentions rests upon a perfection of circumstances which, in the present imperfect condition of civilization, simply does not exist".

Wardle raises these additional objections to legislative barriers: (*a*) that it is rarely possible to foresee that a potentially dangerous insect is likely to become introduced; (*b*) that the cost of maintaining the required inspection forces may be out of all proportion to the possible losses that insect introduction may bring about; and (*c*) that such legislation may act in restriction of international trade and may be used as a weapon by particular agricultural sections that desire economic protection.

The statement by Strong (1923), "the fact that no pest of major importance has become established in the United States since the passage of the Plant Quarantine Act demonstrates in a graphic manner the value of plant quarantine to the United States as a nation", is discounted by Wardle on the grounds that the period of time which had elapsed since the passing of the Act—ten years—was not long enough. We have already quoted the results of thirty-six years of Insect Quarantine operation for the U.S.A. (Deputy, 1948), which is surely sufficient answer to this objection, and we have also given the evidence provided by the wartime breakdown of quarantine precautions in Hawaii.

That the required perfection of circumstances does not exist is an indefinite criticism implying, in part, lack of sufficient knowledge and lack of efficiency on the part of the persons charged with the duties of administering the relevant quarantine procedures. Neither of these difficulties is insuperable, but it is important that quarantine staffs should be adequately trained and suited to their profession.

As experience is gained it becomes increasingly possible to foresee possibilities of pest insect introduction, and as insect and related quarantines become more and more international in their outlook the less credence can we give to this objection.

The critical objection surrounds the relative costs of the administration of such quarantines as compared with the subsequent costs of control or eradication following the establishment of a new pest. When we consider that quarantine is applied in a limited number of ports to ships and aircraft and their cargoes instead of control measures over wide areas of territory or large acreages of crops there seems little room for comparison. Then, when we realize that the quarantine procedures cope with

far more than just individual pest species at the one time, instead of separate control measures for a number of different pests, there can be no doubt that precautionary measures will prove far less expensive. The fact that eradication programmes are seriously considered following the early discovery of a new insect pest is a further denial of Wardle's contention.

Finally, to say that insect quarantine legislation may be used as an economic weapon is not a criticism of the principles of quarantine, but one of the integrity of governments.

If these are the most serious objections to the promulgation of insect quarantine precautions then it must be granted that we have strong reasons, along the lines which have been previously discussed, for the maintenance of such precautions.

9. *The Development of Insect Quarantine Legislation.*

A full discussion of the history of the development of insect and plant quarantine legislation, since the two usually go hand in hand, would be out of place in this address. However, we should realize that such legislation is of comparatively recent date. In California the first promulgations were issued in 1881, for the U.S.A. as a whole not until 1912.

In Australia the Federal Constitution of 1901 empowered the Commonwealth to administer quarantine (Clause 9 of 51). Under the Constitution the first Quarantine Act, which included a Plants Division, which in its turn dealt with insect pests, was passed in 1908 and took effect on July 1, 1909. Until 1921 the Act was administered by the Department of Trade and Customs, but in this year the Department of Health was established by order of the Executive Council and the administration of quarantine became a function of this department, wherein it still remains. The year 1927 saw the foundation of the Divisions of Plant Quarantine and of Veterinary Hygiene as separate divisions of the Department of Health.

Existing procedures do, of course, come under critical review from time to time, and in the case of the Australian Act the most important contribution is found in the Report of the Central Committee appointed by the Australian Institute of Agricultural Science to deal with Overseas Plant Quarantine (Nicholson *et al.*, 1941). Here criticism of existing practice is combined with a detailed series of recommendations concerning improvements in staff and regulations. These are too detailed to be quoted here, but it should be pointed out that at least some of these recommendations have been incorporated in the Regulations under the Quarantine Act, particularly by Statutory Rules No. 92 of 1948 which gives wide powers for the complete destruction of noxious animals or plants following their detection on entry, and by Statutory Rules No. 78 of 1950, which requires the registration of approved authorities who may desire to import nursery stock under permit.

What is of more immediate interest to us in the historical development of insect quarantine precautions is the gradual change in approach that is evident in the legislation of most countries, including Australia.

Early quarantine legislation provided for embargoes against specific known pests, at least from the countries where these pests were known to occur, or restricted entry, subject to the fulfilment of particular provisions, of materials likely to harbour known pests. Inspection on arrival was provided for and any materials subject to restrictions would only be passed through quarantine if found free of the suspect insects, or following suitable treatments to destroy them. Providing the inspecting officer has been suitably trained and knows what to look for in any particular type of material, or has ready access to sources of appropriate information and identification, such a system works reasonably well. There are, of course, some cases wherein it is not possible to detect the pest insect by inspection, e.g., Narcissus Fly in various bulbs. To cope with such cases the material may be fumigated or subjected to heat treatment before shipment, this being done at a time when the bulbs will suffer less damage from such treatment. In other cases provision is now made for the growing of suspect material under quarantine. This may be done by a Federal authority, as in the U.S.A.,

or by the registered importers, as in Australia. A period of at least twelve months is then available for the detection of any pests, disease or insect that may be incapable of detection on entry.

Various ways in which certain commodities, otherwise likely to be subject to embargoes, may receive treatment prior to their consignment or during their period of shipment are discussed by Annand (1950). Of particular interest is the shipment of pre-cooled and refrigerated apples in specially equipped ships from South Africa to the U.S.A., giving a complete mortality of fruit fly larvae, the most dangerous type of pest likely to be contained therein.

Undoubtedly the various quarantine provisions increase in complexity as time goes on, but they do provide more and more protection against pest insects as they become revealed as potential dangers. The tendency is to channel all imports of suspect material through those agencies which would stand to lose most following the introduction of a pest of one of the materials in which they are most interested. And there can be little doubt that such restrictive precautions are ultimately understood to be protective to the importer as well as to the country generally.

There are still cases in which material is imported which is of no interest to anyone, and this applies to the various types of packing used in preparing goods for shipment. In such contingencies the onus is entirely on the quarantine service to see that such packing materials are free of pest insects.

Finally, following on the success of pre-flight treatment of aircraft leaving Hawaii for the U.S.A., particularly to cope with the danger of the introduction of Oriental Fruit Fly, similar arrangements are now the subject of negotiation between Australia, New Zealand and Hawaii. It is considered, on sound evidence (Cooley, 1950), that pre-flight inspection and treatment is a more effective way of dealing with possible insect passengers than similar operations carried out at the end of the journey and, moreover, they are more acceptable to airlines and passengers. There seems little doubt that extensions of this type of operation will come about in the future, especially if reciprocal arrangements between countries can be agreed upon.

Except in the last case, we have dealt with problems usually associated with shipping. Insects harbouring in their host material is one problem, but insects purely as temporary passengers, as they often are on aircraft, dissociated from any host materials, is an entirely different one. Consequently, in recent years, quarantine laws have had to cope with insects arriving in such a manner on aircraft. In the case of Yellow Fever the problem is so serious that International Air Navigation Agreements have been formulated.

Otherwise each country has added to its quarantine laws provisions regarding the treatment of aircraft to ensure that they arrive in an insect-free condition. Further precautions are often taken immediately after landing.

Annand (1950) foreshadows the wider use of point-of-origin inspection and clearance in the future, since it offers greater protection at less cost. He cites the proposal made in 1948 by the United States to the International Civil Aviation Organization. "Contracting States should make arrangements whereby one State will permit another State to station representatives of the public authorities concerned in its territory to examine aircraft, passengers, crew, baggage, cargo, and documentation for customs, immigration, public health and agricultural quarantine purposes, prior to departure for the other State concerned, when such action will facilitate clearance upon arrival in that State."

Perhaps the most standard treatment in use at present for aircraft is the aerosol formulation G–382, containing 3% DDT, 5% of pyrethrum extract (20% pyrethrins), 5% cyclohexanone, 2% lubricating oil and 85% of Freon-12 at a dosage of 5 gm. per 1,000 cubic feet. Admittedly this dosage is not fully effective and pre-flight treatments, when carried out in the absence of passengers, are applied at four times this dosage (Cooley, 1950). Other formulations are discussed by McBride *et al.* (1950), who concluded that the best results were obtained by a combination of residual and aerosol treatments.

In the case of aircraft the problem is not a legislative one but one of technique. Considerable research has been undertaken to disclose a really effective insecticidal technique for application to this special problem, but even though routine aerosol treatments may cope with some of the more obvious Diptera in an aircraft, many other insects remain unaffected. This does not mean that the solution will not be found; eventually it probably will be. Automatic aerosol-dispensing systems for aircraft have been designed and are under trial, and there is little doubt that these would prove an improvement on hand application.

Another approach to the problem is contained in the Report on the Second Session of the Expert Committee on Malaria of the Interim Commission (W.H.O., 1948). This report includes the recommendation "that, whatever regulations be enforced regarding the disinsectization of sea- or aircraft, rigid anti-mosquito sanitation should, as far as practicable, be maintained within the mosquito flight-range of sea- or airports of the country to be protected, so that no imported mosquitoes will be able to survive". The reciprocal procedure, in the country of origin of such mosquitoes, should prove even more effective.

The present importance of aircraft in the transfer of insect species has already been emphasized. It is in this field particularly that uniform legislation and practice is desirable for all countries and varying procedures in different countries can only minimize the effectiveness of precautionary measures generally. The time available for such measures is so brief, and aircraft are liable to pass through many countries, so that changes in procedure will not only be confusing but are likely to evoke varying degrees of co-operation.

We hope, then, that uniform practices, based on critical research, will eventually be adopted on an international rather than a regional scale.

10. *The Broader Aspects of Insect Quarantine.*

We have discussed in some detail the overall background to the problem of insect quarantine, principally because it is a wide field about which relatively few have detailed knowledge of all sections, even among entomologists, and also because its wide scope, covering pests of all horticultural and agricultural plants, stored products, the household, and pests of medical and veterinary significance is deserving of emphasis.

Some general discussion has been given to insect quarantine legislation, but a little more should be said about the implementation of such legislation.

The fact that a port-of-entry inspection service is required has been mentioned, but hand in hand with this must go an identification service for the less obvious of the suspect insect pests that may be intercepted, and efficient treatment facilities for infested material. The identification service must be sufficiently skilled and knowledgeable to make rapid determinations, and the treatment facilities should be sufficiently flexible to cover a range of treatments for reasonable quantities of imported materials. Such facilities do vary from place to place, and it seems only reasonable that those of the major ports of entry should be improved at least to the level of the most efficient.

Beyond this a quarantine service should also provide for prompt and effective action in the way of an eradication programme following the early detection of an insect importation which has escaped detection at entry. In the Australian Act this has been provided for in Statutory Rules No. 92 of 1948. It is not necessary that all the probable requirements for the implementation of such a programme be held in waiting for such an event, but it is necessary that we should know where and how to marshal them when the occasion arises.

In the words of Annand (1947) "quarantines should have two functions, (i) to prevent the entrance of new pests or those not widely distributed, and (ii) to facilitate the movement of commerce by the application of treatments and other safeguards, when such can be used, in lieu of embargoes. They are not intended to serve in place of tariffs, and they must be maintained on a biologically sound basis. To be fully effective they should be based on knowledge of the occurrence, distribution, abundance, hosts, and habits of harmful pests at home and abroad."

This introduces the general background to the operation of quarantine legislation, and Annand also stresses the need for exotic surveys of particularly important imports and the areas from which they come, linked with the findings of inspectors after the arrival of such imports.

In the detection of new pests Annand stresses the importance of initial surveys to establish what is present, and claims that these need to be exhaustive and co-operative and that greater allocations are required for the necessary taxonomic work.

Cooley (1947), writing particularly of the air traffic problem, defines three lines of defence: (i) pest surveys in foreign countries so that we may become familiar with species likely to be dangerous, (ii) inspections at airports, and (iii) continued surveys in the vicinity of ports of entry. The same author also recommends that all vegetation in the vicinity of international airports be continually treated with DDT and other insecticides to prevent establishment of any pests which may escape from arriving planes and that various types of insect traps be maintained in the vicinity of all important air terminals. Such recommendations presuppose the maintenance of an entomological service at major air terminals.

In general, then, we are faced with the need for far more precise knowledge of insect pests on an international basis. For each country to gain its knowledge of exotic pests individually is more than a duplication of effort but, since few countries document their insect pest problems in a form suitable for quarantine purposes, such a procedure may be desirable, at least in special cases, for some time to come. Ultimately, when the type of information required by quarantine services is more widely realized, and there is co-operative effort on an international basis in the preparation of such data and the early circulation of information on new pests the need for exotic surveys will diminish.

But first of all we should know, and document, our own insect pest story, and this applies equally to those which are to us of major and of minor importance. Perhaps such information as we possess is available, but with six States in the Commonwealth and an equal number of journals recording agricultural pest information, the task of abstracting relevant details is a formidable one. The type of documentation envisaged is only accomplished when a specific allocation of staff and money is made for such a project, and it is one of our needs that the specific data on recorded pests, their distributions, habits, life histories, and animals, plants or other materials attacked should be gathered together in one series of publications.*

A prerequisite of such documentation is discussed by Essig (1948), who stresses the need for insect surveys of literature, of collections, and of insect occurrence in the field on a scale sufficiently detailed to provide exact information for such areas with which any particular survey unit can cope. Here again we reveal the need of a wide basic taxonomic knowledge.

Finally, the efficient operation of quarantines depends not only on knowledge within the professional field but it also requires a general public realization of its purposes and a more specific knowledge of individual problems amongst those most concerned with goods likely to be subject to quarantine inspections.

In other words, a public relations programme is also necessary, since lack of co-operation is usually based on ignorance.

In conclusion I should like to emphasize that the time has long since passed when we regarded insect, and also plant, quarantines as restrictive to the commercial exchange of various commodities. The basis on which they operate becomes biologically more sound as time goes on, and the needs of international commerce continually

* This implies a central information service as envisaged by Nicholson *et al.* (1941). It is pleasing to be able to record that for some years now the N.S.W. Department of Agriculture, through its Entomological Branch, has been bringing out an annual insect-pest survey which provides much useful information. For the past two years a section has also been devoted to pests intercepted in quarantine and this provides information of considerable significance.

demand that precautionary treatments and safeguards be developed. A fuller realization of the problems involved is particularly desirable and there is further scope for the encouragement of co-operative effort amongst organizations not directly concerned in the implementation of quarantines.

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The Honorary Treasurer, Dr. A. B. Walkom, presented the Balance Sheets for the year ended 28th February, 1951, duly signed by the Auditor, Mr. S. J. Rayment, F.C.A. (Aust.); and he moved that they be received and adopted, which was carried unanimously.

A vote of thanks to the Acting Honorary Secretary (Dr. W. R. Browne) and the Honorary Treasurer (Dr. A. B. Walkom) for their work for the Society was carried by acclamation.

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

President: Mr. A. N. Colefax, B.Sc.

Members of Council: Lilian Fraser, D.Sc.; Professor J. Macdonald Holmes, B.Sc., Ph.D., F.R.G.S., F.R.S.G.S.; Professor P. D. F. Murray, M.A., D.Sc.; G. D. Osborne, D.Sc., Ph.D.; T. C. Roughley, B.Sc., F.R.Z.S., and A. B. Walkom, D.Sc.

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

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

GENERAL ACCOUNT. Balance Sheet at 28th February, 1951.

LIABILITIES.

	£ s. d.	£ s. d.
Capital—		
Amount received from Sir William Macleay during his lifetime ..	14,000 0 0	
Further sum bequeathed by his Will	6,000 0 0	
		20,000 0 0
Contingencies Reserve		10,303 8 4
Accumulated Funds		30,303 8 4
Suspense	1 13 0	
Bookbinding Account	404 14 1	
Commercial Banking Company of Sydney Ltd.	179 6 3	
Current Liabilities		585 13 4
		£30,889 1 8

ASSETS.

	£ s. d.	£ s. d.
Fixed Assets—		
Commonwealth Loans, at cost	15,048 10 0	
Debentures:		
Metropolitan Water, Sewerage and Drainage Board, at cost	994 7 6	
Science House (one-third share), at cost	14,835 4 4	
		30,878 1 10
Current Assets—		
Cash in hand	10 0 0	
Income Account	19 10	
		10 19 10
		£30,889 1 8

INCOME ACCOUNT. Year Ended 28th February, 1951.

	£ s. d.	£ s. d.
To Salaries		980 5 7
„ Printing Proceedings	705 10 0	
„ Printing Reprints	91 13 3	
„ Blocks	138 9 6	
		935 12 9
„ Insurance		20 6 8
„ Postage	64 9 7	
„ Petty Cash	37 19 11	
		102 9 6
„ Audit	13 2 6	
„ Printing and Stationery	67 15 0	
„ Printing Rules	33 0 0	
„ Expenses	42 5 10	
„ Cleaning	39 0 0	
„ Library	26 7 7	
„ Bank Expenses	3 0 2	
		224 11 1
		£2,263 5 7

	£ s. d.	£ s. d.
By Balance from 1949–50		2 5 7
„ Subscriptions: 1950–51	387 9 0	
Arrears	19 19 0	
In advance	8 8 0	
		415 16 0
„ Entrance Fees		14 14 0
„ Interest		526 1 10
„ Science House		597 0 0
„ Sales		119 2 7
„ N.S.W. Government Grant		100 0 0
„ Fellowships Account (surplus income at 28th February, 1951, transferred)		327 9 6
„ Bank Expenses		1 7 9
„ Rent Refund		3 12 6
„ Grants towards printing		154 16 0
„ Balance to 1951–52		19 10
		£2,263 5 7

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 28th February, 1951, 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 28th February, 1951, as shown by the books. Certificates of the investments have been inspected.

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

Sydney, 20th March, 1951.

A. B. Walkom,
Hon. Treasurer.

2nd March, 1951.

SEROLOGICAL STUDIES OF THE ROOT-NODULE BACTERIA.

IV. FURTHER ANALYSIS OF ISOLATES FROM TRIFOLIUM AND MEDICAGO.

By Hilary F. Purchase, J. M. Vincent and Lawrie M. Ward,
School of Agriculture, University of Sydney.

[Read 28th March, 1951.]

Synopsis.

The present paper summarizes serological data accumulated over a period of about ten years in respect of reference strains of *Rhizobium trifolii* and *Rh. meliloti*. Over this time the antigenic properties of the organisms have shown a high degree of stability and the technique has proved useful for the typing of isolates in field and laboratory studies.

To obtain adequate typing it is necessary to distinguish flagellar and somatic reactions. The latter on its own permits more strains to be distinguished than the former, but maximum differentiation requires both to be taken into account.

Extending the method of analysis used in the earlier papers it has been found that the description of the 12 isolates of *Rh. trifolii* requires at least 2 flagellar and 9 somatic antigens. The corresponding figures for the 16 isolates of *Rh. meliloti* are 4 and 15.

Introduction.

Since the application of improved agglutination techniques to the study of root-nodule bacteria (Vincent, 1941, 1942) fair use has been made of these criteria for the classification and identification of serological strains in field and laboratory studies (Hughes and Vincent, 1942; Kleczkowski and Thornton, 1944; Vincent, 1944 and 1945; Purchase and Vincent, 1949; Read, 1950, private communication). Whilst there is no apparent relationship between serological constitution and the organism's behaviour in association with the host, the method remains a useful technique for distinguishing and grouping strains, a means of studying field distribution, and for "labelling" material for laboratory and field studies.

A comparison of our recent results with those reported in the earlier papers has shown a high degree of stability in antigenic properties; few cases have occurred where a culture has shown any significant change in this regard. The antigenic constitution appears in fact more stable than other characteristics (*cf.*, for example, Kleczkowski and Thornton, 1944; Nutman, 1946).

The earlier papers from this laboratory included reasonably detailed analyses of several strains of both species. The number of fully studied strains has been added to in the intervening years so that a fair battery of testing sera is now available. It has been thought worthwhile, therefore, to record these further studies which provide the basis of our more recent investigations.

Experimental.

Organisms used for the development of antisera.—The isolates are identified by collection numbers and are mostly described in the earlier papers: *Rh. meliloti* (Vincent, 1941) and *Rh. trifolii* (Vincent, 1942). No. 204 has been added to the clover strains, having been obtained as "Clover F" strain from Dr. H. G. Thornton, Rothamsted Experiment Station, England. *Rh. meliloti* No. 52 originated from *Medicago hispida* var. *denticulata* growing at Warracknabeal, Victoria. Additionally it is worth noting that strains 7, 8, 10 and 12 came to us from the United States, the first three from the collection of the University of Wisconsin, and the last via the N.S.W. State Department of Agriculture.

Methods.—The methods of obtaining cultures and using them as antigens for the development and testing of antisera have been largely maintained as in the first paper (Vincent, 1941). It has been generally advantageous to obtain an earlier reading for flagellar (*H*) agglutination at about one hour and advisable to check somatic (*O*) agglutination with heated antigen, particularly in the presence of flagellar agglutina-

tion. Occasional difficulties have been encountered with a less voluminous flagellar agglutination but, provided a two-day motile culture of sufficient density is used, the result has been almost always satisfactory. We have not found it necessary to distinguish *H* by the use of *O*-absorbed sera or by the removal of *O* antibody by heat, although some workers might well prefer this added check (Kleczkowski and Thornton, 1944).

Results.

Strains of Rh. trifolii.—Tables 1 and 2 give the results for flagellar and somatic reactions respectively.

Two major groupings of flagellar antigens are revealed, one represented by strain 36, and the other by strain 46. Following the 1942 treatment these have been classed A and B respectively. The earlier paper also showed by absorption tests that the five members of the first group tested on that occasion were identical. Flagellar reactivity has now been found between 157, 161 and 46—a result at variance with the earlier findings but supported by the agreement between reciprocal tests.

As has been found generally in these species, somatic antigens provide more groupings than do the flagellar. On the basis of what we now know of the somatic cross reactions of these strains the minimum number of somatic antigens would have to be extended from three to seven. Absorption tests have been applied in some detail to the 94–160 group of Table 2, and make it necessary to bring the number of antigens to nine. Some irregularities seem to be associated with antigen II of 94, 61, 111 and 161

Table 1.

Flagellar Cross Reactions of Rhizobium trifolii.

Antigens.	Sera.											
	36	108	61	111	94	91	160	204	46	157	161	64
36	*3* 3	3 3	2 3	2 2	2	2 3	2	2	––	–	–	–
108	3 3	*3* 3	3 3	2 2	2	3 3	2	2	––	–	–	–
61	3 3	3 3	*3* 3	2 2	2	2 3	2	2	––	–	–	–
111	2 3	3 3	3 3	*2* 2	2	2 2	2	2	––	–	–	–
94	3 3	2	3	2	*3*	2	2	2	––	–	–	–
91	3 3	3 3	3 3	2 2	2	*2* 2	2	2	––	–	–	–
160	3 3	2	2	1	2	2	*3*	2	––	–	–	–
204	3	2	2	2	2	2	1	*3*	–	–	–	–
46	––	––	––	––	–	––	–	–	*3* 3	2	2	3
157	––	–	–	–	–	–	–	–	2 –	*3*	2	0–1
161	––	–	–	–	–	–	–	–	2 –	2	*3*	0–1
64	––	–	–	–	–	–	–	–	3 3	2	2	*3*

Note.—Numbers indicate highest dilutions showing agglutination, viz. 1 = 1/25 to 1/50, 2 = 1/100 to 1/200, 3 = 1/400 to 1/800, 4 = 1/1600 to 1/3200 or greater.
Top right-hand figure shows earlier result.

and indicate the possibility that the antigen might be composite and its components variable in their relative proportions between strains and in the one strain at different times.

The findings can now be summarized:

Isolate.	Minimal Antigenic Composition. Flagellar.	Somatic.
36, 108	A	I
94	A	II, IV, VII
61, 111	A	II, V
160	A	IV, VII
91	A	III
204	A	IX
64	B	I
161	B	II, IV, VI
46	B	III
157	B	VIII

Sera of the six strains underlined have been used for typing field isolates (Purchase and Vincent, 1949) and include representatives of both flagellar types and eight of the somatic antibodies.

TABLE 2.

Somatic Cross Reactions of Rhizobium trifolii.

Antigens.	Sera.											
	36	108	64	94	61	161	111	160	91	46	204	157
36	*4* 4	4 4	2	–	–⁻	–	–⁻	–	–⁻	–⁻	–	–
108	4 4	*4* 4	4	– – –	–⁻	–	–⁻ –	–	–⁻	–⁻	–	–
64	3 4	4	*4*	– –	–⁻	–	–	–	–	–⁻	–	–
94	–⁻	–	–	*3*	3 2	3	2	3	–	–⁻	–	–
61	–⁻	–⁻	–	3	*4* 3	3	2 3	–	–	–	–	–
161	–⁻	–	–	3	2⁻	*4*	–	3	–	–⁻	–	–
111	–⁻	–⁻	–	2	4 3	–	*4* 3	–	–⁻	–⁻	–	–
160	–⁻	–	–	3	–⁻	2	–	*4*	–	–⁻	–	–
91	–⁻	–⁻	–	–	–⁻	–	–⁻	–	*4* 4	4 3	–	–
46	–⁻	–	–	–	–⁻	–	–⁻	–	4 4	*4* 4	–	–
204	–⁻	–	–	–	–⁻	–	–	–	–	–⁻	*4*	–
157	–⁻	–	–	–	–⁻	–	–	–	–	–⁻	–	*4*

Note.—Numbers indicate highest dilutions showing agglutination, viz. 1 = 1/25 to 1/50, 2 = 1/100 to 1/200, 3 = 1/400 to 1/800, 4 = 1/1600 to 1/3200 or greater.
Top right-hand figure shows earlier result.

TABLE 3.
Flagellar Cross Reactions of Rhizobium meliloti.

Antigens.	Sera.														
	7	8	12	27 62	51	52	66	74	76	102	126	134	10	47	101
7	*4*	4	4	4 [4]	4	4	4	4	3	4	4	4	2	– [2]	–
8	4	*4*	4	4 [4]	4	4	4	4	2	4	4	4	1	1 [1]	–
12	4	4	*4*	4 [4]	4	4	4	4	3	4	4	4	1	– [1]	–
27, 62	4	4	4	*4* [4]	4	4	4 [4]	4 [4]	3	4 [4]	4	4	1	– [1]	–
51	4	4	4	4 [4]	*4*	4	4	4	2	4	3	4	2	1 [1]	–
52	4	4	4	4	4	*4*	4	4	3	4	4	4	1	–	–
66	4	4	4	4 [4]	4	4	*4* [4]	4 [4]	3	4 [4]	4	4	2	2 –	–
74	4	4	4	4 [4]	4	4	4 [4]	*4* [4]	3	4 [4]	4	4	1	1 [1]	–
76	4	4	4	4 [4]	3	4	4	4	*3*	4	4	4	1	1 [1]	–
102	4	4	4	4 [4]	4	4	4 [4]	4 [4]	3	*4* [4]	4	4	1	1 [1]	–
126	4	4	4	4 [4]	4	4	4	4	4	4	*4*	4	1	– –	–
134	4	4	4	4 [4]	4	4	4	4	3	4	4	*4*	2	– [1]	–
10	2	1	2	± [2]	–	1	1	±	–	2	1	2	*4*	3 [4]	–
47	2	2	3	1 [1]	3	3	1 [2]	1 [1]	–	1 [2]	3	3	4	*3* [3]	–
101	–	–	–	– –	–	–	–	–	–	–	–	–	–	– –	*5*

Note.— ± = variable result at lowest titre ; code otherwise as for Table 1.

Strains of Rh. meliloti.—Tables 3 and 4 give flagellar and somatic reactions of sixteen strains.

Most of the flagellar reactions are those previously seen in strain 27, but strain 10 has the major antigen of 47, and 101 is different from both these groups. Using the notation of the first paper, 10 and 47 are described as Ab, the 27 group as bC and 101 is now characterized as D. The symbol *b* is used to describe a minor antigen that is commonly shared by members of the first two groups.

Somatic antigens provide a basis for further division. Approximate groups are represented by:

7, 27 and 62, 47
52, 102
126, 8, 12
134, 74
66
10, 76, 101
51

although there is a certain amount of cross reaction beyond these limits. Cross absorption tests have shown 7, 27 and 62 to be identical; they have, however, an antigen additional to those of 47 and the latter has an antigen not common to them. No. 76 also appears to have the same antigenic constitution as 101, otherwise there are differences even within the members of the groups set out. The group represented by 126, 8 and 12 shows a wide range of reactivity when they constitute the antigen, but outside the group itself reciprocal tests are mostly negative. It seems that the cells of

TABLE 4.
Somatic Cross Reactions of Rhizobium meliloti.

Antigens.	Sera.														
	7	27 62	47	52	102	126	8	12	134	74	66	10	76	101	51
7	*4*	4^{4}	1^{2}	–	$-^{-}$	–	–	–	–	$-^{-}$	$-^{-}$	–	–	–	–
27, 62	3	4^{4}	2^{2}	–	$-^{-}$	–	–	–	–	$-^{-}$	$-^{-}$	–	–	–	–
47	3	3^{3}	3^{4}	1	$\pm^{1}$	–	–	–	±	$-^{-}$	$-^{-}$	–	–	–	–
52	2	–	1	*4*	2	4	±	–	±	–	–	–	–	–	–
102	–	$-^{-}$	1^{1}	3	4^{4}	1	–	–	–	$-^{-}$	$-^{-}$	–	–	–	–
126	1	$\pm^{-}$	2^{-}	2	2^{3}	*4*	3	3	2	2^{-}	2^{-}	3	2	–	3
8	1	$-^{2}$	3^{1}	2	2^{2}	4	*4*	4	3	2^{2}	2^{3}	2	2	3	3
12	–	$-^{2}$	4^{3}	2	1^{2}	4	4	*5*	4	1^{2}	2^{3}	4	2	3	3
134	–	$-^{-}$	$-^{-}$	–	$-^{-}$	1	–	–	*4*	2^{3}	$-\pm$	–	–	–	–
74	–	$-^{-}$	$-^{-}$	–	$-^{-}$	–	–	–	3	2^{3}	1^{1}	–	–	–	–
66	–	$-^{-}$	$-^{-}$	–	$-^{-}$	–	–	–	1	$-^{-}$	2^{4}	–	–	–	–
10	–	$-^{-}$	$\pm\pm$	1	$-^{-}$	±	–	±	±	$-^{-}$	$-^{-}$	*4*	3	4	1
76	–	$-^{-}$	$-^{-}$	–	$-^{-}$	–	–	–	–	$-^{-}$	$-^{-}$	2	*3*	3	–
101	–	$-^{-}$	$-^{-}$	–	$-^{-}$	–	–	–	–	$-^{-}$	$-^{-}$	3	3	*3*	–
51	–	$-^{-}$	$-^{-}$	–	$-^{-}$	–	–	–	–	$-^{-}$	$-^{-}$	1	±	–	*2*

Note.—± = variable result at lowest titre, code otherwise as for Table 1.

this group are relatively easy to agglutinate, perhaps by a less specific antibody, and only reactions that have reciprocal tests in agreement have been used in stating somatic antigens. Cases 52 against serum 7, 66 *vs.* 134, 10 *vs.* 52, in which the reciprocal test is negative, have also been ignored. Antigen II, previously postulated as common to 66 and 74, would, on similar grounds, be regarded as a doubtful or minor antigen.

The data for cross reaction and absorption tests can be symbolized thus:

Isolate.	Minimal Antigenic Constitution. Flagellar.	Somatic.
47	Ab	I, III
10	Ab	X, XI
7, 27, 62	bC	I, IV
52	bC	III, V, XII
102	bC	III, V, XIII
126	bC	V, VIII, IX
8	bC	VIII, XIV
12	bC	VIII, XV
134	bC	VI, IX
74	bC	II, VI
66	bC	II, VII
76	bC	X
51	bC	XI
101	D	X

Sera of the strains underlined have been used in typing field isolates (Purchase, Vincent and Ward, 1950). These include the three flagellar groupings and all the somatic antigens so far revealed.

Discussion.

These results emphasize the serological heterogeneity that exists within a "species" of *Rhizobium*. There are notably fewer differences in flagellar reaction than somatic, and distinction between the two types is obviously desirable for the more specific recognition of a strain. It is interesting to observe how, with both clover and medic isolates, the one somatic antigen can occur with any of the flagellar groupings.

Acknowledgements.

The work reported in this paper has been supported in part by grants from the Commonwealth Research Committee and the Rural Bank of New South Wales.

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A SEPTORIA DISEASE OF *EUPHORBIA PEPLUS* L.

By Dorothy E. Shaw,
Faculty of Agriculture, University of Sydney.

(Plate i; one Text-figure.)

[Read 28th March, 1951.]

Synopsis.

A *Septoria* disease of Petty Spurge is described, and the Australian distribution is given. The cultural characteristics and morphology of the causal organism are described. The results of investigations concerning the host-parasite relations, the longevity of the spores, the search for the perfect stage, and pathogenicity tests with other plants are given. The literature describing species of *Septoria* parasitizing species of *Euphorbia* is examined, and the name *S. pepli*, n. sp., is proposed for the causal organism.

Introduction.

A leaf and stem spot disease of *Euphorbia peplus* L., caused by a species of *Septoria*, was pointed out to the writer by Professor W. L. Waterhouse in 1947. He had had it under observation for some time, and noted that infection on Petty Spurge was quite widespread around Sydney. At his suggestion an investigation of the disease was carried out, with particular reference to the host range, as some serious diseases of economic plants are caused by species of *Septoria*.

Economic Importance.

Euphorbia peplus L., Petty Spurge, native to Europe and Asia, occurs on the New South Wales coast and tablelands, and in Queensland, Victoria, South Australia and Western Australia, as recorded by Hurst (1942). She listed its reputed medicinal and photographic properties, but to the writer's knowledge it is not used commercially in Australia. Hurst also recorded it as containing a poisonous principle, euphorbin. It is a weed of gardens and waste places, but is easily eradicated. The disease is not of economic importance.

Review of Literature.

Australian Records.

No mention of a leaf and stem spot disease of *E. peplus* was made by Cooke (1892) or by McAlpine (1895). The disease was noted by Waterhouse (unpublished data) in June, 1921, in the Sydney area. Pieces of material collected by him and embedded in wax in 1921 are filed at Sydney University. Also filed are pieces of diseased material in wax from a collection made in July, 1932, again from the Sydney area. A record of a *Septoria* leaf spot disease of *E. peplus* was made by Noble *et al.* (1934), without either date or locality of occurrence. The herbarium specimen lodged at the Department of Agriculture, Sydney, is also without date of occurrence, locality or collector's name. A *Septoria* species is recorded occurring on *E. peplus* in Brittlebank's catalogue of Australian Fungi (unpublished), compiled between 10th May, 1937, and 2nd March, 1940, but no indication of the date or locality is given, and no specimen is filed in the herbarium.*

Overseas Records.

Diseases caused by six species of *Septoria* and two species of *Rhabdospora* were recorded by Saccardo (1884, 1892, 1913)), on eight species of *Euphorbia*, but none on *E. peplus*. Oudemans (1921) listed species of *Septoria*, *Phleospora* and *Rhabdospora* on various *Euphorbia* species in Europe, but none on *E. peplus*. No *Septoria* was recorded for any *Euphorbia* by Grove (1935), although a *Rhabdospora* was noted on one species of *Euphorbia* in Britain.

* Personal communication from Mr. S. Fish, Government Biologist, Department of Agriculture, Victoria.

In a personal communication, Dr. G. R. Bisby, of the Commonwealth Mycological Institute, reported that he could find only one record of a species of *Septoria* on *E. peplus*, and that was of *Septoria euphorbiae* Guep. in the Russian book "Key to Fungi, Vol. 2. Fungi Imperfecti", by A. A. Jaczewski (1917). I am indebted to Dr. Bisby for his translation of the significant paragraph: "p. 102. *S. euphorbiae* Guep. on *Euphorbia amygdaloides*, *E. peplus*. Round, olive-coloured spots. Stylospores 40 to 45μ by 2 to 2·5μ with 3 to 4 indistinct septa." Dr. Bisby also reported that no *Septoria* was recorded on *Euphorbia* spp. for North America by Seymour (Host Index of the Fungi of North America. Cambridge, Mass., 1929), this volume being unavailable to the writer.

No *Septoria* on any species of *Euphorbia* was recorded for South Africa by Doidge and Bottomley (1931), by Brien (1939) for New Zealand, or by Shigekatsu Hirayama (1931) or Nakato Naito (1940) for Japan.

Australian Occurrence.

The disease occurs on Petty Spurge over a wide area around Sydney, and collections were made throughout the area extending from Mangrove Mountain, near Gosford, in the north, Windsor in the west, and Mt. Keira, near Wollongong, in the south, in 1948 and 1949. In 1950, two further collections were made at Canberra, A.C.T., and Wagga, N.S.W.

The disease has not been recorded for Western Australia, South Australia, or for Queensland.* It is not known whether Brittlelank's record was for Victorian occurrence. In Tasmania in 1948 the writer collected diseased Petty Spurge plants at Launceston, Hobart, and Port Arthur.

From the information available at present, the disease is known to occur around Sydney, at Wagga, Canberra and throughout Tasmania.

Appearance of the Disease.

Lesions first appear on the leaves as small, mostly circular areas, pale green in colour, later spreading and turning pale yellow, then light brown, becoming papery and covered with scattered black pycnidia. Many lesions per leaf were recorded (in one case 14 apparently separate ones), but the majority of field specimens examined showed that infection was from one centre only, although sometimes two were observed. The pycnidia occur on both sides of the leaf, but mostly on the undersurface. A few lesions examined had a total lack of pycnidia on the upper surface, although numerous ones were found on the lower. In some cases a slight zonation of pycnidia occurs radially from the centre of infection. The pycnidia are produced singly, only rarely being grouped in twos or threes. As the necrotic tissue enlarges, slight puckering often occurs between this area and the rest of the leaf. The edge of the necrotic area is generally quite regular and definite, but without cicatrix formation. Pycnidial production is usually confined to the necrotic area, but occasionally lesions were found where pycnidia occurred at the edge of the lesions in advance of necrosis. Where several lesions occur per leaf, the diseased areas later coalesce. In the advanced stages of the disease premature leaf fall occurs.

Lesions on the stem occur less frequently than on the leaves. The leaf infection, in many cases, extends to the petiole and thence to the stem. Pycnidia occur on both petioles and stems. Stem infections were produced in the glasshouse, which were so severe as to cause death to the uninfected upper part of the plants.

Pycnidia were recorded on the seed capsules on material from the field, as well as on plants inoculated in the glasshouse. No pycnidia were noted on the seeds.

Cultural Characteristics.

Isolation Methods.

Isolations of the causal organism were first made by the usual method of tissue transplants, pieces of diseased material of about $\frac{1}{4}'' \times \frac{1}{4}''$ being cut from the edge of

* Personal communications from Mr. W. P. Cass Smith, Government Plant Pathologist, Western Australia, Mr. D. B. Adam, Department of Plant Pathology, University of Adelaide, and Professor D. A. Herbert, University of Queensland.

the lesions, or just in front, and taken through 95% alcohol for 5 seconds, mercuric chloride 1 in 1000 for 20 seconds, and three washings with sterile water, then transferred with sterile forceps to freshly poured and cooled plates of potato dextrose agar. It was found, however, that if a contaminant present had escaped the surface sterilization, it usually grew at a rate much in excess of the *Septoria* mycelium, which was subsequently difficult to obtain in pure culture. The method later adopted was to allow the spores to exude from the pycnidia in the leaf, into a drop of distilled water, and to streak a loopful of the spore suspension over the surface of the P.D.A. plates. Bacterial and fungal contaminants were sometimes present, but because of the scattered nature of the *Septoria* spores isolations were not difficult. Transfers were then made to P.D.A. slopes, of single spores or hyphal tips, as well as mass transfer of mycelium. Nine isolations were made from collections, five from within the Sydney area, three from Tasmania, and one from Wagga. Nineteen collections were made from many diseased plants observed in the field, three of these being from Tasmania, one each from Wagga and Canberra, and the rest from a wide area around Sydney.

Media.

The fungus grew on P.D.A., water agar, standard agar, maize meal agar, maize husks and maize cobs, potato cubes, lucerne shoots, lima bean agar, dried pea agar, lentil agar, soaked rye and peanut husks, also on Czapeck-Dox with marmite, and wort agar. It also grew on a water extract of *E. peplus* leaves in agar, and on sterile shoots and stems of *E. peplus*. Growth on water agar was very slow and meagre. Pycnidia, mostly well formed, were produced on all the media, often with abundant pinkish exudate of spores, especially on the sterile stems of Petty Spurge, and on the rye-peanut husk media. P.D.A. proved the most satisfactory media for mycelium and spore production and for maintaining cultures.

Appearance of Cultures.

Spores germinate on P.D.A. usually within twenty-four hours. After three to four days the colonies are visible, being whitish in colour, and distinctly mucose, with a smooth surface and an entire edge to the naked eye. As the colonies develop, the edge becomes slightly irregular and the surface slightly ridged. At seven days most colonies have become black in the centre, and at 17 days are all black, sometimes with a tinge of greeny-grey, with a minute border of white at the edge.

On P.D.A., cultures later produce small greyish patches of very short, pile-like aerial mycelium. Black carbonaceous pycnidia are embedded over the surface, and these, in most cultures, give pink exudates of masses of spores. Where pycnidia occur near the side of a tube, cirri can be easily distinguished under the low power of the microscope. These spore masses are yeast-like in appearance to the naked eye. The mycelial mass later becomes carbonaceous, piled and convoluted in the centre, and with sub-surface hyphae at the edge. The hyphal mass remains very compact and difficult to separate, with growth upwards nearly as great as lateral growth. Seldom is the whole surface of the slope covered with mycelium, and often cracks occur in the agar. After about three months small tufts of white cottony mycelium appear in patches over the surface in some slopes. Colonies are usually non-sporulating about this time. In some cultures more than four months old, hard carbonaceous bodies appeared on the surface and along the cracks in the agar. The structures, when sectioned after fixing in chrom-acetic and stained with gentian violet-orange G, were roughly circular to oval, but measured anything from 200 to 500μ wide (measuring from the innermost walls). The interior had no definite structure, but consisted of wispy strands of fungal material, which could not be distinguished as hyphae. The walls consisted of 6–9 layers of very dark brown, thick-walled, pseudoparenchymatous cells, which pass into a region of brownish, twisted, strongly septate, clearly distinguished hyphae. No development further than this sclerotial-like stage was observed.

Optimum Temperature.

Optimum temperature was determined by growing the fungus in small ($2\frac{1}{4}$") Petri dishes on P.D.A., and incubating over a range of temperatures. Three tests were

carried out at different times. In the first two tests duplicate plates were used, in the third only one plate was inoculated for each temperature, except for 20°C., when duplicate plates were used. All the tests gave approximately the same results for the temperatures available. Inoculum was of the Pennant Hills isolate, approximately 2 mm. square, and readings were taken at four weeks. The readings for the third test are given, as the range available at that time was a little more comprehensive.

TABLE 1.
Growth of the Causal Organism at Various Temperatures.

Temperature. ° C.	Colony Diameter. mm.	Spore Production and Character of Growth.
3	2× 2	No growth discernible.
5	2× 4	Very slight growth.
10	7× 9	Colony black with small white margin ; no spores.
15	13×14	Colony similar to above ; no spores.
20	16×17 (mean of 2 plates)	Colony black with greenish tinge ; on the reverse side, clumps of pycnidia in concentric circles ; abundant spores.
25	10×12	Colony black ; no spores.
30	2× 2	No growth discernible.
Room temp. (light)	13×16	Colony as at 20° C. ; abundant spores.
Room temp. (dark) (June-July)	12×13	Colony as at 20° C. ; very abundant spores.

Optimum temperature for mycelial growth and spore production is around 20°C. Colonies at the other temperatures might have produced spores when older. No measurement was made of the height of the colonies, but this increased with increase in diameter.

Optimum pH.

Optimum pH was determined by growing the fungus on plates of P.D.A. adjusted with N/5 NaOH or N/5 HCl to give a series varying in hydrogen-ion concentration. Two tests were conducted, and the pH was read on a Vane Electronic pH Meter. Duplicate plates were used in the first test, triplicate plates for the second. Readings of pH were taken before inoculation. Inoculum was of the Sandy Bay (Tasmania) isolate, approximately 2 mm. square. Plates were kept at room temperature during May and June, and measured after seven weeks.

TABLE 2.
Growth of the Causal Organism at Various Hydrogen-ion Concentrations.

pH.	Colony Diameter. mm. (Mean of 3.)
3·6	6·0× 9·3
4·8	23·6×25·3
5·6	26·0×29·5
6·8	24·3×26·3
7·7	22·0×24·0
8·6	16·0×18·6

Optimum pH is about 5·6 or a little more alkaline. Specificity is not very marked over a wide central range, the greatest effect being shown on the very acid side at the concentrations taken.

Test for Pathogenicity.

Isolations of the organism were made as outlined previously, and the fungus maintained on P.D.A. slopes. Spores from pycnidia produced in culture were used to inoculate leaves of Petty Spurge seedlings in the glasshouse as outlined under "Host-parasite Relations, Method". Typical symptoms of the disease appeared on the leaves, with production of pycnidia. Isolations made from these lesions yielded the organism which was similar in detail to that isolated initially.

Morphology of the Causal Organism.

Mycelium.

The mycelium in young colonies consists of stellately radiating hyphae, which are minutely guttulate, hyaline, septate, and branch profusely. Pigmentation occurs in hyphae about six days old. Old hyphae (i.e., after a period of months), become very nobbly in outline, olive in colour, often with large refractive globules, but usually without any apparent contents. Young hyphae at the edge of colonies are very fine. Mycelium in colonies 13 days old measured up to 3μ in diameter, and at four months measured about 4μ in diameter. Hyphae in the plant tissues measure $2–3\mu$ in diameter.

Pycnidia.

Pycnidia occur on both sides of the leaf, but mostly on the under-surface, scattered over the centre and sometimes on the marginal green areas of the necrotic spots; singly, only rarely in twos or threes; visible to the naked eye, black in colour, but reddish-brown by transmitted light; globose, immersed but later erumpent; ostiole about one-quarter the diameter of the pycnidium; pycnidial wall smooth, composed of 2–3 layers of pseudoparenchymatous cells; $85–135\mu$ ($65–160\mu$), mean $110{\cdot}19\mu \pm 18{\cdot}98\mu$.

Pycnidiospores.

Pycnidiospores hyaline, straight to very slightly curved, attenuated at one end, with a varying number of guttulae; usually three septa, often two, sometimes one, rarely aseptate or four-septate; $25–44\mu$ ($17–51\mu$), mean $35{\cdot}77\mu \pm 5{\cdot}94\mu$.

Cirri.

Cirri were often found exuded from the ostioles in material examined straight from the field, and practically always from material in the glasshouse, owing to the high humidity. They are colourless under reflected light, and in strong sunlight can be seen with the naked eye as a glistening whitish spot on the pycnidium. The horns vary in length, nearly always curl over, and often adhere to the neighbouring horns. On diseased material from the glasshouse, cirri were noted from quite small pycnidia. Cirri were observed microscopically by placing diseased stems from the glasshouse (with cirri still attached) into lacto-phenol cotton-blue, and by allowing pycnidia produced in culture to exude spores into dilute lacto-phenol. The pycnidiospores are oriented with their long axes parallel to the horn. When material with cirri already exuded is placed into water the spores immediately separate from one another. When pycnidia with unreleased spores are placed in water, the spores are ejected separately, not exuded in cirri.

Observations on Pycnidiospores.

Spore Structure.

Pycnidiospores of all isolates examined were hyaline, the septa being indistinguishable unless stained. Stains used included cotton-blue lacto-phenol, aqueous gentian violet, nigrosin, aceto-carmine, and gentian violet, orcein and carbol fuchsin in lacto-phenol. Cotton-blue lacto-phenol proved to be the best stain to show cell contents. This stain acts quickly, the protoplasm staining blue of varying intensity. Guttulae were of various sizes, sometimes two large ones appearing in each cell, one at each end near the septa, sometimes one large guttula only, as well as numerous small ones. The number of large guttulae was not constant per cell or per spore. Septa were unstained with gentian violet, the spore contents appearing granular with large refractive drops in most cells. In material fixed, sectioned and stained with gentian violet-orange G,

nuclei were clearly distinguishable in the spores and conidiophores. Spores mounted in water and examined with dark field illumination, showed the cell contents as circular areas of light of varying size and intensity, as shown in Plate 1, B, by MacMillan and Plunkett (1942).

Septation of Spores.

Because of the confusion in the literature regarding the number of septations in most species of *Septoria*, this aspect of the causal organism was particularly observed. MacMillan and Plunkett (1942), following on the work of Garman and Stevens* (cited by the afore-mentioned but unavailable to the writer), have shown that there is a great inadequacy on this point for most published descriptions of *Septoria* species. Sprague (1944) and MacMillan and Plunkett consider that the number of septations of the spores is usually 1, 3 or 7, depending on whether there are 1, 2, or 3 nuclear divisions in the spores, and that there is simultaneous division of the end cells, after formation of the primary septum. MacMillan and Plunkett concluded that the spores become mature on attaining the 3-septate condition, but not before, and that an even number of septa in the spores is anomalous. These authors found it difficult to account for the very large number of observations in the literature for even-numbered septate spores. Sprague (1944) found that some species infecting grasses are characterized by 2-septate spores, while five septa are common in others. He concluded that in some species the number of nuclear divisions evidently is dependent on the available cell nutrients; that large spores produced in humid winter weather may have two or even three nuclear divisions, while later in the season, when the weather is warmer and drier, the same species may produce aseptate or 1-septate spores.

Septa are indistinguishable in unstained spores. Stained with cotton-blue lactophenol, the septations are visible, but the granular nature of the cells does not make for easy observation. The best method found was as follows: diseased material with pycnidia was placed in a drop of water on a slide, and the spores allowed to exude. After a minute or so, the tissue was lifted from the slide, and a drop of iodine in potassium iodide in 80% alcohol was added, this being a modification of the method used by Brodie and Neufeld (1942). The cover slip was lowered, and the septation counts made immediately. The spores, with this method, appear a homogeneous golden-brown, with the septa, under slightly reduced light, clearly distinguished.

TABLE 3.

Septation of Spores from Different Collections, at Various Intervals from Time of Collection, and from Culture.

Collection.	No. of Spores Examined.	Time from Collection.	Percentages of Spores in the Various Septate Classes.					
			0	1	2	3	4	5
Mangrove Mtn.	200	2 weeks.	—	10·0	28·5	60·5	1·0	—
Mt. Keira	200	2 months.	0·5	17·5	37·0	44·5	0·5	—
P. Arthur, Tas.	200	4 months.	—	19·0	46·5	33·0	1·0	0·5
Sandy Bay, Tas.	200	4 months.	—	10·5	36·0	53·5	—	—
Sandy Bay, Tas.	100	6 months.	—	6·0	15·0	79·0	—	—
*Sandy Bay, Tas.	142	—	—	1·9	46·0	52·1	—	—
Penshurst	100	11 months.	1·0	21·0	38·0	40·0	—	—

* Spores from culture.

The results shown in Table 3 indicate that the maximum number of septa in mature spores is three, practically no further division taking place until germination. The first cell-division in the spore would appear to take place early, because of the very small number of aseptate spores which appear in the counts. Spores in which

* Garman, P., and F. L. Stevens, 1920.—"The genus *Septoria*." *Ill. State Acad. Sci. Trans.*, 13 : 176-219.

two cell-divisions have taken place (giving four-celled spores) would most probably be spores produced under optimum conditions. The large percentage of 2-septate spores could only be explained where only one cell divided after the formation of the primary septum. It is to be noted that a large number of 2-septate spores was also produced in culture. Counts from all the above collections are of the same general type, i.e., 3>2>1-septate spores (except the Port Arthur isolate, where the 2-septate spores predominate), with 0-, 4-, and 5-septate spores occurring only very rarely. The relative percentage of 3-, 2-, and 1-septate spores is most likely conditioned by nutrition. Age, under the conditions of storage of the material, did not appear to affect the relative percentages greatly.

Germination of Spores.

1. *Method and manner of germination.*

Germinations were studied on plates of P.D.A., the media having been strained, and only that amount which would just cover the bottom poured into Petri dishes. Spores from a water suspension were streaked over the surface with a loop. With this method, each streak of spores could be followed under the microscope with ease. Germination conformed in general to that described by MacMillan and Plunkett (1942) for 20 representative spores of *S. apii-graveolentis*. These workers noted that, at the end of four hours, the two end-cells had divided, and the tapered end of the spore had increased in length more than the other cells. At twelve hours the end-cells had divided, and at 24 hours the two original centre-cells had divided, and the outer cells of this division had sent out tubes. The spores were originally all 3-septate, and the germination was quite symmetrical.

In the present study, it was noted that germination was not always symmetrical, and counts were made of the positions of emergence of germ tubes. Readings were taken on 200 spores from the Penshurst collection, taken at random for both readings, on P.D.A.

TABLE 4.
Germination of Spores at 24 and 50 Hours.

Type of Germination.	24 Hours. %	50 Hours. %
Not germinated	4	3
Germ tube at 1 end	38	1
1 side	6·5	1
both ends	33	11
both sides	1·5	2
1 end, 1 side	12·5	1
2 ends, 1 side	4	17
1 end, 2 sides	0·5	9
both ends and more than one side	—	55

As indicated in Table 4, emergence of germ tubes was asymmetrical, although by the second reading at 50 hours, emergence had proceeded towards the "normal" type expected from a 3-septate spore, as shown by MacMillan and Plunkett. Spores from the Penshurst collection included many with one and two septations, and the asymmetrical emergences were most likely a reflection of this condition. The above workers considered that spores with less than three septations were immature, but it is to be noted that spores in this study which would be classed as "immature" were capable of germination, as shown in Table 4, where 96% had germinated in 24 hours.

Germinations on water agar were slower than on P.D.A. (e.g., in one test, 94% had germinated on P.D.A. in 48 hours, against 74·5% on water agar), and hyphae were shorter, with fewer branches. For this reason, strained P.D.A. was used in preference to water agar, although the latter is a little clearer. Germinations in water were comparable with those on P.D.A. Spores retained their identity in most cases, up to approximately 48 hours on P.D.A., but for a shorter time in water.

No secondary spores borne directly on the mycelium were observed, as noted by Weber (1922) and Sprague (1944) for several species of *Septoria*. Anastomoses between germinating spores occurred in water, but none were observed on P.D.A. or water agar.

2. *Effect of Temperature on Germination.*

Several loopfuls of a spore suspension in water were placed on coverslips, which were then inverted over van Tiegham cells containing several drops of water, and sealed with vaseline. After seven days cotton-blue lacto-phenol was run in, to fix and stain the hyphae, the coverslips were removed and placed on clean slides for observation.

TABLE 5.
Germination of Spores and Degree of Development at Different Temperatures.

4° C.	8° C.	13° C.	Room Temp. July.	25° C.	30° C.	37° C.
+	+	++	+++	+	–	–

The results of the temperature test for germination agree fairly well with that for vegetative growth, as in Table 1.

Spore Size.

1. *Length.*

Great discrepancy exists in the literature regarding methods employed for mounting and measuring, and methods of recording measurements, and the position has been reviewed by Bisby (1945) and Ramsbottom (1948). There are also wide differences in opinion as to the number of items, e.g., spores, which are required to be measured. Many workers have not recorded the number measured. Bisby (1945) suggested 20 or so, to include spores at both ends of the range. Cochrane (1932) measured 1,000 spores of each of the two species studied. Beach (1919) measured 200 spores for each test when checking the effect of various microclimates on the length of *Septoria* spores.

In this study, spores were allowed to exude from pycnidia into a drop of water on a slide, for not longer than two minutes, when lactophenol cotton-blue was added, to prevent swelling and to stain the hyaline spores. One thousand spores were measured, from different isolates and environments, and the results examined to see if there was any difference between the spores of seven collections, between the Tasmanian and Sydney area collections, and between the spores from diseased material and those from culture. In some of the collections, material was limited.

Examination of the results in Tables 6 and 7 shows that the means range from 32μ to 41μ, and variation between groups is no greater than variation within groups. The greatest number of long spores was produced in culture. Other workers have found that even slightly different environments affect the length of *Septoria* spores, e.g., MacMillan and Plunkett (1942), found that spores of *S. apii-graveolentis* from pycnidia measured 36·8μ (average of 50 spores), while spores from cirri measured 44·5μ (average of 20 spores). Moore, cited by Hughes (1949), found that the average length of spores of *S. lactucae* increased from 27·5μ to 35μ after a week of dull or wet weather. Beach (1919), measuring 200 spores for each test, with *S. tritici* and *S. verbascicola*, found that size was affected by environmental conditions such as bright and dull light, moist and dry culture conditions, and summer and winter development. While the readings shown in Table 6 are not sufficiently comprehensive for a detailed comparison, it is considered that the differences in length of spores of the various isolates can be accounted for by differences in environment at time of spore production.

TABLE 6.
Length of Spores from Different Isolates.

Isolate.	Month of Collection.	Source.*	No. Measured.	Mean. μ.	Standard Deviation. μ.
Sandy Bay, Tas.	January.	N.	200	32·38	5·100
Sandy Bay, Tas.	January.	C.	100	33·46	4·676
Port Arthur, Tas.	January.	N.	200	35·60	5·821
Launceston, Tas.	January.	N.	200	37·37	4·901
Pennant Hills (7)	May.	C.	100	41·11	5·091
Rydalmere	May.	C.	50	39·71	4·525
Penshurst	July.	N.	100	33·52	6·225
Pennant Hills (9)	August.	N.	50	38·08	3·994

* N. = nature, C. = culture.

TABLE 7.
Comparison between Groups.

	Tasmania μ.		Sydney Area μ.		Bulked Mean μ.	Bulked Stan. Dev. μ.
Nature	32·38 35·60		33·52 38·08		35·01	5·778
	37·37		41·11			
Culture	33·46		39·71		37·77	5·775
Bulked	34·88 Mean	5·564 Stan. Dev.	37·84 Mean	6·184 Stan. Dev.	35·77 Mean	5·939 Stan. Dev.

2. *Width.*

Spores were prepared for measuring as described under the previous section. Three hundred spores were measured, at the widest part, using a 20× eyepiece with a calibrated ocular micrometer, and fifty were measured using a filar micrometer.

TABLE 8.
Width of Spores.

Method.	Isolate.	Source.	Number Measured.	Mean. μ.	Standard Deviation. μ.
Filar micrometer	Penshurst.	N.	50	1·8975	0·2204
Ocular micrometer	Sandy Bay.	C.	100		
	Sandy Bay.	N.	100	1·9384	0·1430
	Launceston.	N.	50		
	Pennant Hills.	C.	50		

No difference between isolates was detected. The use of the calibrated ocular entailed making estimates for those spores whose widths fell between graduations. Although greater accuracy is obtained by using the filar micrometer, whose graduations are only 0·178μ apart, the former method is quicker, and is sufficiently accurate to

warrant its use under most circumstances, if a large number of spores are to be measured.

Size of Pycnidia.

Diseased material was mounted in lactophenol to prevent shrinking and swelling, and a coverslip gently lowered on top to avoid squashing. Measurements were made from the outside of the pycnidial wall on those pycnidia whose ostiole was uppermost, i.e., if the adaxial surface of the leaf was uppermost, only adaxial pycnidia were measured. Readings for each collection, however, were made on pycnidia on both sides of the leaf. After a preliminary examination of the pycnidia, it was decided that their practically spherical formation required only one measurement. Where length and width differed, the diameter measured was the one which happened to lie parallel with the graduated scale of the eyepiece.

Table 9.
Size of Pycnidia from Different Isolates.

Isolate.	No. of Pycnidia Measured.	Mean. μ.	Standard Deviation. μ.
Sandy Bay, Tas.	200	117·55	18·694
Port Arthur, Tas.	100	107·44	18·712
Pennant Hills (7)	50	102·34	15·760
Rydalmere	100	110·33	17·847
Penshurst	50	104·04	18·241
Pennant Hills (9), ...	100	105·06	18·093
Bulked	600	110·19	18·982

As shown in Table 9, the mean of the bulked readings was $110{\cdot}19\mu \pm 18{\cdot}982\mu$. Measurements of pycnidia grouped in twos and sometimes in threes fell within the range of solitary pycnidia, and are not included in the above figures.

The mean of 50 measurements of ostioles of pycnidia on diseased leaves was $29{\cdot}24\mu$, ranging from 17μ to $47{\cdot}6\mu$.

Host-Parasite Relations.

Method.

Seedlings of *E. peplus*, raised from seed, or transplanted from the field, were grown in pots in the glasshouse. Leaf surfaces were difficult to wet, and the best method proved to be moistening with the fingers, followed by spraying from an atomizer. Several loopfuls of inoculum were placed on both surfaces of the leaves, the inoculum consisting of a water suspension of spores, either from pycnidia on leaves, or from pycnidia in culture. Seedlings were incubated from 48 to 72 hours, then placed on benches in the glasshouse.

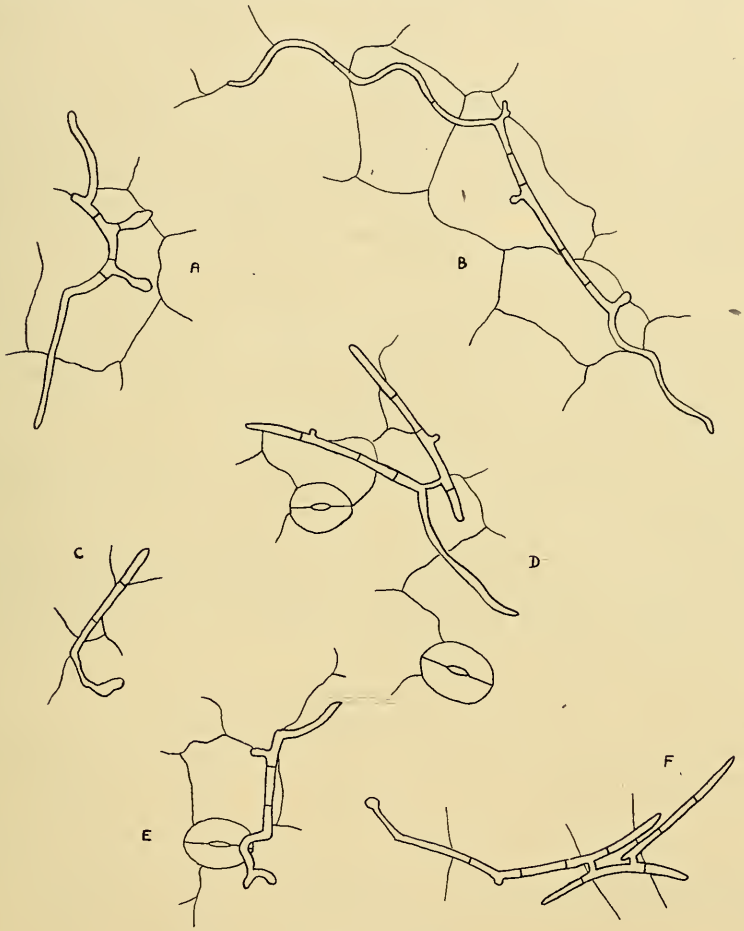
Leaves were picked and fixed after 24 and 48 hours, and thereafter every two days until pycnidia were abundant. Several methods of fixing and staining were tried, including staining with Pianese 111*b* as recommended by Weber (1922), but the method finally followed was as follows: leaves were fixed in Farmers (absolute alcohol and glacial acetic acid 3:1) for 20 minutes, washed several times in 95% alcohol, decolourized in 95% alcohol for 18–24 hours, and either mounted in lactophenol cotton-blue permanently, or taken from it to lactophenol after ten minutes. This method was found to be very satisfactory. The leaf tissue after treatment was quite colourless, and the spores and hyphae on the leaf surface stained blue, standing out vividly. Spores in pycnidia stained in deepening amounts of blue, depending on the maturity. Hyphae in the tissues were quite colourless when first mounted, but after several months appeared faintly blue. Material mounted in this way and examined after fourteen months was in good condition. The hyphae were clearly visible below the epidermis,

and although the chloroplasts by this time were stained blue, this assisted observations by making cell boundaries easily discernible.

Stem tissue was stripped, fixed, stained and mounted as above.

Observations.

Spores had germinated on the leaf surface after 24 hours, usually from one end, sometimes from both, more rarely from a side branch. The infection hyphae were usually not much thinner than the width of the spore. Many germ tubes terminated in small, appressoria-like bodies, usually at the junction of two epidermal cells. In many cases hyphae were observed to pass alongside or over stomates. No entry was



Text-figure 1.

Camera-lucida drawings of spores germinating on the leaf surfaces. × 300. A, B and C, spores germinating on the upper surface. D, fusion of spores germinating on the under surface, with germ tube passing by stomate. E, spore germinating on the under surface, with germ tube passing over stomate. F, multiple fusion of spores germinating on the uppper leaf surface.

observed through stomates, and there appeared to be no attraction for the hyphae to do so. One case only was observed where the hypha ended at a stomate, and in that case there appeared to be further development.

Germination was similar on both leaf surfaces. Branching was observed only rarely, and spores retained their identity longer than on P.D.A. The number of septa

did not increase in most spores during germination. Anastomoses were frequently observed between two spores, sometimes between three spores.

At a later stage, hyphae were observed in the leaf tissue, spreading out radially from the infection centre, branching and passing beneath the epidermis, and around the cells, mainly in the mesophyll region. Later, knots of hyphae were noted below the stomates, sometimes not directly beneath, but always in the sub-stomatal cavity. On no occasion did a knot develop on one hypha only: pycnidial formation therefore is probably symphogenous.

On a few leaves, notably in one collection kept wrapped in moist paper for 24 hours, hyphae were observed issuing from the stomates above immature pycnidia. These "aerial" hyphae measured approximately 3μ wide, and were from several to 70μ long. In many cases not just one hypha projected from the stomate, but two or three, and some cases were observed where bunches of five to eight short hyphal tips projected through the stomates.

Pycnidia were apparent to the naked eye after about 14 days. The most mature pycnidia occurred at the centre of the lesions, and radially from these were immature pycnidia, aggregations of hyphae under stomates, and then hyphae ramifying through the tissue. Hyphal tips were quite distinct, and measured about 3μ across, being just slightly wider than the older hyphae. Tips were located up to 500μ in advance of pycnidia formation. In the undiseased tissue, the chloroplasts appeared distributed evenly around the cell walls, and remained so even with the advance hyphae passing around them. In the region between the advance hyphae tips and the pycnidia, the chloroplasts lose their discreteness, and the cells appear collapsed. The boundary between the normal-appearing cells and the collapsed cells was usually quite distinct. Not all the stomates had pycnidia forming under them, but where a stomate nad been missed in the first place, it often showed aggregations at a later stage, i.e., young pycnidia could form in the zone of older mature pycnidia.

Strippings from stems showed a similar condition, with hyphae mostly running up and down the stem, and pycnidia being more linearly placed, instead of zoned. Pycnidial formation was symphogenous.

Examination of healthy Petty Spurge leaves showed that stomates occur on the abaxial surface on the average of eight to a field (magnification ×840), while very few occur on the adaxial surface, most fields having none, or two or three, at certain parts, e.g., along the sides of the main vein. This would account for the predominance of pycnidia on the lower surface of the leaves.

TABLE 10.
Viability of Spores at Various Periods After Collection.

Collection.	Age at Test.	No. of Spores Counted.	Germinated. %
Mt. Keira	2 months.	170	94
	3½ ,,	200	87
	5 ,,	200	71
	7 ,,	100	0
Mangrove Mtn.	7 ,,	200	12
Pennant Hills (9)	10 ,,	200	0
Penshurst	11 ,,	300	0

Diseased tissue was also fixed in Flemming's weaker solution and Farmers Fluid, the former being stained with gentian violet-orange G, the latter with carbol fuchsin-light green. Sections were cut at 8μ and 10μ. No cicatrix was ever observed at the edge of the lesion. Hyphae ramified throughout the tissue, and the stages in pycnidial formation were noted: hyphae loosely woven below the stomates, later developing into a knot, followed by the development of the pycnidial wall. The pycnidia were subepi-

dermal, and later erumpent with a widened ostiole. Spores were produced on one-celled pycnidiophores. Nuclei were clearly visible in sections stained with gentian violet-orange G.

Longevity of Spores.

Germination tests were made with spores from diseased material which, after the initial test, was kept between paper at room temperature. Several loopfuls of the spore suspensions were streaked across strained P.D.A. plates, and germination counts were made at 48 hours. Spores from all isolates gave more than 95% germination at the initial tests.

Spores retained within the pycnidium under the above conditions of storage were viable for about six months.

Source of Inoculum and Transmission of the Causal Organism.

Diseased plants of Petty Spurge were found in the field throughout the year, with the exception of late spring, and further search might have revealed infected plants even during this period. These diseased plants, therefore, provide an immediate source of inoculum. Pycnidia on fallen leaf and stem fragments could also liberate spores, given favourable conditions of moisture, and provide an additional source of inoculum in the absence of growing infected plants.

To determine whether the disease is seed-borne or not, tests were carried out as follows:

A collection was made of the ripest capsules on heavily diseased plants at Penshurst. In the laboratory, seeds (most of which had left the capsule cases) were picked out with forceps. The cases were floated and turned over in distilled water in watch glasses and examined under low power. Many pycnidia were noted on them. The cases were drawn up onto the sides of the watch glass with forceps, and the residue water examined with reduced light. Many spores were noted. The seed was turned over in distilled water in watch glasses and examined under low power. No pycnidia were noted on the seed, but spores were found in the water residue. The seed was then sown in pots containing sterilized soil, and the residue water with the spores sprayed over the seed. The seedlings were examined every day after emergence, but no sign of disease was apparent on the stems or leaves. Random seedlings were selected at four weeks, washed in fast running tap water, and several times in distilled water, and plated on P.D.A. No *Septoria* mycelium grew from the tissue. Capsules and seeds from diseased plants at Allawah were examined as above. Pycnidia were found on the cases, and spores in the washing, but no pycnidia were detected on the seeds.

Ripe seed capsules were collected from Petty Spurge plants in an isolated patch at the University, the plants being apparently quite free from disease. The capsules and seeds were examined as above, and as no pycnidia or spores were observed, the seed was presumed to be clean. The seed was divided into four groups of about 40 seeds each, and treated as follows:

(*a*) Seed sown in pots in sterilized soil (control).
(*b*) Seed sown in pots in sterilized soil, and the surface of the soil sprayed with a suspension of spores and mycelium of the Pennant Hills isolate.
(*c*) As (*b*), but from the Sandy Bay isolate.
(*d*) Seed soaked for 24 hours in a spore and mycelium suspension, then sown in pots in sterilized soil.

The seedlings were examined after emergence, up to a period of eight weeks, but no sign of disease was observed on the stems or leaves. Random seedlings were washed as above, and plated on P.D.A., but no *Septoria* mycelium grew from the tissue.

Seeds from heavily diseased plants were surface sterilized and plated on P.D.A., but no *Septoria* mycelium developed.

Although the above tests are not conclusive, it seems unlikely that mycelium is carried in the seed, and although spores are carried on the surface, no infection was established from these. It must not be overlooked that spores in pycnidia on shed

capsule cases could constitute a source of inoculum, for example, if splashed up by the rain on to the leaves of young seedlings.

Search for the Perfect Stage.

The perfect stage of some species of *Septoria* has been recorded, and the literature was examined to note the environment favourable for perithecial production. Stevens (1925) cited Klebahn, who recorded *Mycosphaerella sentina* as the perfect stage of *S. piricola*, occurring on over-wintered leaves of apple and pear. Stevens also recorded *Leptosphaeria phlogis* as the perfect stage of *S. phlogis*. Roark (1921) showed that a *Mycosphaerella*, occurring on over-wintered leaves and in pure culture (media not given), was the perfect stage of *S. rubri*. Weber (1922) recorded *Leptosphaeria avenaria* as the perfect stage of *Septoria avenae* Frank, perithecia occurring in oatmeal agar and potato dextrose agar cultures. Stone (1916) showed that *Mycosphaerella grossulariae*, occurring on dead over-wintered leaves of currant and gooseberry, was the perfect stage of *S. ribis*, and that *Mycosphaerella aurea*, found on old leaves of *Ribis aureum*, was the perfect stage of *S. aurea*. Thompson (1941) recorded *Mycosphaerella populorum* as the perfect stage of *S. musiva* on poplars, and *Mycosphaerella populicola* as the perfect stage of *S. populicola*, the ascigerous stages occurring on over-wintered leaves. Ruggieri (1936) reported a *Mycosphaerella* as the perfect stage of *S. aurantiorum*, having obtained perithecia in pure culture. Klebahn (1934) found that a *Mycosphaerella* on overwintered leaves of chestnut was the perfect stage of *S. castanicola*. Wollenweber (1938) found perithecia of *Sphaerella linorum*, the perfect stage of *S. linicola*, on flax straw in the Argentine. Johnson (1947) found a *Leptosphaeria* on wheat, and rarely, barley leaves in Canada, and also obtained perithecia on corn meal agar, this being the perfect stage of *S. avenae* Frank F. sp. *triticea*. Cochrane (1932) could not find the perfect stages of *S. apii* or *S. apii-graveolentis*, either in culture, on artificially wintered leaves, or in response to treatment with ultra-violet light.

During the present study, all cultures on P.D.A. were periodically examined for any evidence of the perfect stage, some slope cultures being kept for more than a year, Cultures on the various types of media used, on P.D.A. in various environments, and cultures used for temperature tests were examined, in case a necessary factor or combination of factors giving optimum conditions for perithecial growth had been supplied.

Cultures of the various isolates were opposed in all combinations on P.D.A., in nearly all combinations on corn meal agar and on sterile lucerne shoots. These cultures were kept for more than five months.

Heavily diseased leaves were placed on and just below the surface of soil sterilized for four hours, in Petri dishes, and were (*a*) held at approximately 2°C. for four months, then at room temperature, or (*b*) moistened periodically at room temperature.

Diseased leaves on plants infected in the glasshouse were allowed to fall onto the surface of the soil in the pots; some pots were kept in the glasshouse for six months, others were put into the open, and the decomposing leaves examined from time to time. A patch of heavily diseased plants was marked off in a garden at Hurstville, and allowed to remain undisturbed. The diseased leaves shed on to the soil surface, and later the stems, were examined. The Petty Spurge leaves are so delicate that they do not retain their identity for long on the soil surface.

No evidence of a perfect stage was found under any of the above conditions.

Pathogenicity Tests with Other Plants.

In order to determine the host range of the fungus, plants of the family Euphorbiaceae, being species of *Euphorbia* and *Ricinus*, were inoculated in the glasshouse. The writer particularly desired to determine whether the species of *Euphorbia* reported as hosts of species of *Septoria* were susceptible or not to the fungus under study, but difficulty was experienced in obtaining seed, as most of the species mentioned are of European-Asian habitat, and are not present in Australia. Black

(1922) recorded *E. exigua* as present in South Australia, and the C.S.I.R. Bulletin No. 156 (1942) listed *E. exigua* and *E. Esula* as present in Australia, but seed of these species was unobtainable at Sydney Botanic Gardens, Adelaide University (Waite Institute), Melbourne Botanic Gardens and the Tasmanian University. Seed was also requested through the medium of the Australian Plant Disease Recorder, circulating through all the States. Seed of *E. Esula*, *E. exigua*, *E. serrata*, *E. silvatica*, *E. palustris*, *E. aspera*, *E. angulata* and *E. amygdaloides* was requested from overseas institutions by the Plant Introduction Office, C.S.I.R.O., and viable seed of *E. Esula* and *E. exigua* was eventually obtained.

Plants not of the family Euphorbiaceae, but known to be hosts of other species of *Septoria*, were also inoculated, together with other grasses, weeds and ornamentals.

The inoculum consisted of a suspension of spores, either from pycnidia on fresh leaves, or from cultures of the various isolates. The plants were either transplanted from the field, raised from seeds, or grown from cuttings. Seedlings of *E. peplus* were inoculated at each test.

Plants inoculated were as follows:

Euphorbia helioscopia L., "Sun Spurge".
E. Drummondii Boiss, "Caustic Weed".
E. Lathyris L., "Caper Spurge".
E. terracina L., "False Caper".
E. splendens Bojer (*E. Millii* Desm., *Sterigmanthe splendens* Kl. et Garcke), "Crown of Thorns".
E. neriifolia L.
E. Bojeri Hook (*Sterigmanthe Bojeri* Kl. et Garcke).
E. exigua L.
E. Esula L.
E. pulcherrima Willd. ex Klotzsch, "Poinsettia".
Ricinus communis L., "Castor Oil".
Lycopersicon esculentum Mill., "Tomato".
Linum usitatissimum L., "Flax".
Pastinaca sativa L., "Parsnip".
Apium graveolens L., "Celery".
Apium leptophyllum (DC) F. Muell.
Triticum vulgare Host. "Federation" wheat.
Triticum monococcum L., "Einkorn" wheat.
Avena sativa L., "Richland" oats.
Hordeum vulgare L., "Kinver" barley.
Secale cereale L., "Open-pollinated rye".
Zea Mays L. (var. *indentata*).
Poa annua L., "Winter grass".
Poa pratensis L., "Kentucky Blue grass".
Bromus unioloides H.B.K., "Prairie grass".
Lolium multiflorum Lam., "Italian rye grass".
Hordeum bulbosum L.
Agrostis alba L.
Digitaria adscendens (H.B.K.) Henrard.
Dianthus spp., "Carnation".
Malva parviflora L., "Small-flowered Mallow".
Sonchus oleraceus L., "Sow Thistle".
Geranium sp., "Geranium".
Geranium dissectum L.
Erodium cygnorum Nees, "Blue-flowered Crowsfoot".
Erodium moschatum (L.) L'Hér., "Crowsfoot".
Oxalis corniculata L.
Stellaria media (L.) Vill.

No infection was obtained in any of the above species, while the *E. peplus* controls gave lesions and pycnidia. The plants were kept under observation for weeks after inoculation, in case development of the fungus was slower than in "Petty Spurge".

No *Septoria* disease was detected in the field on plants of *E. helioscopia* at Hobart, Castle Hill and Hurstville, or on *E. Drummondii* at Allawah and Sydney University, or on plants of the latter species sent from Toowoomba, Queensland. At Hurstville, several plants of *E. helioscopia*, growing in a patch of severely diseased *E. peplus*, showed complete immunity.

Judged by the species tested, it appears as if the causal organism has a limited host range. Specificity by *Septoria* species for one or a few hosts has been noted by other workers, e.g., Beach (1919) working with 15 species, Weber (1922*a*, 1922*b*, 1923) with eight species, Cochrane (1932) with two species, Thompson (1941) with two species, and Sprague (1944) working with many species on grasses.

Name of the Causal Organism.

The history of the genus *Septoria* has been reviewed by Wakefield (1940) and Sprague (1944). The former's recommendation that *Septoria* Sacc. (1884) described from type species *S. Cystisi* Dem. be conserved against *Septoria* Fr. (1828), which was based on non-pycnidial species, was upheld by Sprague. *Phleospora* Wallr. (1833), based on non-pycnidial species, is an exact synonym of *Septoria* Fr. (1828). Grove (1935), Clements and Shear (1944) and Ainsworth and Bisby (1945) followed Saccardo's use, employing *Phleospora* for the forms with incomplete pycnidia. The writer, on the above authorities, retains the genus as described by Saccardo (1884) on page 474.

From examination of fresh diseased material and microtome sections, it is evident that the causal organism of the disease of "Petty Spurge" conforms to *Septoria* Sacc. The filiform nature of the spores, their length in relation to their width (ratio approximately 15-20:1), the yeasty, later carbonaceous, scanty mycelium and distinct black pycnidia (to the naked eye), distinguish it from *Stagnospora*, whose spores are typically cylindrical (although grading into more filiform types), with a length:width ratio of less than 10:1, with a cottony appearance on P.D.A., and with pale brown, less prominently distinguished pycnidia to the naked eye (Sprague, 1944; Clements and Shear, 1941). The pycnidia are too well-formed for *Phleospora*, and lesions occur too often on the leaves to consider *Rhabdospora*.

The only species of *Septoria* recorded on *Euphorbia* spp. are as follows:

1. *S. bractearum* Mont., 1849. The spore length is given as 50μ. It was described on *E. serrata*. (Saccardo, 1884.)
2. *S. Kalchbrenneri* Sacc. The type of this species is Rabenhorst *Fungi europaei* 1854, issued as *S. euphorbiae* Kalchbrenner in *Hedwigia*, 1865, p. 158, *nec* Guep. No spore measurements are given. It was described on *E. silvatica*, *E. palustris* and *E. aspera*. (Saccardo, 1884.)
3. *S. Euphorbiae* Guep., 1879. The spore measurements are given as "40–45μ × 2–2½μ, with 3–4 indistinct septa. It was described on *E. Esula* and *E. angulata*. (Saccardo, 1884.)

The rest of the very brief descriptions of the above three species is more or less the same.

Oudemans (1902), after examining the Exsiccati of Desmazieres, recommended that *S. bractearum* Mont. should become *S. Euphorbiae* Desm., and that *S. Euphorbiae* Guep. should yield place to *S. Guepini* Oud. *S. Kalchbrenneri* Sacc. remained unchanged.

4. *S. media* Sacc. et Brun. A fairly full description is given. The spots are described as having a dark reddish margin, with spores 50–55μ × 1μ. It was described on *E. palustris*. (Saccardo, 1892.)
5. *S. euphorbicola* Hollós, 1910. The description of this species is fuller, and the spots are given as 1 mm. in diameter, pycnidia 140–160μ in diameter, and spores 16–20μ × 2–2·5μ. It was recorded on *E. procera*. (Saccardo, 1913.)
6. *S. Hariotiana* Sacc., 1906. A full description is given: the spots 1 mm. in diameter, with a dark purple margin, pycnidia 120–125μ in diameter, spores 3–4 septa, 30–32μ × 3μ. It was recorded on *E. palustris*. (Saccardo, 1913.)

Because of the inadequacy of the description of *S. Kalchbrenneri* Sacc., a request was made to the Commonwealth Mycological Institute for further information, if it was available, and Dr. G. R. Bisby kindly supplied the following notes: "The Kew specimen of this No. 584 consists of three leaves bearing spots 1–3 mm. in diameter, roundish, visible on both sides of the leaf, at first brownish, then ashen, particularly on the upper surface of the leaf, at all times surrounded by a slightly raised, distinct, reddish brown margin; pycnidia circa 100–200μ wide, brown, with an ostiole which becomes 35μ or more wide; spores (25) 30–35μ × 2–2·5μ, somewhat elevate and tapering

to 1–1·5μ at one end, hyaline, 0–3 septate, straight or somewhat curved. Most of the pycnidia appear to open on the upper surface of the leaf."

The only reference in the literature to a *Septoria* disease of *E. peplus* is in Jaczewski's "Key to Fungi", Vol. 2, p. 107, 1917: "*S. euphorbiae* Guep. on *E. amygdaloides*, *E. peplus*. Round, olive-coloured spots. Stylospores 40 to 45μ by 2 to 2·5μ with 3 to 4 indistinct septa." (Jaczewski was apparently unaware of the entry in *Revue Mycologique*, 1902, whereby *S. euphorbiae* Guep. became *S. Guepini* Oud.). It is not known whether Jaczewski was referring to *E. amygdaloides* Lam. or *E. amygdaloides* L. Hooker and Jackson (1895) listed *E. amygdaloides* L. as being synonymous with *E. sylvatica* L., on which a *Septoria* disease had already been described, namely, *S. Kalchbrenneri* Sacc. Hooker and Jackson also listed *E. amygdaloides* Lam. as a synonym of *E. nicaecnsis* All., and *E. nicaeensis* (St. Am. Fl. Agen., 192) as a synonym of *E. Esula* L. It was on *E. Esula* L. that *S. euphorbiae* Guep. (now *S. Guepini* Oud.) was originally described. It is not known whether the Russian organism was identified on the grounds of morphological similarity. The spore sizes given in the Russian text are the same as those given by Saccardo (1884).

The fungus under study, with spores 35·8μ ± 5·9μ long by 1·9 ± 0·17μ wide and pycnidia 110·2 ± 19·0μ and with unrestricted spots, differs in spore size from *S. Euphorbiae* Desm. (once *S. bractearum* Mont.) (spores 50μ), and from *S. media* Sacc. et Brun (spores 50–55μ by 1μ); and in pycnidia and spore size from *S. euphorbicola* Hollos (spores 16–20μ, pycnidia 140–160μ). *S. Euphorbiae* Desm. was also recorded by Oudemans (1921) on *E. exigua*, and no infection was obtained on this plant with the organism from *E. peplus*.

The fungus more closely resembles *S. Hariotiana* Sacc., *S. Guepini* Oud. and *S. Kalchbrenneri* Sacc. The spores of *S. Hariotiana*, however, are given as 3μ wide, and the length of the spores of *S. Guepini* as 40–45μ, and these are respectively wider and longer than the spores under study. The pycnidia of *S. Kalchbrenneri* (100–200μ) are larger than those on Petty Spurge. *S. Guepini* was recorded on *E. Esula*, but no infection was obtained on this plant with the organism under study. The appearance of the lesions caused by *S. Hariotiana* and *S. Kalchbrenneri* on their hosts, differs markedly from those caused by the *Septoria* on *E. peplus*.

It is realized that the same organism can sometimes produce quite dissimilar lesions on even closely related hosts, and that the difference in spore sizes of some of the above species could, perhaps, be accounted for by natural variation or environment. However, it is considered that the fungus is sufficiently different morphologically (as far as can be determined from the brief description of some of the other species), and with regard to host range, to be described as a new species. In correspondence with the C.M.I., Dr. Bisby was of the opinion that this would be the best course to follow. It is therefore proposed to name the fungus *Septoria pepli*, n. sp.

Septoria pepli, n. sp.

Pycnidiis amphigenis, sed vulgo hypogenis, in orbicularibus non limitatis maculis; sparsis aut raro aggregatis, atris, globosis, innatis vel dein erumptibus, ostiolatis, 85–135μ (65–165μ); sporulis hyalinis, rectus vel leniter curvatis, sursum attenuatis, guttulatis, 3-septatis, saepe 2-, raro 0- vel 4-septatis, 25–44μ (17–51μ) × 1·5–2·0μ (1·3–2·5μ).

Hab. in foliis et in cauli *E. peplus* L. in N.S.W., A.C.T. et Tasmania.

Pycnidia on both sides of the leaves, but mostly on the undersurface, in circular, unrestricted spots, singly or rarely aggregated in twos or threes, visible to the naked eye, black, but reddish-brown by transmitted light, globose or slightly elongate, immersed but later erumpent; ostiole about one-quarter the diameter of the pycnidium; pycnidial wall smooth, composed of 2–3 layers of pseudoparenchymatous cells; 85–135μ (65–165μ); spores hyaline, straight or slightly curved, tapering at one end, with a varying number of guttulae, 3 septate, often 2-, rarely 0- or 4-septate; 25–44μ (17–51μ) × 1·5–2·0μ (1·3–2·5μ).

Hab. on leaves and stems of *E. peplus* L., around Sydney, and at Wagga, N.S.W., in the A.C.T. and Tasmania.

Type specimen collected at Pennant Hills, December, 1949.

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DESCRIPTION OF PLATE I.

Fig. 1.—Leaves of *Euphorbia peplus* L. showing lesions caused by *Septoria pepli* n. sp. × 2.

Fig. 2.—Six months old culture of the fungus on P.D.A., showing "staling". Note the convoluted centre and the sub-surface hyphae at the edge. × 2.

Fig. 3.—Pycnidium produced in culture, on rye and peanut husks, with spores exuded in a cirrus. Mounted in cotton-blue lactophenol. × 100.

Fig. 4.—Section through pycnidium showing filiform spores. Cut at 8μ and stained with gentian violet-orange G. × 400.

PRESERVATION TECHNIQUES FOR SCARABAEID AND OTHER INSECT LARVAE.

By P. B. Carne, B.Agr.Sc., Division of Entomology, C.S.I.R.O.

[Read 28th March, 1951.]

Synopsis.

Methods commonly employed in preserving insect larvae are compared and the use, especially for scarabaeid larvae, of Peterson's "KAAD" fixative is recommended. The various fixatives in use are compared in regard to price; a modified cheaper form of Peterson's fixative, giving equally good results, is described.

The probable function of the fixative components is discussed and evidence recorded which suggests that the discoloration of preserved larvae is due to tyrosinase activity; *in vivo,* the tyrosinase is inhibited by a dehydrogenase system. The very rapid distension of larvae killed in KAAD or its modification is discussed in the light of recent work on insect cuticle.

Detailed recommendations are given for the cleaning, fixing and storage of larval Scarabaeidae.

Introduction.

The writer has experimented with a variety of methods of preserving insect larvae. Much of his earlier collected material, and of that obtained from the collections of earlier workers, shows marked faults, resulting from the use of unsatisfactory methods of preservation. While ethyl alcohol is used almost universally as a storage fluid, previous fixation is essential with most species; larvae killed and stored directly in alcohol become blackened and distorted and almost valueless for scientific study.

The purpose of this paper is to compare preservation techniques in common use, to bring to notice a valuable new fixative devised by Alvah Peterson (Peterson, 1943, 1948), and to discuss the functions of the constituents of the latter.

Definition of a Satisfactory Fixative.

An ideal fixative would have the following characteristics:

(*a*) Larvae fixed in it should be distended and turgid, neither soft and flaccid, nor hardened and shrivelled. (*b*) The larvae so fixed should retain normal, or close to normal, coloration (Lepidopterous larvae present much greater difficulties in this regard than do Scarabaeid larvae), with no darkening of the softer parts, nor bleaching of the head capsule. An increase in body opacity is desirable for morphological work where setal patterns are to be studied. (*c*) The fixative fluid should be reasonably inexpensive, as large quantities are used in the field collecting of larvae; and (*d*) the fixative should be one which may be used cold, and in which the larvae may be held for prolonged periods without deterioration. This is particularly desirable on collecting expeditions, when regular transference of larvae from fixative to storage fluid is sometimes inconvenient.

Preservation Techniques Compared.

The bulk of the larval collections seen by the writer have been treated by one or other of the following methods. The following comments are based upon a critical comparison of these methods, using series of larvae of *Adoryphorus couloni* Blackb., *Semanopterus* sp. and *Sericesthis* sp., and on the writer's general observations on the preservation of a wide range of species of soil-inhabiting larvae. The compositions of the fixatives are given below.

a. By direct killing in a storage fluid of 70–95 per cent. ethyl alcohol or in methylated spirits.

This technique, which appears to be frequently used, is most unsatisfactory for scarab larvae. Darkening of the cuticle begins within 24 hours of killing, and older specimens are completely blackened, and may become either very soft or hardened, according to the strength of alcohol used.

b. By direct killing in a storage fluid of 4 per cent. formalin.

This technique is equally unsatisfactory, severe discoloration occurring in time. Formaldehyde vapour from the specimens is a continual source of irritation to the eyes during their examination.

c. By killing and fixing in boiling water, and subsequent storage in 70–95 per cent. ethyl alcohol, or in 4 per cent. formalin.

Quite good results can be obtained by this method, and darkening on storage is prevented to a great extent. Small larvae appear to respond better than large larvae, which may fail to become, or to remain, turgid. Collapse is frequent if the larvae are held in actively boiling water; much better results are obtained if the larvae are placed in a beaker of boiling water, which is then allowed to cool. If the high temperature is maintained, the fat lining the body wall is melted, and is deposited about the gut. Any heat treatment is undesirable when larvae are to be dissected.

d. Killing and fixing in one of the acetic-formalin fixatives, e.g., Carls, Blés, or Bouin, and transfer to 70 per cent. ethyl alcohol.

Carls' or Blés' fixatives can give good results in the laboratory where careful attention can be given to time and temperature of fixation. Overfixation, resulting in hardening and buckling of the body wall, is the common error. Such overfixation makes examination of setal patterns extremely difficult, and special "renovation" techniques may be necessary before determination of the larva is possible. These fixatives can be used cold for longer periods, but larvae should be sorted into size groups, because in the period required to ensure adequate fixation of large larvae, small larvae in the same series becomes grossly overfixed. However, where collections are being made at a number of localities, this introduces difficulties in that the number of containers to be carried is multiplied.

Bouin easily results in overfixation, and imparts an undesirable picric staining to the larvae, which is difficult to remove.

e. Killing and fixing in Carnoy's fixative and storage in 90 per cent. ethyl alcohol.

Killing and fixing in cold Carnoy gives excellent results, although larvae become somewhat soft and transparent if allowed to remain in the fixative for more than a few days.

Larvae fixed by methods *a–d* invariably die with their mandibles closely opposed or overlapping, and these cannot be moved apart, the articulations becoming rigid, so that dissection of the mouthparts is difficult. On the other hand larvae fixed in Carnoy die with the mandibles opposed, but the articulations remain quite flexible and are easily dissected.

f. Killing and fixing in Peterson's KAAD fixative, or derivatives thereof, and storing in 95 per cent. ethyl alcohol.

The use of Peterson's KAAD results in larvae in an ideal state of preservation. The larvae are well distended, firm and completely free of any discoloration. There is an increase in opacity of the body wall.

Although Peterson states that best results are obtained by fixing for periods not longer than four hours, the writer has not observed any deterioration when larvae are left in the fixative for periods of up to three weeks. Best results for scarab larvae are given by fixation for not less than 2–3 hours.

As the writer's use of KAAD began only two months prior to the drafting of this paper, he has not seen larvae so preserved for periods longer than this. It is the writer's observation that, with all other preservation techniques, any tendency towards deterioration becomes evident within a week of treatment. Peterson states that the larvae retain their good condition for "a prolonged period".

Larvae killed in KAAD almost invariably die with the mandibles apart, the articulations remaining flexible. Important taxonomic characters occur on the mandibles, and dissection may often be avoided when the mandibles remain apart.

The fixative is expensive, containing approximately 8 per cent. dioxane. For this reason the writer has tried omitting this component, with results equal to those

obtained with the complete fixative. The acetic acid content may be reduced to 25 per cent. of that recommended by Peterson, or may be omitted altogether if the larvae are previously killed in hot water.

For purposes of gross dissection, larvae fixed in KAAD are considerably superior to those prepared by any of the other methods described. Dr. M. F. Day, of the Division of Entomology, C.S.I.R.O., has kindly examined mid-gut tissues of cetoniid larvae so treated. He found that histologically the mid-gut was fairly well preserved, considering the gross method of fixation employed, and that staining of the tissues was satisfactory.

Discussion.

The writer has rarely seen any discussion of the possible function of components of fixative mixtures, and has attempted to gain some understanding of these functions.

Firstly, all fixatives known to the writer contain acetic acid and alcohol. It is generally stated that acetic acid, together with the alcohol, is responsible for precipitation ("fixation") of the body protein, and that for most larvae its presence is necessary to prevent subsequent blackening.

The fact that hot water treatment prevents discoloration suggests that the blackening is an enzymatic process. That the enzyme is probably tyrosinase is supported by the following observations. Blackening is prevented by acids, suggesting that inactivation of the enzyme results from denaturation of the protein portion of the enzyme. Tyrosinase is known to contain copper in its prosthetic group and to be inactivated by cyanide. Larvae killed in cyanide do not blacken when stored in alcohol but will do so if first placed in an alcoholic solution of cupric chloride. The period of immersion in hot water necessary to destroy the enzyme varies from one minute at 100°C. to 30 minutes at 55°C. with *Semanopterus* sp.

The rapidity with which larvae blacken depends upon the treatment, which suggests that there is some system present which prevents blackening. Dennell (1949) considers that the tyrosinase in the larvae of *Calliphora erythrocephala* is prevented from acting upon its substrate by the presence of a dehydrogenase system which maintains a low redox potential in the insect tissues. Destruction of this system allows the redox potential to rise and the tyrosinase to act upon its substrate. Chloroform inhibits dehydrogenase systems and *Adoryphorus* and *Sericesthis* larvae placed in chloroform vapour are completely blackened an hour after anæsthesia. When killed in ethyl acetate vapour these larvae show no trace of blackening in the same period of time, which suggests the presence in these larvae of a tyrosinase-inhibiting dehydrogenase system.

Hurst (1940) has observed that a polar substance of low dielectric constant such as alcohol, is greatly assisted in its passage through the lipoid layer of insect cuticle by the presence of a non-polar compound of high dielectric constant, such as kerosene. The very rapid distension of larvae killed in Peterson's "KAAD" appears to be due to this phenomenon. Scarab larvae placed in either ethyl alcohol or kerosene die very slowly, and distension takes place very slowly. Death occurs very rapidly in a mixture of these two substances, and larvae are fully distended in less than an hour. The rate of entry of alcohol may be reduced by lowering the proportion of kerosene in the mixture, and Peterson found this necessary with some soft-bodied larvae, which otherwise burst before equilibrium was established.

Some kerosenes are not completely miscible with alcohol-acetic acid mixtures, and Peterson finds that adding dioxane results in complete miscibility. While Peterson considers that the dioxane itself may improve the quality of some larvae, the writer has found larvae preserved in KAA equally good. The KAA becomes cloudy during fixation to a much greater extent than does KAAD, although the cloudiness may be greatly reduced by the use of absolute rather than 95 per cent. alcohol in preparing the fixative. The fixative may be filtered and used again a number of times.

Composition and Estimated Costs of Fixatives.*

Bouin.—Picric sat. aqueous soln. 71 per cent., formalin 24 per cent., glacial acetic 3 per cent., approx. 7s. per gallon.

Carls.—Water 57 per cent., absolute alcohol 28 per cent., formalin 11 per cent., glacial acetic 4 per cent., approx. 4s. per gallon.

Blés.—70 per cent. alcohol 90 per cent., formalin 7 per cent., glacial acetic 3 per cent., approx. 3s. 6d. per gallon.

Carnoy.—Absolute alcohol 60 per cent., chloroform 30 per cent., glacial acetic 10 per cent., approx. £1 1s. per gallon.

KAAD.—Kerosene 8 per cent., 95 per cent. alcohol 70 per cent., glacial acetic 14 per cent., dioxane 8 per cent., approx. £1 per gallon.

KAA(1).—Kerosene 8 per cent., 95 per cent. alcohol 77 per cent., glacial acetic acid 15 per cent., approx. 9s. per gallon.

KAA(2) (with acetic acid content reduced).—Kerosene 8 per cent., 95 per cent. alcohol 87 per cent., glacial acetic 5 per cent., approx. 5s. per gallon.

While there is probably little to choose between Carnoy and KAA(2), it will be seen that the price of the former is approximately four times that of the latter.

Other Faults in Preserved Larvae.

When larvae are immersed in any fluid other than actively boiling water, regurgitation of part of the gut contents occurs. The black fluid coagulates on the mouthparts. The latter possess taxonomically important structures, which must be examined in detail for specific determination; the coagulated material must therefore first be removed. This is a tedious operation, and one likely to damage delicate structures: it may be made unnecessary either by starving the larvae for several days before killing, so that the regurgitated fluid is colourless and leaves no deposit, or the larvae may be anæsthetized before placing in the fixative, when no regurgitation occurs. Many scarab larvae are remarkably slow to succumb to cyanide, and the most rapid anæsthesia is brought about by carbon dioxide or chloroform. Deep anæsthesia is necessary, or the larvae recover sufficiently in cold fixative to regurgitate.

Tubes containing preserved larvae must be sealed to prevent evaporation, otherwise the percentage alcohol content of the fluid decreases rapidly, due to the higher volatility of alcohol over water in the mixture. Browning and changes of texture of the larvae then occur which are highly undesirable. If some evaporation does occur, the tube should be topped up with an alcohol of higher strength than that originally used.

Recommended Procedure for Preservation of Scarabaeid Larvae.†

(*a*) Handle larvae with blunt forceps, and remove superficial dirt by blowing, or by gentle washing in cold water. With some cetoniid larvae, a soft brush may be necessary to dislodge adhering soil. Such cleaning movements should be made in a caudal direction to avoid damage to the setae clothing the body.

(*b*) Anaesthetize the larvae deeply in carbon dioxide, or chloroform or ethyl acetate vapours.

(*c*) Kill and fix in Peterson's KAAD or KAA for not less than two hours.

(*d*) Wash larvae in alcohol briefly and store in 95 per cent. alcohol. Not more than two-thirds of the effective length of the tube should contain larvae, which should always be well covered by alcohol.

Larvae other than Scarabaeids.

Peterson's KAAD or KAA has been tried with a number of larval types. Excellent fixation was given with larvae of Carabidae, Elateridae, Cerambycidae, Chrysomelidae, Asilidae, and Lepidoptera. The fixative appears to be unsatisfactory for some Calliphorid larvae.

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* Based on Australian prices as at July, 1950.

† This refers to larvae killed in the laboratory. In the field, anæsthesia may have to be omitted, and cleaning postponed until transfer to storage fluid in the laboratory.

Acknowledgements.

The writer is indebted to Dr. R. H. Hackman, Division of Industrial Chemistry, and Drs. M. F. Day and K. H. L. Key of the Division of Entomology for advice and comment.

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THE ANATOMY AND MORPHOLOGY OF THE OPERCULUM IN THE GENUS *EUCALYPTUS*.

PART I. THE OCCURRENCE OF PETALS IN EUCALYPTUS GUMMIFERA (GAERTN.) HOCHR.

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(Plates ii–iii, and two Text-figures.)

[Read 26th April, 1951.]

Synopsis.

The nature of the operculum present in the genus *Eucalyptus* has been for many years the subject of a considerable amount of conjecture, and a number of conflicting interpretations as to its morphological nature have been proposed.

In the young buds of *E. gummifera*, four minute imbricate petals have been found, which gradually fuse together to form an inner corolline operculum. This inner operculum remains quite distinct from the outer operculum which is probably calycine in origin.

There is, therefore, a close morphological relationship between the flowers of this species and the two New Caledonian genera *Piliocalyx* and *Acicalyptus*, which may also indicate a close phyletic relationship.

Introduction.

Although a considerable volume of literature dealing with the anatomy of the genus *Eucalyptus* has accumulated, no investigations have yet been carried out on that unique organ, the operculum, most attention having been focussed upon the wood anatomy, leaf structure, etc. This is somewhat surprising, as the exact nature of the operculum has been the subject of a considerable amount of conjecture since 1788 when the genus was first described by L'Héritier.

Historical.

In his original description, and after consideration of the one species only (*E. obliqua*), L'Héritier held the operculum to be corolline in nature. On the other hand, Jussieu (1812) considered that it was formed by the fusion of two bracts. Robert Brown (1814), however, came to the conclusion that the operculum had different origins in different groups of species. He thought that in most species it represented a fusion of the calyx and corolla; in those species with double opercula, the inner structure represented the corolla, and the outer one the calyx; and in the genus *Eudesmia* R.Br., now *Eucalyptus* L'Hér., Series *Eudesmiae* (Blakely, 1934), the operculum was formed from the corolla alone. Hooker (1860) concluded that the operculum was a combined calyx and corolla, but Bentham (1866) was uncertain as to the correct interpretation of the organ, although he considered it to be most likely corolline in nature. He noted the presence of an additional outer operculum in some species, but regarded the nature of this outer organ as doubtful. Bentham thought that this outer operculum would eventually be found to be present in nearly all species but that it was deciduous so early that it was not noticeable in most buds. Maiden (1923) regarded the operculum as corolline in origin except in those species with double opercula where he considered the inner one to be corolline and the outer one calycine. He predicted that eventually all species would be found to have double opercula, the outer calycine one being deciduous very early in most species. Naudin (1883), Deane (1900), Andrews (1913), Hutchinson (1926), Blakely (1934), Rendle (1938), and Osborne (1947) all considered the operculum to be formed from the fused petals, whereas von Mueller (1879–84) concluded that the organ was nearly always calycine in nature. Hardy (1935, 1939), however, thought the operculum was either a modified corolla or a fusion of both calyx and corolla, but he considered the evidence insufficient to determine definitely which interpretation was the correct one.

In view of these conflicting opinions, it was thought that a study of the organogeny of the operculum would definitely decide which of these interpretations should be adopted.

The Present Status of the Problem.

It is apparent from the descriptions of the various species that there can be no general interpretation of the morphological nature of the operculum, and that the species fall roughly into three groups: (1) the Eudesmiae with four minute calyx teeth surmounted by a single operculum; (2) those species with distinct double opercula throughout most or all of the stages of bud development, notably the Corymbosae-peltatae; and (3) those species with a single operculum only throughout most or all of the bud's development. This last group includes the majority of Eucalypt species. These three groups coincide with those of Robert Brown (1814).

There are still good grounds for considering group (1) (Eudesmiae) to be a separate genus closely related to *Eucalyptus*. Also, group (3) is probably derived from group (2) by suppression of one of the opercula or by the fusion of both structures. Consequently, an examination of the opercula in group (2) is the most likely to provide information regarding the fundamental nature of the organ. It may also assist in interpreting the morphological nature of the single operculum in group (3).

Materials and Methods.

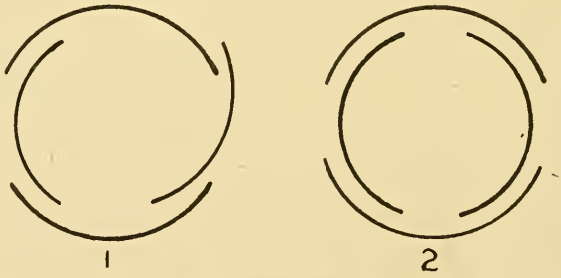
The Bloodwood *E. gummifera* was the first species to be examined as it is a common tree on the Hawkesbury sandstone in the vicinity of Sydney, and so little difficulty was experienced in collecting adequate material. The buds used in this study were collected from three different localities—Avalon, Roseville, and National Park.

The buds at different stages were fixed under reduced pressure in F.A.A. or F.P.A. and embedded in paraffin in the usual way. Staining was carried out with Safranin and Delafield's Haematoxylin using the method of Boke (1939).

The photographs were taken on Kodak Process Pan plates at a magnification of × 30, and have been reproduced at the same magnification.

The Anatomy of the Operculum.

An examination of the very young buds of *E. gummifera* revealed the presence of four minute, imbricate petals, inserted between the staminal ring and outer operculum (Plate ii, figs. 1 and 2). The petals are simple in construction with a uniform epidermis and no cuticle, whilst a constant feature is the presence of many large, well-defined oil glands (Fig. 2). The petals are attached by a broad base, and have a peculiar arrange-



Text-figures 1 and 2.

1. The petal arrangement in *Eucalyptus gummifera*.
2. The expected petal arrangement when the phyllotaxis is opposite and decussate.

ment in that they are not symmetrically imbricate. For example, in the case of three of the petals, the right (or left) edge overlaps the left (or right) edge of the petal next to it, whilst the fourth petal has both right and left edges enclosed by the petals on either side (Text-fig. 1 and Plate iii, fig. 8). As Eucalypts have basically a phyllotaxis of one-half (Jacobs, 1936), one would expect a simple dimerous arrangement as shown in Text-figure 2.

This arrangement described above leads to one petal being folded and enclosed by the other three, so that when the bud is cut transversely, the upper part of the folded petal is sectioned somewhat longitudinally (Plate iii, fig. 7).

As the bud develops, the petals gradually fuse together to form a solid inner operculum, which remains quite separate from the outer conspicuous operculum (Plate iii, figs. 10 and 11). The calyx tube grows faster than both the operculum and the fused petals, and as the proportional volume occupied by the fused petals becomes less and less, they spread out to form an almost flat cap just under the operculum proper (Plate iii, fig. 11). There is always a small space between the two structures and they fall together when the stamens unfold. A comparison of the ratio opercular volume to bud volume in Plate ii, fig. 1 and Plate iii, fig. 11, shows the much more rapid growth of the calyx tube.

Hardy (1935, 1939) has pointed out that the operculum is not a solid mass of tissue as most authors have assumed. Instead, a distinct lobing at or near the apex of the operculum marks the presence of a minute pore, which may either run right through the organ, or only part of the way, according to the species under consideration. Hardy found this pore or traces of it in 55 species, and there seems little doubt that it will be found to be of general occurrence in the genus.

In *E. gummifera* this channel is lined with cuticularized elongated cells, and runs completely through the organ (Plate iii, fig. 9). It nearly always emerges at one side of the operculum near the apex, and rarely through the apex itself (Plate ii, fig. 3; Plate iii, fig. 9). At its upper end the channel is usually three lobed (Plate ii, fig. 4) but lower down it becomes a single elongated slit (Plate ii, fig. 5). It is eventually obliterated as the bud matures.

Discussion.

Angophora is generally considered to be the genus with the closest affinity to *Eucalyptus*, the two genera being the only members of the Subtribe Eucalypteae (Bentham and Hooker, 1862–67). However, in view of the occurrence of four minute petals in *E. gummifera* as described above, it now seems more likely that the genera most closely related to *Eucalyptus* will be found to be the two genera *Piliocalyx* Brong. and Gris., and *Acicalyptus* A. Gray. (Bentham and Hooker (1862–67) placed *Piliocalyx* in the *genera anomala*, and *Acicalyptus* in the Subtribe Metrosidereae.)

Acicalyptus is confined to the Fiji Islands and New Caledonia. Its buds are Eucalypt-like and four-angled, with a beaked operculum which falls off, revealing four minute imbricate petals inserted on the margin of the calyx tube by broad bases. These petals lightly cohere, thus forming a lid which falls in one piece when the operculum is detached. There are numerous inflexed stamens but the ovary has only two loculi. The fruit is unknown (Gray, 1854).

Piliocalyx also possesses an operculum covering four small, unequal imbricate petals which cohere to form an inner operculum. The stamens are indefinite and the fruit is unknown (Brongniart and Gris, 1865). One species is found on Lord Howe Island (von Mueller, 1873), but otherwise the genus is known only from New Caledonia. Both these genera, therefore, bear flowers having a very close morphological relationship to those of *E. gummifera*, and a closer examination of them should prove of great interest, as this similarity in floral morphology may well denote a close phyletic kinship.

It seems likely also that on investigation a situation similar to that described for *E. gummifera* will be found to hold for all other species of *Eucalyptus* with double opercula (mainly the Corymbosae-peltatae), and that by fusion or loss, the single operculum of the majority of Eucalypts has been formed. However, the position of such species as *E. camaldulensis* Dehnh. (Series Exsertae) and *E. microtheca* F. Muell. (Series Buxeales) described by Maiden (1923) as having double opercula, is still obscure.

The presence of the opercular channel described above, may well indicate that the operculum is calycine in nature, especially in view of the lobed nature of the channel near the apex. In this connection it is significant that Hardy (1935, 1939) recorded this channel in two other members of the Corymbosae-peltatae, *E. calophylla* R.Br. and

E. ficifolia F. Muell., the former having four symmetrical lobes at the apex of the operculum, and the latter either four, three or two lobes irregularly arranged, "but approximating to a symmetrical arrangement of four about the axial point". Although Hardy considered the operculum, in the latter species at least, to be a combined calyx and corolla, for simplicity he termed the lobes "petaline vestiges".

However, it has been found (Willis, unpub.) that in *E. ficifolia* (and almost certainly in *E. calophylla*) there are four imbricate petals similar to those reported above for *E. gummifera*, but larger and not completely concrescent. They are pressed closely to the inside surface of the operculum but not fused to it, indicating that the operculum is most likely calycine in nature and is not a composite structure.

The indistinct lobing or lack of lobing, and the incomplete nature of the opercular channel found in such series as the Pachyphloiae and the Piperitales indicates that fusion takes place earlier and earlier in the ontogeny as the species becomes more advanced.

Jacobs (1936) has shown that the phyllotaxis of *Eucalyptus* is basically opposite and decussate. The alignment of juvenile leaves in two rows and the varying arrangements of mature leaves are caused by the growth in length of the stem between each pair of leaves, the twisting of the petioles, and the twisting of the internodes between each leaf pair. Consequently, the petals of a *Eucalyptus* flower would be expected to show two dimerous whorls instead of the arrangement described. The arrangement of the petals of *Piliocalyx* and *Acicalyptus* is at present unknown, but if they show an arrangement similar to that shown by *E. gummifera*, it will be additional confirmation for the close morphological relationship to *Eucalyptus* postulated above for these two genera.

Summary.

1. The presence of four small imbricate petals in *E. gummifera* is demonstrated.

2. The petals have an unusual unsymmetrical arrangement instead of the expected two dimerous whorls.

3. These petals fuse during the development of the bud forming an inner operculum.

4. The outer operculum has a distinct channel or slit running through it which is obliterated before the bud reaches maturity.

5. The relationship between *E. gummifera* and the two genera *Piliocalyx* and *Acicalyptus* is discussed.

6. There is some evidence indicating that the outer operculum represents a fusion of the sepals.

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EXPLANATION OF PLATES II-III.

(All photographs × 30.)

Plate ii.

Fig. 1.—Longitudinal section through young bud showing insertion of petals.

Fig. 2.—Transverse section of young bud just below the level of the stigma showing the four imbricate petals. Two of the petals are beginning to fuse.

Fig. 3.—Transverse section of operculum of young bud showing lateral position of the entrance to the opercular channel.

Fig. 4.—Transverse section slightly lower than Fig. 3 showing triple nature of the channel near the apex of the operculum.

Fig. 5.—Transverse section slightly lower than Fig. 4 showing the opercular channel.

Fig. 6.—Transverse section slightly lower than Fig. 5 showing three imbricate petal segments.

Plate iii.

Fig. 7.—Transverse section slightly lower than Fig. 6 showing the four imbricate petals. The characteristic infolding of the fourth petal beneath the other three is clearly shown.

Fig. 8.—Slightly oblique transverse section at the level of the stigma showing the four imbricate petals.

Fig. 9.—Longitudinal section of bud showing petals and opercular channel.

Fig. 10.—Longitudinal section showing gradual fusion of petal segments.

Fig. 11.—Longitudinal section of mature bud showing the outer calycine operculum, and the inner operculum formed from the fusion of the petals. The irregularly pentagonal objects just below the inner operculum are transverse sections through the filaments of inflexed stamens.

SOME NOTES ON *ATHROTAXIS*.

By Charles G. Elliott.

(*Communicated by Dr. Patrick Brough.*)

(Sixteen Text-figures.)

[Read 26th April, 1951.]

Synopsis.

This paper records some observations on *Athrotaxis* made in Tasmania in 1946-47. The relationships between the three species of the genus are briefly discussed. The pollen of *Athrotaxis* differs from other Taxodiaceae in the absence of a germ pore or germinal papilla. The intine is 2-layered. Female cones often contain larvae of a fly. Some features of the gametophytes described by earlier workers are commented on in the light of more recent work on *Sequoia* and *Sequoiadendron*. *Athrotaxis* differs from all other Taxodiaceae in the absence of cleavage polyembryony. All the embryo initials contribute to a single dicotyledonous embryo. The relationships between *Athrotaxis* and *Sequoia* and *Sequoiadendron* are briefly discussed, but no conclusions reached.

Introduction.

It is now more than 20 years since Saxton and Doyle (1929) published their fragmentary account of the life history of *Athrotaxis selaginoides*. Since then a description of the stem apex (Cross, 1943) is all that has been published on the morphology of the genus. On the other hand, the life histories of *Sequoia sempervirens* and *Sequoia gigantea* have been worked out (Looby and Doyle, 1937, 1942; Buchholz, 1939*a*, 1939*b*). Buchholz considers the two species sufficiently distinct to be placed in different genera, and instead of Lindley's invalid *Wellingtonia* has proposed the genus *Sequoiadendron* for *S. gigantea* (Buchholz, 1939*c*). While some still consider the two to belong to one genus (Doyle, 1945), many have accepted *Sequoiadendron* (see especially Stebbins, 1948). This, together with the discovery in China of *Metasequoia glyptostroboides*, the morphology and ecology of which are being investigated by a number of botanists,* makes it highly desirable to know something more about *Athrotaxis*. During 1946-47, at the University of Tasmania, I carried out some observations mainly on *A. cupressoides* Don, and though results were far from complete, the following points seem worthy of record.

Relationships between the Three Species.

No one in Tasmania could agree with Dallimore and Jackson's (1948, p. 207) remark that the three forms "might well be regarded as gradations of one species". The two common species, *A. cupressoides* and *A. selaginoides*, are quite distinct, both in the morphological characters used in taxonomy, such as the shape of the leaves and cone-scales, and ecologically. *A. cupressoides* forms stands or occurs as single trees by the side of tarns and along streams, while *A. selaginoides* is a taller forest tree generally growing on sloping ground. It does sometimes grow beside tarns, but I have not observed it in such habitats when *A. cupressoides* is found there. Where the two species occur near one another, their habitats are distinct, as has been noted by Sutton (1928). *A. laxifolia* is rare, and does not form stands. Many people entertain the possibility that it is a hybrid between the other two species, although there is little substantial evidence for the view at present. However, many more trees than exist in any one locality would be needed to show much segregation of characters.

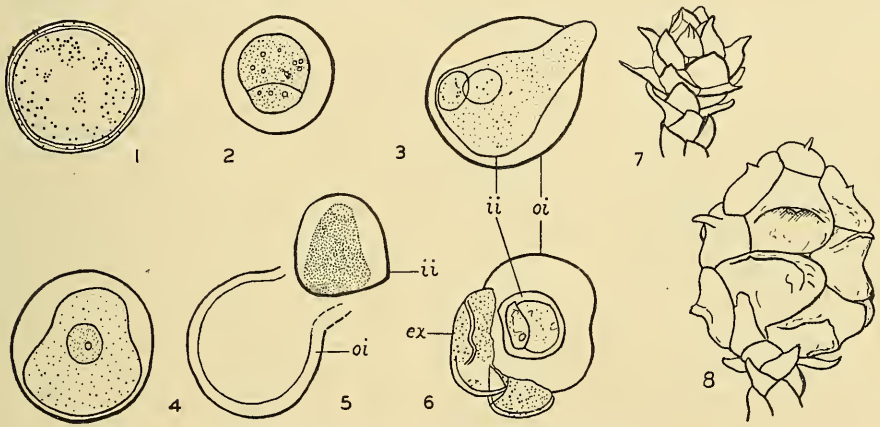
Male Cones and Pollen.

The male cones of *Athrotaxis cupressoides* can first be distinguished from vegetative tips about mid-February, and their development proceeds until May, when spore mother cells are found. Cones collected at Lake Dobson (Mt. Field National Park) on 25th

* A bibliography is given by Chu and Cooper (1950).

August, 1946, and fixed in the field, contained microspores, but in some, the uppermost sporangia had quadrinucleate protoplasts with the spindles of the second meiotic division still present. Meiosis thus occurs about the second or third week of August. The pollen is mature about a month later. I have not observed the shedding of pollen in the field, but twigs with male cones collected at Lake Dobson on 9th September, 1946, and placed in jars of water in the laboratory at Hobart shed pollen on 17th September, and cones collected at the Hugel Lakes (Lake St. Clair National Park) on 14th September, 1947, shed pollen in Hobart on 18th September.

The pollen of *Athrotaxis*, in common with that of other Taxodiaceae and Cupressaceae, lacks air bladders, nor are there any male prothallial cells. As in other members of these families, the exine is thin and is thrown off by the swelling of the intine when the mature pollen grain comes into contact with water. The pollen of *A. cupressoides* is spherical or subspherical, and has no trace of any germ pore or germinal papilla. The diameter of acetolysed grains is 27·2 ± 0·27μ. Three of the layers of the exine recognized by Erdtman (1948) can be observed in *Athrotaxis*. The nexine, about 2μ thick, is made up of an endonexine and an ectonexine of approximately equal thickness. The sexine is represented by minute granulae, irregularly scattered, and less than 1μ in diameter (Text-fig. 1).



Text-figures 1-6.—*Athrotaxis cupressoides.*

1. Acetolysed pollen grain. 2. Pollen, mounted in water, from which the exine has come off, showing the protoplast surrounded by a gelatinous "halo". 3, 4. Pollen after four days in water, showing enlargement of the protoplast within the "halo". 5. Pollen after eight days in M/4 sucrose. Protoplast with its wall (*ii*) emerging from the "halo" (*oi*). 6. Pollen mounted in potash. *ex*, exine; *ii* and *oi*, inner and outer layers of the intine. Text-figure 1, × 640; all others, × 400.

Text-figures 7-8.—Cones of *Athrotaxis cupressoides*. × 2.

7, about the time of fertilization, 14th December, 1946. 8, with nearly mature seed, 24th February, 1947.

The intine itself consists of two layers. When fresh pollen grains are mounted in water, the grains first become turgid, and the average diameter is 30μ. After the exine is thrown off, the contents of the grain are seen to be surrounded by a spherical gelatinous "halo", the average diameter of the latter being 38μ (Text-fig. 2). The pear-shaped "cell" within the halo is closely surrounded by a wall of its own, especially well seen in dry pollen mounted in potash (Text-fig. 6), which we may call the "endintine" (*ii*), and the halo then is the "exintine" (*oi*). After four days in water or sugar solutions the protoplast contained within the endintine has elongated considerably, and although the shape of the protoplast is irregular, the exintine still preserves a spherical form except where it is actually forced out of position (Text-figs. 3, 4). When the cell surrounded by the endintine emerges (Text-fig. 5), the exintine is seen to have a definite thickness. A two-layered intine does not appear to have been

described before in a conifer, but since only the exine is preserved in fossils, it has monopolized the attention of pollen morphologists to the exclusion of the intine.

The pollen of *Athrotaxis* differs markedly from that of *Sequoia*, *Sequoiadendron*, and *Metasequoia*, in all of which there is a prominent germinal papilla, and it likewise differs from *Cryptomeria*, *Taxodium*, and *Glyptostrobus*, which also have a germinal papilla of some sort. It resembles more closely *Cunninghamia* and the Cupressaceae (Wodehouse, 1935; Erdtman, 1943; Sterling, 1949).

Female Cones.

Young female cones have not been distinguished from vegetative tips before mid-September. In some localities production of cones varies from season to season. Cones of *A. cupressoides* were found near Lake St. Clair both in 1946-47 and 1947-48. But in the Mt. Field National Park, near the easterly limit of its distribution, *A. cupressoides* formed no cones in 1946-47, although *A. selaginoides* several miles away did form cones with fertile seeds. The same trees of *A. cupressoides* at Lake Dobson, however, bore cones in 1947-48. Text-figure 7 is a sketch of a cone about the time of fertilization. A fully grown cone is shown in Text-figure 8. Eames (1913, pp. 32, 33) has referred to the arrangement of the vascular bundles in the cone scales. The ovules are in a single row, and have their micropyles directed towards the cone axis. Cones of *A. cupressoides* have frequently been found to contain larvae of a fly. Heavily infested cones were deformed. The larvae appeared to be eating the ovules.

Female Gametophyte.

Observations on the development of the female gametophyte are very incomplete. As Saxton and Doyle (1929) reported, during the enlargement of the megaspore the nucellus is soon consumed up to a thickness of one cell. In this respect *Athrotaxis* seems to be more advanced than *Sequoia* and *Sequoiadendron*. An important feature is that in the free nuclear stages the nuclei are not evenly distributed round the embryo sac but are congregated at the end away from the micropyle, where they are two deep (Text-fig. 9). In this respect *A. cupressoides* resembles *Sequoia sempervirens* and differs from *Sequoiadendron giganteum* (Looby and Doyle, 1942). Saxton and Doyle's (1929) Figure 8 of *A. selaginoides* shows nuclei distributed round the embryo sac in a single layer, though more densely packed lower down. Looby and Doyle (1942) have shown that in *Sequoiadendron* alveolation proceeds evenly all round the embryo sac. In *Sequoia*, however, while alveoli are formed against the central vacuole, in the lower part where nuclei are not in a single layer, walls form cutting out cells of irregular arrangement. In *A. selaginoides*, Saxton and Doyle's Figure 18 shows that wall formation takes place by the method in *Sequoia*, with alveoli being formed at the vacuolar edge of the basal portion.

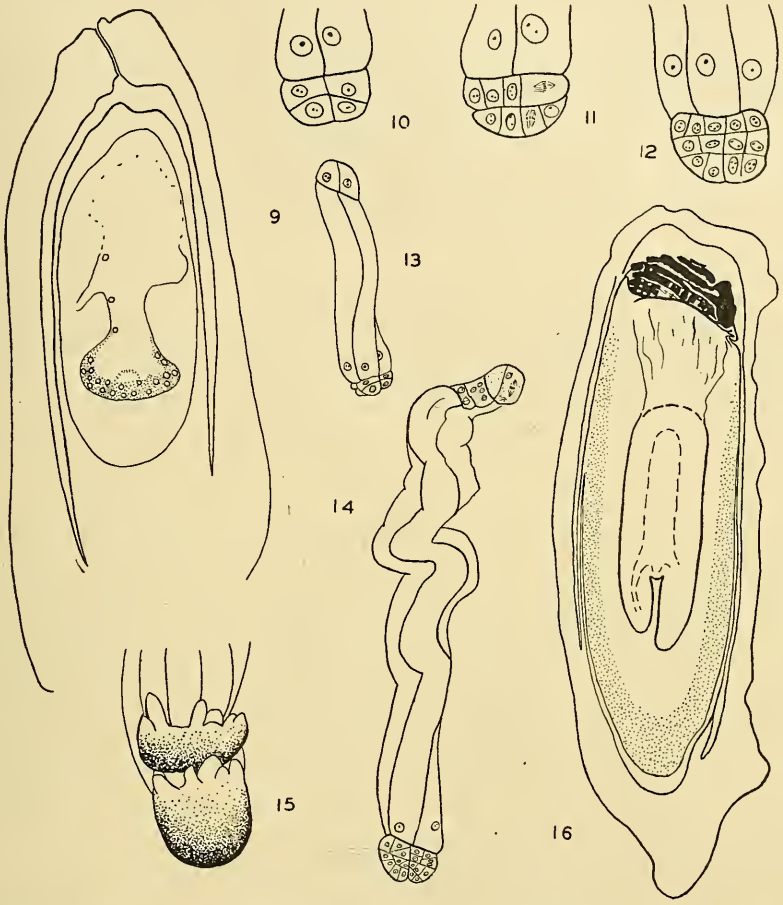
Another feature reported by Saxton and Doyle in which *Athrotaxis* resembles *Sequoia* and not *Sequoiadendron* is that the pollen tube grows over the surface of the nucellus. This is apparently also the case in *Metasequoia* (Sterling, 1949).

Embryo.

Proembryo stages were not found. The earliest stage observed showed eight cells in two tiers of four cells below the four-celled prosuspensor (Text-figs. 10, 13). The early growth of these embryo cells (Text-figs. 11, 12) gives rise to a single embryonic mass which may show some lobing (Text-fig. 14) and whose origin from four primary cells is generally apparent for some time. However, cleavage of this embryo, such as occurs in *Sequoiadendron* and *Taxodium*, was found never to take place.

There is no primary suspensor. A massive secondary suspensor is produced by the single embryo. An early stage of development of embryonal tubes is seen in Text-figure 15. As the suspensor elongates and its upper part becomes folded, the nucellus and rather indefinite prothallial tissue are included in the folds, and all together form a compact mass at the micropylar end of the mature seed (Text-fig. 16). The embryo has two cotyledons. Rosette cells are present in the early stages (Text-figs. 13, 14). Nuclear divisions are numerous in the chalazal part of the gametophyte, but unfortunately in no case could the chromosome number be counted; however, it does not

appear to be large. Embryo systems are frequently found in pairs, the result presumably of the fertilization of two adjacent archegonia by the two male cells (Text-fig. 15). Thus *Athrotaxis* exhibits only Simple Polyembryony as defined by Buchholz. In this respect it is unique in the Taxodiaceae.



Text-figures 9-16.—*Athrotaxis cupressoides.*

9. Longitudinal section of ovule at free nuclear stage, showing micropyle, integument, etc. Embryo sac badly shrunken, but it shows nuclei congregated at lower end in two layers, 14th December, 1946. × 60. 10. 8-celled embryo, 27th January, 1947. × 168. 11. Embryo with two tiers of cells each of more than four cells, 27th January, 1947. × 168. 12. Three-tiered embryo, 27th January, 1947. × 168. 13. Embryo system with two rosette cells, 4-celled prosuspensor, and 8-celled embryo, similar to Text-figure 10. 27th January, 1947. × 72. 14. Embryo system with rosette cells and lobed multicellular embryo, 19th January, 1947. × 72. 15. Embryos of two different systems showing early stage in development of embryonal tubes, 26th January, 1947, × 72. (Material from which Text-figures 10-13 is taken is from a more exposed locality at a higher altitude than those which gave Text-figures 14-15, hence the earlier dates of the latter. Text-figures 10-15 from dissected embryos.) 16. Longitudinal section of nearly mature seed, 24th February, 1947. × 24.

Free nuclear stages in the gametophyte were found in mid-December, and nearly mature embryos late in February.

Discussion.

Athrotaxis shows some significant differences from both *Sequoia* and *Sequoiadendron* in its morphological features—in its pollen grain, simple polyembryony; also in its one-cell-thick nucellus. It agrees with *Sequoia* in the method of wall formation in the

embryo sac, thin megaspore membrane, and two cotyledons. It resembles *Sequoiadendron* in its mature leaves being of one type only, in the presence of a prosuspensor and rosette cells, and one might expect in general features of proembryo development. It is clearly impossible to derive the *Athrotaxis* type of embryogeny with its prosuspensor from the *Sequoia* type which has none; but it may have been derived from that in *Sequoiadendron*. Buchholz (1940, 1948) has rightly suggested that *Athrotaxis*, *Sequoiadendron* and *Sequoia* constitute a distinct subfamily, the Sequoidae. But it must be borne in mind that Florin (1940) has shown that while *Athrotaxis* was widely distributed in the Southern Hemisphere in Tertiary times, "no representatives of this genus are known with certainty from the Northern Hemisphere" (p. 90). Reports of the southern occurrence of *Sequoia*, Florin shows, were the results of misdeterminations. On the other hand, *Sequoia* was abundant in Europe and *Metasequoia* in North America (Chaney, 1948). It is clear that the position of *Athrotaxis* is not merely intermediate between *Sequoia* and *Sequoiadendron*, but we are not yet able to define their relationships more precisely.

Acknowledgements.

I am greatly indebted to Professor Joseph Doyle, of University College, Dublin, who agreed that some notes should be written on this work before his own observations from trees growing in Ireland are published.

My thanks are also due to Drs. E. I. McLennan and I. C. Cookson, of the University of Melbourne, and to Dr. P. Brough, of the University of Sydney, for their interest in this work.

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THE PARAMPHISTOMES (TREMATODA) OF AUSTRALIAN RUMINANTS.

PART I. SYSTEMATICS.

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(Plates iv–v.)

[Read 26th April, 1951.]

Synopsis.

A study has been made of the species of Paramphistomidae occurring in the rumen and reticulum of Australian cattle.

Identifications were based on the system devised by Näsmark 1937, involving an examination of the acetabulum, genital atrium and pharynx, as seen in median sagittal sections.

The species previously known as *Paramphistomum cervi*, was found to consist of *Ceylonocotyle streptocoelium* (Fischoeder, 1901) Näsmark, 1937, and *Calicophoron calicophorum* (Fischoeder, 1901) Näsmark, 1937, whilst the species previously known as *P. cotylophorum* was determined as *P. ichikawai* Fukui, 1922. A fourth species was present among the material examined but as yet remains undetermined.

In view of the importance given by Edgar (1938), Roberts (1934), Ross and Gordon (1936) to Paramphistomes as causal agents of parasitic gastro-enteritis in sheep and cattle in Australia, investigations were commenced into their bionomics, pathogenicity, and control. Three species of Amphistome flukes have been recorded from Australian cattle (Seddon, 1947), namely, *Paramphistomum cervi* (Zeder, 1790), *P. explanatum* (Creplin, 1847), and *P. cotylophorum* (Fischoeder, 1901). *P. cervi* is recorded from Queensland, New South Wales, Victoria, Western Australia and Tasmania; *P. explanatum* from Queensland; and *P. cotylophorum* from Queensland and New South Wales. *P. cervi* and *P. cotylophorum* are noted as occurring also in sheep.

The author (Durie, 1949) published a preliminary note implicating the Planorbid snails, *Glyptanisus gilberti* and *Segnitilia alphena* as the intermediate hosts of *P. cervi* and *P. cotylophorum* respectively. These observations were based on the recovery of flukes, identified as those two species, from lambs fed cysts obtained from naturally infested snails. Subsequent attempts to infest snails experimentally with miracidia, considered to be those of *P. cervi*, were unsuccessful, and it seemed evident that the flukes that had been identified as *P. cervi* probably consisted of more than one species. A careful, taxonomic study of the Australian species was therefore considered essential before further work on the bionomics of these parasites could be attempted.

Materials and Methods.

The bulk of the material examined has been collected from the rumen and reticulum of cattle slaughtered at abattoirs near Brisbane, Queensland, and drawn from the coastal and sub-coastal areas of the State. Additional material has been obtained from other States through the courtesy of slaughtering inspectors and veterinary research laboratories.

It is evident from the literature, Fischoeder (1901), Stiles and Goldberger (1910), Maplestone (1923), Travassos (1934), Dawes (1936, 1946) and Näsmark (1937), that the family Paramphistomidae is a very difficult one from the systematic point of view. This has been discussed fully by Näsmark (1937), who attempted to obtain a clearer conception of the family's classification by careful studies on serial sections, particularly median sagittal sections, in which attention was largely directed to the muscle structures of the acetabulum and pharynx.

Näsmark's system has been used by the author in the studies reported here and is considered a satisfactory one, at least, in so far as the Australian species are concerned.

The measurements of body length and breadth were made on entire specimens fixed in Carnoy's fluid, whereas all other measurements were made on median sagittal sections. Ova dimensions were obtained from eggs deposited in physiological saline.

It was noted very early in these studies that *Gigantocotyle* (*Paramphistomum*) *explanatum* (Creplin, 1847) Näsmark, 1937, was not represented in the Australian material under examination. This species has a readily recognized and distinct musculature of the acetabulum and pharynx (Näsmark, 1937), and specimens received from Ceylon were easily identified on this character. *G. explanatum* occurs in the gall bladder and bile ducts of bovines (Dawes, 1946; Näsmark, 1937). In view, therefore, of the absence of reports from Australia of amphistomes occurring in these parts of the body, together with the fact that the species was not represented among the hundreds of amphistomes obtained for examination from various parts of Australia, it is highly probable that *G. explanatum* is not present in this country and that records of its occurrence by Roberts (1934) and Ross and Gordon (1936) are erroneous.

Two and possibly three species have been recognized among the flukes previously identified as *P. cervi*. *Calicophoron calicophorum* (Fischoeder, 1901) Näsmark, 1937, is very common and widespread and is probably the most prevalent amphistome in Australian cattle. *Ceylonocotyle streptocoelium* (Fischoeder, 1901) Näsmark, 1937, is the second species, whereas the third species as yet remains undetermined, but appears to be closely related to *C. calicophorum*.

A re-examination of the species previously recorded in Queensland and New South Wales as *Paramphistomum cotylophorum* has shown it to be *Paramphistomum ichikawai* Fukui, 1922. A detailed description of each of these species is given below.

Ceylonocotyle streptocoelium (Fischoeder, 1901) Näsmark, 1937.

Host: *Bos taurus*—rumen and reticulum.

Distribution: Beaudesert, Queensland; Gympie, Queensland.

Length 4·5 mm. (3·0–5·0 mm.), breadth 2·4 mm. (2–3 mm.); D.V. measurement 1·4 mm. (1·1–1·8 mm.); dorsal line curved, curvature greater in the posterior third of the body; ventral line plain to slightly concave. Acetabulum conforms to Näsmark's *Streptocoelium* type opening postero-ventrally, its maximum diameter 1·0 mm. (0·7–1·2 mm.), the ratio of its diameter to body length being 1:4·5 (1:3·5–1:5·0). Pharynx conforms to Näsmark's *Paramphistomum* type, 0·40 mm. (0·30–0·46 mm.) in length; ratio of pharynx length to body length 1:10·0 (1:9–1:12). Oesophagus 0·22 mm. (0·17–0·25 mm.) in length; oesophageal sphincter present. Genital atrium with genital sphincter, conforms to Näsmark's *Streptocoelium* type; ratio of genital atrium to acetabulum diameter 1:3·9 (1:3·5–1:4·5). Testes moderately lobed, oval to rectangular in shape, situated tandem and measuring 0·5 mm. in length and 1·0 mm. in D.V. direction. Egg 0·148 × 0·074 mm. (0·154 × 0·070 – 0·145 × 0·078 mm.).

Acetabulum (Pl. iv, fig. 1).—The acetabulum conforms to Näsmark's *Streptocoelium* type. The circular muscle series are characterized by their relatively few muscle units, with the interior series presenting a greater number than the exterior series. There is no division into de_1 and de_2 circular. De and di circular correspond closely in structure and in the number of units to ve and vi circular. The de series shows a slight variation in the size of the units, these being smaller externally and increasing in size internally. The number of units present in 10 specimens is shown in Table 1.

Pharynx.—The pharynx conforms to Näsmark's *Paramphistomum* type. The internal circular muscle layer consists of small closely packed units. The internal surface of the pharynx is smooth or with very small papillae. The interior longitudinal layer appears as a clearly developed band and extends inwards for about one-quarter the width of the pharynx. The middle circular layer is absent. The radial muscles are not strongly developed but are clearly visible. The exterior circular layer is rather indistinct with small units. The exterior longitudinal layer is indistinct and narrow. The basally circular layer is strongly developed and the series appear to be arranged in two rows. A slight trace of the anterior sphincter is present, but both the lip sphincter and posterior sphincter are absent.

Genital Atrium (Pl. iv, fig. 2).—The genital atrium of this species is much smaller than that of *P. ichikawai*, and possesses both a genital sphincter and sphincter papillae.

The genital papilla is rather thick and variable in shape. Sphincter papillae, although present, are not as strongly developed as described by Näsmark (1937). The genital sphincter consists of several bundles of closely packed fibres. It is quite conspicuous, but again not as strongly developed as described by Näsmark (1937). The ventral atrium is only slightly developed.

TABLE 1.

C. streptocoelium: *Unit Series of Circular Musculature of the Acetabulum from a Median Sagittal Section.*

de.	di	vi	ve
12	32	37	15
14	30	25	15
17	32	29	15
15	30	27	13
15	30	30	14
14	31	22	12
12	28	25	13
14	29	26	14
13	31	28	14
17	32	26	13

Discussion.

The specimens differ from Näsmark's description mainly in body length (7·6 mm.), but the measurements of the pharynx and other structures, except the oesophagus, agree closely with his description. Consequently any ratios given by Näsmark involving body length are greater than those given by the author.

Body length is regarded as a useful character to define the approximate size of a species, and to differentiate species which vary greatly in size. However, the length of the body in living specimens is an extremely variable one, as flukes actively elongate and contract continually. In fixed specimens the body length may vary according to the type of fixative and method of fixing employed and is therefore considered unsuitable for determining critical ratios.

In specimens belonging to the genus *Ceylonocotyle* Laurer's canal and the excretory canal (Pl. iv, fig. 3) do not cross one another, a character shared also by the genera *Nilocotyle* (Näsmark, 1937) and *Buxifrons* (Näsmark, 1937). *Ceylonocotyle* may be separated from these, however, by certain features of the acetabulum, and particularly by the absence of strongly developed radial muscles.

C. streptocoelium may be distinguished from other members of the genus by the absence of a strongly developed oesophageal bulb and lip sphincter, and from the closely allied *C. orthocoelium* by the presence of a genital sphincter and an oesophageal sphincter (Pl. iv, fig. 4). In the living state it may be separated from *P. ichikawai*, which it resembles closely in size, colour and shape, by the absence of any noticeable thickening around the genital pore. Both species are found in the rumen, with *C. streptocoelium* in the reticulum as well.

The genital atrium in the specimens examined differed slightly from the description of the *Streptocoelium* type given by Näsmark (1937), but this is probably due to the fact that Näsmark's material was poorly preserved.

The relationship between dimensions of the pharynx, genital atrium and acetabulum is shown in Plate v, figure 5.

PARAMPHISTOMUM ICHIKAWAI Fukui, 1922.

Host: *Bos taurus*—rumen only.

Distribution: Coastal districts, Queensland.

Length 5·7 mm. (3·12–7·0 mm.), breadth 2·7 mm. (2–3 mm.); D.V. measurement 1·80 mm. (1·40–2·17 mm.); dorsal line slightly curved, but more strongly so in posterior two-thirds; ventral line plain to slightly concave (Pl. v, fig. 6). Acetabulum conforms to Näsmark's *Paramphistomum* type, opening postero-ventrally, its maximum diameter 1·3 mm. (1·12–1·50 mm.), and the ratio to body length is 1:4·3 (1:3·8–1:4·7). Pharynx conforms to Näsmark's *Paramphistomum* type, 0·60 mm. (0·52–0·80 mm.) in length; ratio of pharynx length to body length 1:9·5 (1:8·2–1:13·2), oesophagus 0·28 mm. (0·17–0·50 mm.) in length. Genital atrium conforms to Näsmark's *ichikawai* type, measures 0·53 mm. (0·45–0·62 mm.) in external diameter; ratio of genital atrium diameter to acetabulum diameter 1:2·5 (1:2–1:2·9). Testes 0·75 mm. long by 1·0 mm. in D.V. direction, lobed, oval, somewhat "shamrock" shaped, and are situated tandem to each other. Egg 0·143 × 0·064 mm. (0·129 × 0·067–0·148 × 0·059).

Acetabulum (Pl. v, fig. 7): The acetabulum conforms to Näsmark's *Paramphistomum* type. The dorsal, exterior, circular series is divided into de_1 and de_2 circular. The ventral exterior circular series corresponds to de_1 circular and shows no division into two groups. The de_1 circular series is well developed and is strongest outwards. The division between de_1 and de_2 circular is fairly clearly marked. The de_2 circular series is weakly developed in comparison to de_1 circular with the units spaced at irregular intervals. The di series is well developed, with units attaining their maximum size in the centre. Vi circular corresponds closely in structure and number to di circular, and ve circular corresponds similarly to de_1 circular. The number of units in each series was found to be variable, especially in regard to de_2 circular, and, in some cases, considerable difficulty was experienced in obtaining an accurate count. The acetabulum, however, conformed to Näsmark's *Paramphistomum* type plan in all specimens examined, and the musculature was more strongly developed than in *C. streptocoelium*. The number of unit series in each group taken from 10 specimens is shown in Table 2.

TABLE 2.

P. ichikawai: *Unit Series of Circular Musculature of the Acetabulum from a Median Sagittal Section.*

de_1.	de_2.	di	vi.	ve.
23	6	40	48	17
19	9	43	42	14
19	8	46	48	15
20	8	43	43	16
20	8	39	43	17
20	5	36	37	17
23	12	43	44	18
19	9	40	46	15
19	10	31	38	20
20	3	37	46	16

Pharynx: The pharynx conforms to Näsmark's *Paramphistomum* type. The internal circular muscle layer consists of small units increasing slightly in size towards the anterior end. The internal surface of the pharynx is papillated slightly in the anterior portion. The interior, longitudinal layer extends inwards to about one-third the width of the pharynx; the interior margin is clearly defined. The middle circular layer is absent. The radial musculature is clearly visible but not strongly developed. The exterior circular layer is somewhat indistinct anteriorly but clearer towards the posterior end. The exterior longitudinal layer is narrow but clearly visible. The basally circular layer contains small units which lie in two rows towards the interior edge. The anterior sphincter, lip sphincter and posterior sphincter are absent.

Genital Atrium (Pl. v, fig. 8): The genital atrium belongs to Näsmark's Group II B1, which embraces forms with no genital sphincter, but with sphincter papillae. The genital papillae are thick and clumsy. The genital atrium conforms to Näsmark's

ichikawai type. The tissue of the walls of the genital atrium is thick and muscular, with well-developed radial musculature, and could quite easily be mistaken for a sucker. This is particularly the case in living specimens, where the structure shows a typical "sucker-like" appearance. However, sections show that, although the atrium tissue is clearly divided from the rest of the body tissue, a true delimiting membrane, characteristic of the genus *Cotylophoron*, is lacking.

Specimens of this species in the living state are pink to white in colour and appear to be confined to the rumen, as they have never been observed attached to the reticulum, even when heavy infestations are present. They closely resemble *C. streptocoelium* in size and colour, but may be distinguished from that species by the "sucker-like" genital atrium.

Discussion.

The above description agrees closely with that of Näsmark for *P. ichikawai* but differs slightly in body length dimensions. Measurements of other structures are in close agreement. The remarks made in regard to body length in the description of *C. streptocoelium* apply equally to this species. *P. ichikawai* exhibits a remarkably constant ratio between the genital atrium diameter and acetabulum diameter, and differs markedly from *C. streptocoelium* in this respect.

Calicophoron calicophorum (Fischoeder, 1901) Näsmark, 1937.

Host: *Bos taurus*—rumen and reticulum.

Distribution: Coastal and sub-coastal regions of Queensland, New South Wales, Victoria, Western Australia, South Australia and Tasmania.

Length 11·1 mm. (10–12 mm.), breadth 6·6 mm. (5·8–7·5 mm.); D.V. measurement 2·9 mm. (2·1–3·9 mm.); dorsal line evenly curved, truly conical in shape, with maximum breadth at the posterior end; ventral surface slightly concave. Acetabulum conforms to Näsmark's *Calicophoron* type, 2·4 mm. (1·60–3·2 mm.) in diameter; ratio of acetabulum diameter to body length 1:4. Pharynx conforms to Näsmark's *Calicophoron* type, 1·4 mm. (0·93–1·5 mm.) in length; ratio of pharynx length to body length 1:8. Oesophagus 0·9 mm. (approx.). Testes placed diagonally side by side, deeply lobed. Genital atrium conforms to Näsmark's *Calicophoron* type. Egg 0·133 × 0·080 mm. (0·126 × 0·072–0·147 × 0·090 mm.).

Acetabulum: The acetabulum conforms to Näsmark's *Calicophoron* type. The circular musculature is well developed and the dorsal, exterior, circular layer is not divided into de_1 and de_2 circular. In this species the circular musculature of the dorsal half of the acetabulum corresponds almost exactly to the musculature of the ventral portion. The de circular layer is well developed and consists of large well-formed units, largest in the centre and decreasing in size interiorly and exteriorly. The units of the di circular layer reach their maximum size close to the exterior edge and gradually decrease interiorly. Ve and vi circular correspond to de and di series. The number of units in the circular musculature is shown in Table 3.

Another series of units (Pl. v, fig. 9) is present in this type of acetabulum, which has not been described in any of the other types of Näsmark (1937). This series consists of small units, about 15 in number and about one-tenth the size of the largest units of the other circular musculature. It connects the exterior ends of de and di circular in the dorsal half with a corresponding series connecting ve and vi circular in the ventral portion. As this series has not been previously described, the term lateral, circular layer is proposed.

Pharynx: The ventral, circular, muscle layer consists of very small, closely packed units, increasing slightly in size towards the posterior end. The interior, longitudinal layer is narrow and rather indistinct in comparison with that in the *Paramphistomum* type, and the interior border is not clearly marked. The middle, circular layer is absent. The radial muscles are single fibres showing little ramification. The exterior, circular layer is indistinct, with the units somewhat diffuse and not clearly visible. The exterior, longitudinal layer is narrow but distinct. The basally circular layer is

weakly developed and is confined to a single row of units. A trace of the anterior sphincter is present, but the posterior sphincter and the lip sphincter are absent.

Genital Atrium (Pl. v, fig. 10): The genital atrium conforms to Näsmark's *Calicophoron* type and is highly characteristic of the species (Näsmark, 1937), forming a useful diagnostic character in living flukes. It is eversible and may either be found protruding from the genital region of the body, surmounted on a genital pillar, or retracted well within the body, as illustrated in Plate v, figure 10. Surrounding the genital pore or pillar, depending on the degree of contraction of the atrium, is a flattened circular area, bounded by a small circular ridge and, in living specimens,

TABLE 3.

C. calicophorum : *Unit Series of Circular Musculature of the Acetabulum from a Median Sagittal Section.*

de.	di.	vi.	ve.
13	40	44	18
12	41	45	16
18	40	41	16
13	36	39	13
20	45	48	25
23	44	48	27
21	46	50	23

swift circular waves of contraction are visible passing around the area. The genital sphincter is well marked and consists of closely packed units, the radial musculature being strongly developed. The sphincter papilla is also well developed and appears as a large closely packed area at the base of the genital papilla. Both the genital sphincter and sphincter papillae are more strongly developed than in either *C. streptocoelium* or *P. ichikawai.*

Discussion.

Näsmark (1937) described two species in the genus *Calicophoron*, namely, *C. calicophorum* and *C. ijimai*, which differ only in regard to the pharynx. Apart from purely anatomical differences, he gives a range of pharynx length measurements for both species which, in his opinion, are distinct enough to differentiate between them. His measurements are 1·50–2·0 mm. for *C. calicophorum* and 0·95 mm. (average of six specimens) for *C. ijimai.* Measurements of pharynx length made by the author on Australian specimens identified as belonging to the genus *Calicophoron* gave a range of 0·73 mm. to 1·50 mm. with lengths occurring throughout the range. This suggests that the pharynx is of the type belonging to *C. ijimai.*

According to Näsmark (1937), the pharynx of both species varies anatomically in several respects, particularly with regard to the interior, circular, muscle layer and to the presence of a well-marked posterior sphincter. Specimens of *C. ijimai* have both these characters strongly developed, while in *C. calicophorum* these structures are poorly developed or absent. In the series examined by the author the pharynx of some specimens varied in the size of the interior circular layer, but in no instance was a well-developed posterior sphincter seen.

In view of this lack of agreement with Näsmark's description of *C. ijimai*, and also because the type material of *C. calicophorum* was obtained from Queensland by Fischoeder, it has been tentatively decided to consider the species as *C. calicophorum* pending investigation into its life history.

Summary.

A taxonomic study has been made of the Paramphistomidae occurring in domestic ruminants in Australia.

Three species were recognized, namely, *Ceylonocotyle streptocoelium* (Fischoeder, 1901) Näsmark, 1937, *Paramphistomum ichikawai* Fukui, 1922, and *Calicophoron calicophorum* (Fischoeder, 1901) Näsmark, 1937. There is possibly a fourth species, as yet undetermined.

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EXPLANATION OF PLATES IV-V.

Plate iv.

Ceylonocotyle streptocoelium.

1. Median sagittal section through the acetabulum showing structure and arrangement of the circular musculature, × 60. de, Dorsal exterior circular layer; di, Dorsal interior circular layer; Ra, Radial muscle fibres; vi, Ventral interior circular layer; ve, Ventral exterior circular layer.

2. Median sagittal section through the genital atrium, × 184. GP, Genital papilla; GS, Genital sphincter, SP, Sphincter papillae; ♂, ductus ejaculatorius; ♀, uterus.

3. Median sagittal section through Laurer's canal and the excretory canal, × 60. EC, Excretory canal; LC, Laurer's canal.

4. Median sagittal section through part of the pharynx and oesophagus, showing a well-developed oesophageal sphincter, × 184. INT, Intestine; Oe, Oesophagus; OeS, Oesophageal sphincter; Ph, Pharynx (portion of).

Plate v.

Ceylonocotyle streptocoelium.

5. Median sagittal section, showing the position and size of the pharynx, genital atrium and acetabulum, × 18. Ac, Acetabulum; DuE, Ductus ejaculatorius; EB, Excretory bladder; GA, Genital atrium; Oe, Oesophagus; OV, Ovary; Ph, Pharynx; PM, Pars musculosa; T, Testes; Ut, Uterus.

Paramphistomum ichikawai.

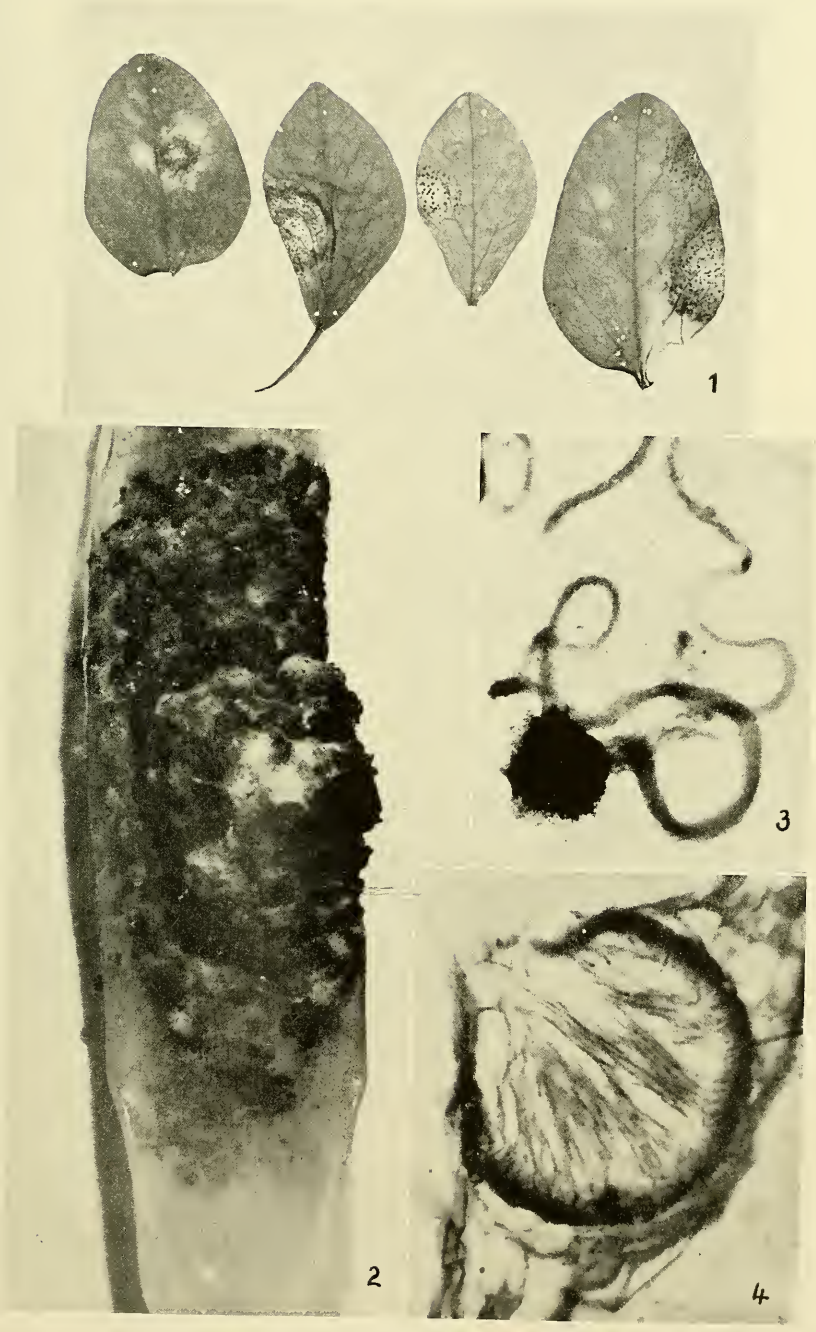
6. Median sagittal section, showing the position and size of the pharynx, genital atrium and acetabulum, × 15. Ac, Acetabulum; GA, Genital atrium; Oe, Oesophagus; Ph, Pharynx.

7. Median sagittal section of the acetabulum showing structure and arrangement of the circular musculature, × 42. de_1, Dorsal exterior circular layer 1; de_2, Dorsal exterior circular layer 2; di, Dorsal interior circular layer; Ra, Radial muscle fibres; ve, Ventral exterior circular layer; vi, Ventral interior circular layer.

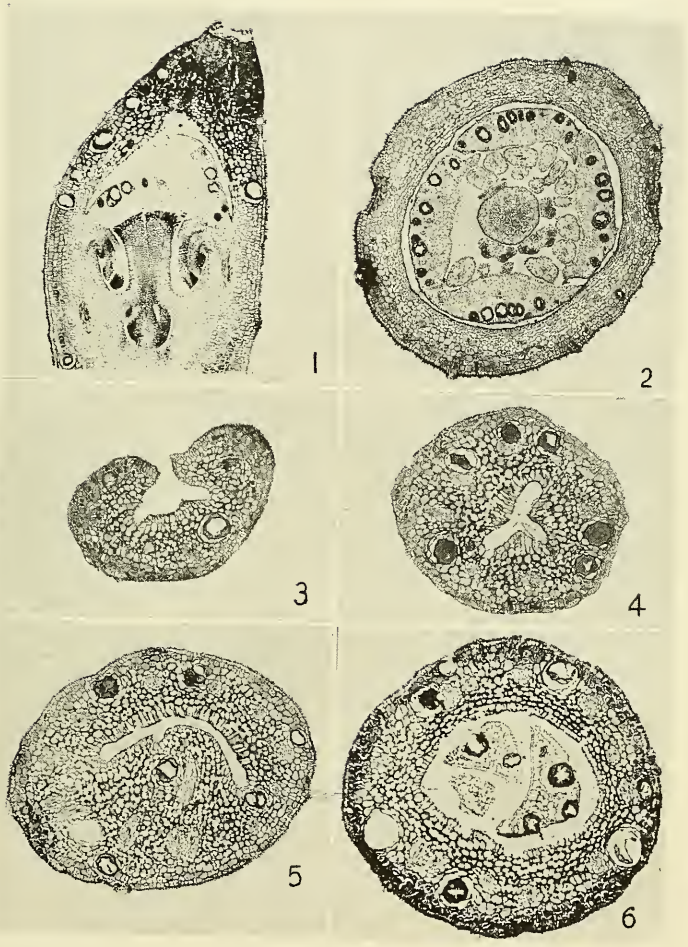
8. Median sagittal section through the genital atrium, × 60. GP, Genital papilla; SP, Sphincter papillae; Ra, Radial muscle fibres; ♂, Ductus ejaculatorius; ♀, Uterus.
Calicophoron calicophorum.

9. Median sagittal section through portion of the acetabulum showing the lateral circular muscle layer, × 180. l, Lateral circular muscle layer; ve, Portion of ventral exterior circular layer; vi, Portion of ventral interior circular layer.

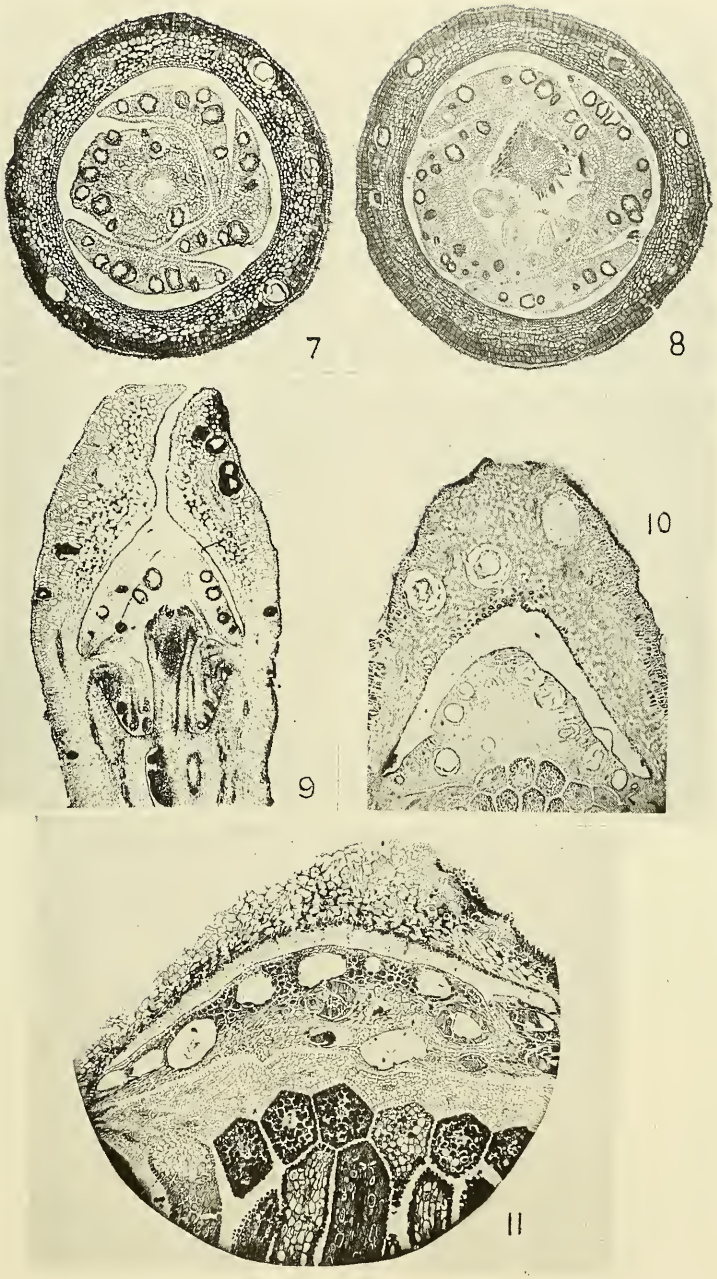
10. Median sagittal section through the genital atrium, × 60. GP, Genital papilla; GS, Genital sphincter; Ra, Radial muscle fibres; SP, Sphincter papillae.



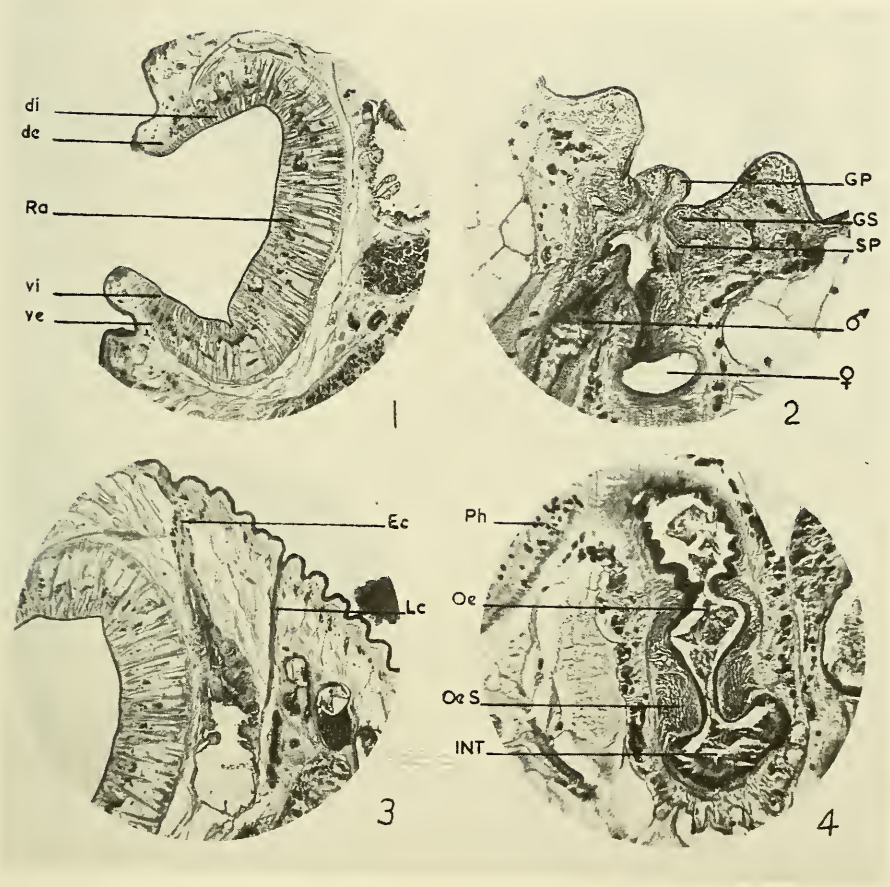
Septoria pepli on leaves of *Euphorbia peplus*.



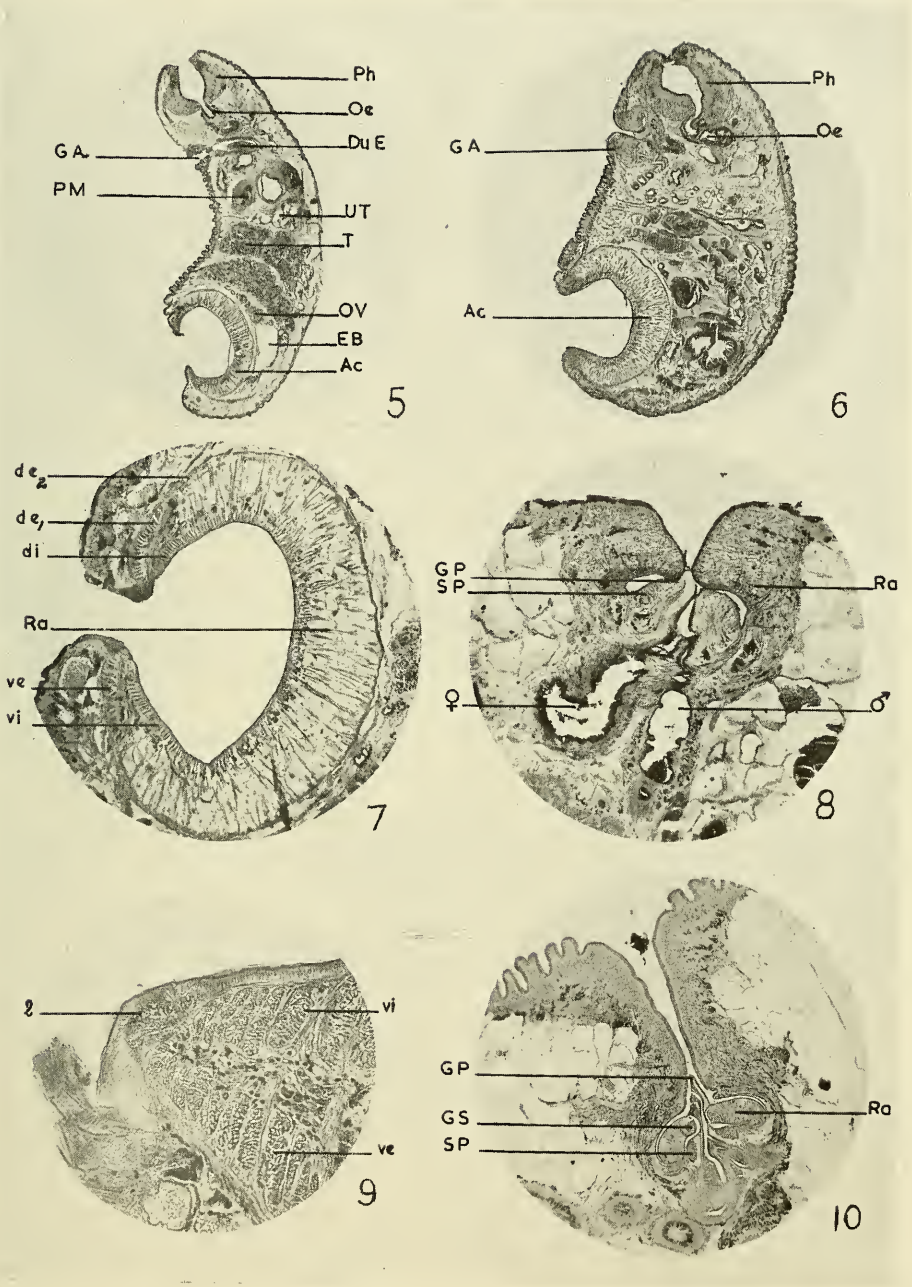
Operculum in *Eucalyptus gummifera.*



Operculum in *Eucalyptus gummifera.*



Ceylonocotyle streptacoelium.



5, *Ceylonocotyle streptocoelium*. 6-8, *Paramphistomum ichikawai*.
9-10, *Calicophoron calicophorum*.

A REVIEW OF THE AUSTRALIAN SPECIES OF *SARCOCHILUS* (ORCHIDACEAE).

By the Rev. H. M. R. Rupp, B.A.

(One Text-figure.)

[Read 27th June, 1951.]

Synopsis.

Sixteen valid species of the genus are recognized in this review, including one (*S. tricalliatus*) newly admitted to specific rank. Nine excluded species are listed at the end of the review.

Some different conceptions of the character of *Sarcochilus* are briefly discussed, and a description of the genus as understood by the author is given. The remainder of the paper consists of notes on the individual species. In the case of *S. australis* Lindl., which F. M. Bailey recorded for Queensland under the synonym *S. parviflorus*, the author expresses the view that there are no authentic records of this species occurring north of Gosford, N.S.W., and that the Queensland record should probably be applied to *S. spathulatus* Rogers.

Considerable difficulty is experienced in attempting to decide between varying interpretations of the genus *Sarcochilus*, which Pfitzer places between *Grosourdya* Rchb. f. and *Dendrocolla* Bl., in the sub-tribe Aerideae of the tribe Sarcanthinae. The late J. J. Smith, in *Blumea*, I, 1 (1930), pp. 194–215, described *Sarcochilus* as distinguished by a long straight column with a very short foot, and a lip with a very small pit at the base. If this description is to be generally accepted, it seems to me that it will mean the removal of all our Australian species to some other genus or genera. For with the possible exception of *S. australis* Lindl., they are all distinguished by a short column with a long foot, to which the lateral sepals are usually adnate; and in most instances the "pit" or sac, situated below the mid-lobe of the labellum, is relatively large. As I have not been able to ascertain whether J. J. Smith's interpretation as given above is generally acceptable, in this review I have retained the older conception of the genus, in which the column is short with a long foot. So far as I am aware, no one up to the present has proposed to remove the Australian species on the ground of their incompatibility with J. J. Smith's description. On other grounds, various authors have from time to time transferred to other genera quite a number of Australian plants previously included in *Sarcochilus*, as will be seen from the list of "Excluded Species" at the end of this review. The latest of these removals is proposed by the present writer in the *Victorian Naturalist*, Vol. 67 (1951), 206, where Mueller's *S. divitiflorus* is made the type of a new genus to be known as *Rhinerrhiza*. With the exclusion of this plant, there remain sixteen Australian species to be reviewed, viz.:

1, *S. Fitzgeraldii*; 2, *S. Hartmannii*; 3, *S. falcatus*; 4, *S. Weinthalii*; 5, *S. australis*; 6, *S. spathulatus*; 7, *S. olivaceus*; 8, *S. Harriganae*; 9, *S. dilatatus*; 10, *S. Longmanii*; 11, *S. Bancroftii*; 12, *S. Ceciliae*; 13, *S. Hillii*; 14, *S. tricalliatus*; 15, *S. eriochilus*; 16, *S. minutiflos.*

Before proceeding to review these in detail, however, I wish to submit the following brief description of the genus itself as I understand it.

Sarcochilus R.Br.

Epiphytes or rock plants, usually rather small. Stems short. (Exception in Australia, *S. Fitzgeraldii.*) Leaves from broadly lanceolate to linear, often more or less falcate and usually distinctly channelled above. Racemes emerging below the leaves. Flowers from a few mm. to 3 cm. in diameter, racemose, often numerous and showy, in some species very fragrant. Sepals and petals approximately equal, free, relatively broad at least in the distal portion, the lateral sepals usually more or less dilated at the base and adnate to the foot of the column. Labellum articulate at the base of the column-foot, spurless, trilobate. Lateral lobes erect, relatively large, curving inward;

mid-lobe usually very short, with a rather conspicuous sac or protuberance below, projecting in front; disc with a few stalked calli. Column short, with a long foot; anther operculate; stigma semicircular to oblong; pollinia 2.

An illuminating article on the genus by the late Dr. R. S. Rogers will be found in the *Australian Orchid Review*, Vol. II, No. 3 (Sept., 1937), pp. 9–12. One or two corrections are required. (The name is several times misspelt *Sarchochilus*, but this is probably a printer's error.) On p. 10 the author states, "In habit the genus *Sarcochilus* may be distinguished from *Thrixspermum* by the elongated inflorescence of the former, on which all the flowers of a raceme open on the same day, or else begin to bloom suddenly in series on a gradually lengthening inflorescence". This is not correct, at least so far as Australian species are concerned. The only Australian species with elongated racemes on which all the flowers open on the same day is *S. divitiflorus* F. Muell., now removed from the genus. I know of no species in which the flowers begin to bloom suddenly in series on a gradually lengthening inflorescence, nor can I find any observer who does. Dr. Rogers remarks that *Thrixspermum* had not been reported from Australia at the time of writing; but Schlechter in 1911 (*Orchis*, v. 55) had removed *S. platystachys* F. M. Bail. to that genus, and the transfer is not likely to be challenged. Rogers gave the number of Australian species of *Sarcochilus* in 1937 as "17 (perhaps 18)". Presumably he included *S. phyllorhizus* F. Muell. (now transferred to *Chiloschista*) as well as *S. platystachys*. I do not know what his possible 18th species was, but he felt some uncertainty as to the status of *S. falcatus* var. *montanus*, which R. D. Fitzgerald originally published as *S. montanus*. Fitzgerald's reduction of it to a variety of *S. falcatus*, however, has been generally endorsed. The exclusion of *S. phyllorhizus*, *S. platystachys*, and *S. divitiflorus* would reduce the number given by Rogers to 14; but to these are now added *S. Harriganae* and *S. tricalliatus*, the latter being described here as a species for the first time.

A Key to the Species.

1. Sepals and petals from broad-lanceolate to almost orbicular.
   2. Stems often rather long, scrambling on rocks, with somewhat flaccid leaves. Flowers white or pink with maroon blotches ..... *S. Fitzgeraldii.* 1.
   2′. Stems always short.
      3. Robust plant; leaves in the typical form large, rigid, deeply channelled. Flowers white with maroon centre ..... *S. Hartmannii.* 2.
      3′. Plants less robust than the last. Leaves shallowly channelled, often more or less falcate.
         4. Flowers white or pink.
            5. Leaves moderately broad, light green, falcate. Flowers up to 3 cm. in diameter white with orange and reddish-purple markings on the lateral lobes of the labellum, and often on the labellar sac ..... *S. falcatus.* 3.
            5′. Leaves linear, channelled. Small plants with small flowers.
               6. Leaves more or less spotted, dull green.
                  7. Flowers bright pink, almost campanulate ..... *S. Ceciliae.* 12.
                  7′. Flowers pink or white, expanding widely ..... *S. Hillii.* 13.
               6′. Leaves not spotted, light green. Flowers white; labellum with three conspicuous calli ..... *S. tricalliatus.* 14.
                  8. Lateral lobes of labellum densely pubescent or hairy ..... *S. eriochilus.* 15.
                  8′. Lateral lobes of labellum glabrous. Flowers very diminutive ..... *S. minutiflos.* 16.
         4′. Flowers neither pink nor white.
            9. Flowers brick red ..... *S. Bancroftii.* 11.
            9′. Flowers never red.
               10. Flowers cream, blotched with dull purple ..... *S. Weinthalii.* 4.
               10′. Flowers yellow ..... *S. Longmanii.* 10.
1′. Sepals and petals narrow for their basal third, then expanding rather broadly.
   11. Sepals dilated into a rhomb above the narrow basal portion ..... *S. dilatatus.* 9.
   11′. Sepals expanding to lanceolate above the narrow basal portion.
      12. Lateral lobes of the labellum spathulate.
         13. Labellar sac with bright purple markings ..... *S. spathulatus.* 6
         13′. Labellar sac pale green ..... *S. Harriganae.* 8.
      12′. Lateral lobes of the labellum oblong to ovate.
         14. Flowers old-gold or olive-green ..... *S. olivaceus.* 7.
         14′. Flowers brownish-green; labellum white with purple and yellow markings ..... *S. australis.* 5

1. *S. Fitzgeraldii* F. Muell., Fragm., vii, 1870, 115; Benth., Fl. Austr., vi, 1873, 293; R. D. Fitzg., Austr. Orch., i, 3, 1877; Austr. Orch. Rev., i, No. 1, 1936, 10, and ii, No. 3, 1937, 9-10; Rupp, Orch. N.S.W., 1943, 136.

This is the largest and, in the opinion of many, the most beautiful, of all Australian species of the genus. Mueller (*l.c.*) hints at the possibility of its proving to be a variety of *S. falcatus* R.Br.; while Bentham, followed by F. M. Bailey, states, "Stem, foliage, and general aspect of *S. falcatus*". It is difficult for anyone well acquainted with both plants to perceive this supposed resemblance. Fitzgerald makes no allusion to it. *S. falcatus* is a true epiphyte, always found on trees, short-stemmed, with light green leaves and short racemes. *S. Fitzgeraldii* is an extensively spreading, branching plant which scrambles along cliffs and on rock-ledges in deep ravines; the leaves are dark green, and the racemes are on long, stout peduncles. Bentham probably lacked a sufficiency of good material, and of course he had never seen the plant growing; but it is curious that Bailey, who must surely have seen it in southern Queensland, should have repeated Bentham's remark without comment.

The precise colouring of the flowers varies a good deal, but typically it may be described as white with crimson or maroon blotches. Plants are occasionally found with pure white flowers. The variety *aemulus* (These Proceedings, 69, 1944, p. 73) was found by the present writer some 20 miles from the site of Fitzgerald's original discovery at the Naroo Falls on the Bellinger River, N.S.W. Its flowers are light crimson with deep maroon blotches.

Although the species is not uncommon in gorges of the eastern slopes of the Dividing Range in northern New South Wales and southern Queensland, its distribution appears to be confined to these areas. There are no definite records of its occurrence south of the Hastings Valley in New South Wales, nor has it been found north of the Brisbane River in Queensland. It responds fairly well to cultivation, provided the requisite humidity and temperature are available; it does best in moderate shade, with a rock to scramble on.

2. *S. Hartmannii* F. Muell., Fragm., viii, 1870, 248; F. M. Bailey, in Q'land Fl., v, 1902, 1551, plate lxvii; Austr. Orch. Rev., i, No. 1, frontispiece; Rupp, Orch. N.S.W., 1943, 137.

Although obviously closely related to the preceding species, this species is quite distinct, with a different habit. It grows on both rocks and trees, and likes a bright, sunny situation. It is a more variable plant than *S. Fitzgeraldii*. In the typical form the stem is erect, but short; the leaves are large, rigid, and deeply channelled. Bailey, however, identified Fitzgerald's *S. rubicentrum* (Austr. Orch., ii, 1, 1884) with *S. Hartmannii*, and his view is generally accepted; but there is some difference between the two forms, *rubicentrum* being less erect, with smaller leaves and flowers. There is some mystery about the habitat of the plant figured by Fitzgerald; see footnote to the description of *S. Hartmannii* in Orch. N.S.W., *l.c.* Diligent search by several capable collectors in the Cairns district during the past twenty years has failed to discover any orchid resembling Fitzgzerald's plate, and it seems probable that the plant he received from E. Ramsay had been cultivated at Cairns. The experience of botanists and collectors suggests that the habitat of *S. Hartmannii* is even more restricted than that of *S. Fitzgeraldii*, and is practically confined to the Macpherson Range in southern Queensland, and one or two localities just on the New South Wales side of the border.

The flowers of *S. Hartmannii* vary a good deal in dimensions; sometimes they are as large as those of *S. Fitzgeraldii*, but more commonly they are smaller. They are in a more compact raceme, borne on a long, stout peduncle. Usually they are white with maroon spots at the base of the perianth; but pure white flowers are sometimes found. The species is more easily cultivated than *S. Fitzgeraldii*.

Synonymy.—Sarcochilus rubicentrum Fitzg., Austr. Orch., ii, 1, 1884.

3. *S. falcatus* R.Br., Prodr., 1810, 332; Benth., Fl. Austr., vi, 1873, 293; Fitzg., Austr. Orch. i, 5, 1879; Austr. Orch. Rev., i, 3, 1936, frontispiece; Rupp, Orch. N.S.W., 1943, 132; Barrett and Nicholls, "Gems of the Bush", 1934, 9.

Generally known as the "Orange Blossom Orchid", this attractive little species is a familiar wildflower in many parts of the coastal belt of eastern Australia, and it ascends to a considerable altitude on the Dividing Range and its spurs. As might be expected in view of its extensive distribution, it varies considerably from the typical form; but the variations rarely tend to obscure its identity. R. D. Fitzgerald, indeed, described and figured one form (Austr. Orch., *l.c.*) as a distinct species (*S. montanus*); but subsequently, in Moore and Betche's "Handbook of the Flora of N.S.W.", he reduced this to a variety of *S. falcatus*. In the foothills of many mountain ranges, intermediates between it and the type-form are so numerous that it is hardly desirable to perpetuate the varietal status. One of the most distinctive forms known to me is found growing on the Negrohead Beech (*Nothofagus Moorei*) near Barrington Tops, about sixty miles north of Newcastle, N.S.W. This plant is more robust than usual, and the flowers are of a rich cream colour, with a tuberose perfume. Another distinct form occurs on the Atherton Tableland in North Queensland, more than a thousand miles away. In this case the plant is very small, but the flowers are well above average size, heavily stained with deep purple markings, and with a distinctive perfume.

As indicated above, the range of *S. falcatus* is very extensive. From the Cann River in eastern Victoria to the Atherton Tableland in North Queensland, the distance is approximately 1,500 miles, but in and near the rain forests of many areas along this great stretch of country, the "Orange Blossom" may be found.

Synonymy.—Thrixspermum falcatum (R.Br.) Rchb. f., Beitr. 46, and Xen. Orch., ii, 122.

4. *S. Weinthalii* F. M. Bail., Q'land Agr. Journ., xiii, 1903, 346, and xxviii, 1912, 448; also in Compr. Cat. Q'land Pl., p. 534; Rupp, Orch. N.S.W., 1943, 134.

This plant when not in bloom is hardly distinguishable from smaller forms of *S. falcatus*. The flowers, numbering from 3 to about 12, are cream or white, blotched with dull reddish-purple, and the lateral lobes of the labellum are very narrow, with purple spots. The species seems to be very rare, being known only in one or two localities in southern Queensland, and near Kyogle in the far north of New South Wales.

5. *S. australis* (Lindl.) Rchb. f., Walp. Ann., vi, 501, and Xen. Orch., ii, 122; Rupp, Orch. N.S.W., 1943, 134, plate xxiii; Fitzg., Austr. Orch., i, 3, 1877 (as *S. parviflorus*).

This very attractive little orchid was for many years better known as *S. parviflorus* Lindl. But Lindley had originally named it *Gunnia australis*, and the priority of the latter specific name is beyond question. As it happens, it is a far more suitable name than *parviflorus*; for while there are several species with smaller flowers, no other extends so far south, this being one of the only two epiphytic orchids occurring in Tasmania, where it was discovered by Ronald Gunn more than a century ago.

The species is recorded by F. M. Bailey for southern Queensland, but the record is very vague, and no Queensland specimens are known at present. In my opinion, *S. australis* does not extend farther north than the rain forests near Gosford in New South Wales. I believe that the Queensland records should be applied to the allied species *S. spathulatus* Rogers, which resembles *S. australis* both in habit and in superficial appearance. It probably passed for the latter for many years, for it was not till 1927 that the late Dr. Rogers described and named *S. spathulatus* from specimens found on Tamborine Mountain in southern Queensland. For more than twenty years I have tried to trace *S. australis* at least as far north as the Hunter Valley in New South Wales; but Gosford remains the nearest approach (50 miles south of the Hunter). Unless direct evidence of the occurrence of this species in Queensland is forthcoming, I think it should be deleted from the orchid flora of that State.

It is one of the daintiest and most attractive of the smaller Australian orchids. Occasionally stems are elongated to as much as 20 cm.; but more usually they are quite short. Racemes in well-developed plants are often numerous, each bearing from 5 to about 14 very fragrant flowers, brownish-green with a white labellum, variably splashed with purple, red, or yellow. Column relatively longer than in other species. The plant is most frequently found growing on twigs of small trees and shrubs, in moist gullies.

In Tasmania it is confined to rain forests in the north and west of the State. In Victoria, Mueller recorded it from Apollo Bay; but this is the only known record west of Port Phillip. It is not uncommon from the Dandenong Ranges eastward. In New South Wales there are records from Braidwood, Picton, Campbelltown, the Blue Mountains, National Park, northern arms of Port Jackson, Hawkesbury River, and Gosford.

Synonymy.—Gunnia australis Lindl., Bot. Reg., 1834, sub t. 1699; Hook. f., Fl. Tasm., ii, 1860, 33, t. 128; *Sarcochilus parviflorus* Lindl., Bot. Reg., 1838, Misc. 34; Benth., Fl. Austr., vi, 1873, 294; Fitzgerald, Austr. Orch., i, 3, 1877; *Sarcochilus Gunnii* F. Muell., Fragm., i, 1859, 90; *Sarcochilus Barklyanus* F. Muell., *l.c.*, 89; *Thrixspermum parviflorum* Rchb. f., Xen. Orch., ii, 122; *Thrixspermum australe* Rchb. f., *l.c.*

6. *S. spathulatus* Rogers in Trans. Roy. Soc. S. Austr., li, 1927, 1; Rupp, Orch. N.S.W., 1943, 136; Barrett and Nicholls, "Gems of the Bush", 1934, 8.

I cannot agree at all with Murray Cox (Cultural Table of Orchidaceous Plants, 1946, p. 274) that this species in any way resembles *S. Hillii*; except perhaps in its habit of growing on twigs. It does, however, closely resemble *S. australis*, and could easily be mistaken for that species. The plant is, I think, consistently smaller, and the stem is never elongated. The flowers are quite as large as those of *S. australis*, and are somewhat similarly coloured, but they are never numerous. The specific name was chosen in allusion to the conspicuously spathulate lateral lobes of the labellum.

The species was discovered on Tamborine Mountain, Queensland, in 1925, by Mrs. H. Curtis; just a week later I found it in the southern foothills of Barrington Tops in New South Wales. Between these two localities it is not uncommon in coastal rain forests; it has not been seen south of the Hunter Valley, or north of the Brisbane River.

7. *S. olivaceus* Lindl., Bot. Reg., 1839, Misc. 32; Benth., Fl. Austr., vi, 1873, 293; Fitzg., Austr. Orch., i, 5, 1879; Rupp, Orch. N.S.W., 1943, 134.

Bentham remarks, "Sepals and petals of a dull pale purple or yellowish-brown". This is a very unsatisfactory description; there is no purple at all. It is difficult to define the colour; Fitzgerald's plate does not do it justice. I think "old gold" is as near as one can get to it—an uncommon shade of golden green. The flowers are deliciously perfumed, and are more numerous than Bentham supposed—I have counted 11 on one raceme. When not in bloom this species is sometimes mistaken for *S. falcatus*; but the leaves are thinner, and of a darker green. Bentham united Mueller's *S. dilatatus* with *S. olivaceus*, but there are ample grounds for specific distinction. W. H. Nicholls has described a distinct form from North Queensland as var. *borealis*. (N. Q'land Naturalist, Dec., 1939.) It has darker flowers, blotched with deep red-brown.

The species extends from at least as far south as the Shoalhaven River in New South Wales, northward into the tropics of Queensland.

Synonymy.—Thrixspermum olivaceum Rchb. f., Xen. Orch., ii, 122.

8. *S. Harriganae* Rupp in These Proc., lxiii, 1938, 128.

Unfortunately the type specimen of this species was inadvertently destroyed, and at present no others are available. It is a rare plant, apparently confined to part of the Dorrigo highlands in northern New South Wales. The plant itself somewhat resembles a small *S. falcatus*, but the leaves are usually marked with irregular rows of dark dots. The dull-green flowers almost suggest a natural hybrid *S. olivaceus* × *S. spathulatus*; their general conformation agrees with the former, while the lateral lobes of the labellum are definitely spathulate. The dorsal sepal is very broad.

9. *S. dilatatus* F. Muell., Fragm., i, 1859, 191; Rogers, Trans. Roy. Soc. S. Austr., li, 1927, 291.

As stated above, Bentham united this little species with *S. olivaceus*. Rogers, however, makes it clear that Mueller was justified in giving it specific rank. It never attains the dimensions often reached by *S. olivaceus*, and the flowers (1 to 5) are correspondingly smaller. The sepals and petals are pale green basally, shading to deep brown at their distal ends. In the sepals the narrow claw forming the basal half is dilated terminally into a rhomb; in the petals it merely becomes spathulate. The whitish labellum is unlike that of *S. olivaceus*.

S. dilatatus has not yet been found outside southern Queensland. Mr. Trevor Hunt, of Ipswich, writes, "I have found this species always in the thick, semi-dry vine scrubs of the hilltops, at elevations up to 1,000 ft. These scrubs are in the nature of residuals of the once dense scrubs covering hilly parts of the coast plain". Recently I received numerous specimens from Mr. W. W. Abell, of Durong State School, near Tingoora, on the Kingaroy line.

10. *S. Longmanii* F. M. Bail., Q'land Agr. Journ., xxiii, 1909, 261; ibid., xxviii, 1912, 449; Compr. Cat. Q'land Pl., p. 532.

Bailey's description of this species calls for no comment. The plant closely resembles *S. Weinthalii*, but the flowers are a little smaller, and of a light yellow colour. It is a rare species, being recorded only on the slopes of the main Dividing Range in the Toowoomba district of southern Queensland.

11. *S. Bancroftii* F. M. Bail., Q'land Agr. Journ., xxviii, 1912, 450; Compr. Cat. Q'land Pl., p. 532.

Nothing is known of this species at present beyond Bailey's description and figure. The latter shows a small plant similar to *S. Weinthalii* and *S. Longmanii*. The only record is that of Bancroft from Eidsvold, Queensland, in 1912. It is most desirable that efforts should be made to re-discover this orchid, the flowers of which are described as "brick-red". In this respect it must present a striking contrast to all the other species.

12. *S. Ceciliae* F. Muell., Fragm., v, 1865, 42, t. 42; Benth., Fl. Austr., vi, 1873, 294; Barrett and Nicholls, "Gems of the Bush", 1934, 8; Rupp, Orch. N.S.W., 1943, 137.

In Mueller's plate the enlargements of an individual flower are excellent; but the figure of the plant itself (natural size) with two racemes and several leaves, shows the latter far more acuminate than is usual, and the flowers expanded too widely. The photograph by W. H. Nicholls depicts the flowers more naturally; they are almost campanulate, like inverted bells. ("Fairy Bells" is a popular name for this species.) The flowers are typically of a bright pink colour; a white-flowering form (var. *albus* Hunt) has been found in south-east Queensland. *S. Ceciliae* is a very small plant, but when growing, as it often does, on rock-ledges, it usually occurs in dense masses, the numerous flowers being quite conspicuous. If growing on trees the plants are generally solitary. The species is found in coastal forests and rocky gullies from the Macleay River in New South Wales northward into the Queensland tropics, occasionally extending to the ravines of the tablelands.

Synonymy.—Thrixspermum Ceciliae (F. Muell.) Rchb. f., Beitr., 71.

13. *S. Hillii* F. Muell., Fragm., ii, 1860, 94; ibid., vii, 1870, 98; Benth., Fl. Austr., 1873, 295; Fitzg., Austr. Orch., i, 3, 1877; Barrett and Nicholls, "Gems of the Bush" (1934), 8; Rupp, Orch. N.S.W., 1943, 138.

When not in flower, this tiny plant could be mistaken for a small *S. Ceciliae*; but it is strictly an epiphyte, and has not been recorded on rocks. Plants, however, are sometimes crowded in great numbers on the trunks of small trees such as *Backhousia myrtifolia*. The flowers expand more widely than those of *S. Ceciliae*; they are white or pink, and are very fragrant. The species has a fairly extensive range, from the south coast of New South Wales at least as far north as Rockhampton in Queensland.

Synonymy.—Dendrobium Hillii F. Muell., Fragm., i, 1859, 88; *Thrixspermum Hillii* (F. Muell.) Rchb. f., Beitr., 71.

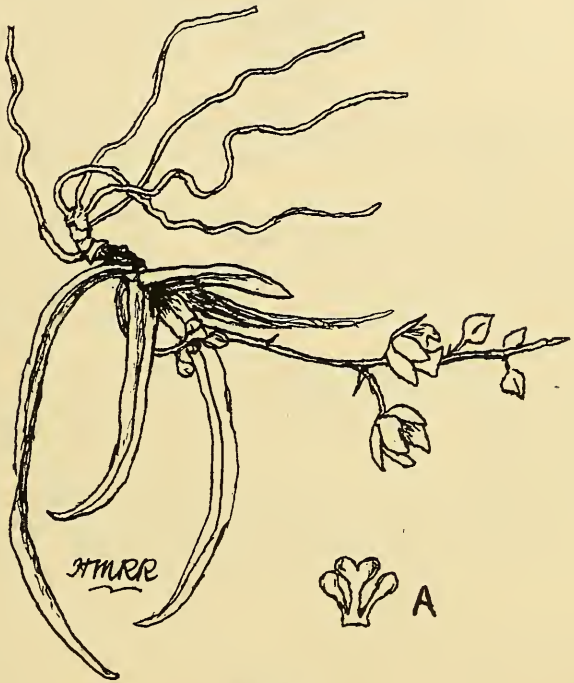
14. *S. tricalliatus* (Rupp) Rupp, n. sp. (Text-fig. 1).

Planta parva caule brevissimo. Folia pallida, immaculata, linearia, canaliculata, usque ad 7 cm. longa. Flores 2–5, albi, inodorati. Sepala petalaque latissime lanceolata, patentia, circa 5 mm. longa. Labelli lobi fere aequales, intus rubri; lobus intermedius marginibus aurantiacis, paulum pubescens. Discus callis clavatis conspicuis 3, callus intermedius magnus, anceps. Columna non dentata.

A small plant with a very short stem. Leaves pale green, unspotted, linear, channelled, up to 7 cm. long. Flowers white, 2 to 5, without any perfume. Sepals and petals very broadly lanceolate, about 5 mm. long, spreading. Labellum trilobate,

the three lobes approximately equal; midlobe with orange margins, only slightly pubescent. Disc with three rather stout clubbed calli, the middle one larger than the others, and double-headed. Column devoid of teeth.

Specimens sent to me in 1935 from Mount Dryander, by Mr. K. MacPherson of Proserpine, North Queensland, flowered the next year in February. At the time I thought the plant could be regarded as a northern variety of *S. Hillii*, and I provisionally named it *S. Hillii* var. *tricalliatus* (N.Q. Naturalist, May, 1936, 31). But for some years past I have felt that the differences are sufficient to warrant the raising of the Mount Dryander plant to specific rank. It has not been found in any other locality.



Text-fig. 1.

Sarcochilus tricalliatus, n. sp. Nat. size. A, the 3 calli on the disc of the labellum (enlarged).

15. *S. eriochilus* R. D. Fitzg., Journ. Bot., xxix, 1891, 153; Rupp, Orch. N.S.W., 1943, 137.

I regret that I have nothing to add to the remarks made on this species in the work last cited. Apparently it is extremely rare. As the Tweed River, on the New South Wales–Queensland border, is the only locality where it has been recorded, it is possible that the clearing of the forests along that stream has exterminated it.

16. *S. minutiflos* F. M. Bail., Compr. Cat. Q'land Pl., pp. 845-847.

This species has been recorded only from Eidsvold in Queensland. There are specimens in the Brisbane and Sydney Herbaria, but beyond these little is known of it. Following is Bailey's description: "On branchlets of shrubs and trees. Roots very long and slender, white and more or less curled. Stem very short. Leaves several, slender, 2–4 inches long and about 2 lines broad, sometimes dotted. Racemes mostly very slender, from 2 to 6 inches long, sometimes forked, bearing throughout their whole length, or nearly so, very numerous minute flowers. Flowers on slender pedicels of about two lines, nearly globular from the incurving of the sepals and petals, of a greenish white sometimes tinged with pink, and less than two lines in

diameter. Bracts minute. Sepals somewhat longer than the petals. Labellum small, lateral lobes purplish, blunt, ovate-oblong, middle lobe stalked, for the greater part composed of a globular mass of glandular white hairs. Discal calli orange yellow. Column short, anther lid stained with purple. Capsules narrow, straight, 2–2½ in. long."

Excluded Species.

S. Armitii F. Muell., Fragm., ix, 49 (*Cleisostoma Armitii* F. Muell., *l.c.*).

The rightful position of this plant has not been definitely settled. The type in Mueller's herbarium is too fragmentary to be of very much use, and no other specimens have been clearly recognized as such. My own opinion now is that *Saccolabium orbiculare* (Rupp) Rupp, in Vict. Nat., 67, 1941, 220, is really identical with Mueller's plant, and should in future be known as *Saccolabium Armitii*.

S. Baileyi F. Muell., Herb., is *Taeniophyllum Muelleri* Lindl., Herb., Benth., Fl. Austr., vi, 291.

S. Beckleri (F. Muell. ex Benth.) F. Muell., Cens. Austr. Pl., 1882, 111, is *Sarcanthus Beckleri* (F. Muell. ex Benth.) Rupp, Vict. Nat., *l.c.*

S. calcaratus (F. Muell.) F. Muell., Fragm., ii, 192, is *Sarcanthus tridentatus* (Lindl.) Rupp, Vict. Nat., *l.c.*, 218.

S. divitiflorus F. Muell. ex Benth., Fl. Austr., vi, 292, is *Rhinerrhiza divitiflora* (F. Muell.) Rupp, Vict. Nat., Vol. 67, 1951, 206.

S. Newportii F. M. Bail., Q'land Fl. v, 2014, is *Bulbophyllum Newportii* (F. M. Bail.) Rolfe, Orch. Rev. (London), xvii, 94.

S. phyllorhizus F. Muell., Fragm., v, 201, is *Chiloschista phyllorhiza* (F. Muell.) Schltr., Engl. Bot. Jahrb., lvi, 492.

S. platystachys F. M. Bail., 1st Suppl. Syn. Q'land Fl., 56, is *Thrixspermum platystachys* Schltr., "Orchis", 1911, v. 155.

S. tridentatus (Lindl.) Rchb. f., Walp. Ann., vii, 98, is *Sarcanthus tridentatus* (see *S. calcaratus* above).

I desire to acknowledge the assistance of Mr. Trevor E. Hunt, of Ipswich, Queensland, and Mr. H. K. C. Mair, B.Sc., of the New South Wales National Herbarium, who have both read the MSS. of this review and have offered useful suggestions.

AUSTRALIAN RUST STUDIES.

VIII. PUCCINIA GRAMINIS LOLII, AN UNDESCRIBED RUST OF LOLIUM SPP. AND OTHER GRASSES IN AUSTRALIA.

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[Read 27th June, 1951.]

Synopsis.

A stem rust which attacks *Lolium* spp., *Dactylis glomerata* L. and about 30 other grasses is described. Aecidial, uredospore and teleutospore stages show that it is a type of *Puccinia graminis* Pers. Spore morphology and cultural studies make it clear that it is not one of the known subspecies of the cereal stem rusts, nor is it one of the described subspecies which attack grasses.

Its host range has been studied and its distribution determined in all the States of Australia and in New Zealand. The occurrence of physiologic races of the rust has been shown by differential reactions of plants of *Lolium perenne* L., *L. rigidum* Gaud., and *Arrhenatherum elatius* (L.) J. et C. Presl. In many grasses there are wide differences between the resistance and susceptibility of individuals within the species.

The name *Puccinia graminis lolii* is proposed for the rust.

Introduction.

Stem rust of cereals and grasses is caused by the highly specialized fungus *Puccinia graminis* Pers. The following subspecies (or varieties) are generally recognized: (i) a group of three which attack cereals, viz., *P. graminis tritici* E. and H., *P. graminis avenae* E. & H., and *P. graminis secalis* E. and H.; and (ii) a group of subspecies which attack grasses. Three of these have been studied intensively in U.S.A., viz., *P. graminis poae* E. and H., *P. graminis agrostidis* E., and *P. graminis phlei-pratensis* (E. and H.) Stak. and Piem. In addition, European workers have described four others, viz., *P. graminis airae* E. and H., *P. graminis calamagrostis* Jacz., *P. graminis aperae* Jacz., and *P. graminis arrhenatheri* Jacz. Little is known of these.

McAlpine (1906) recorded *P. graminis* on cereals and a number of grasses, but made no inoculation studies or determinations of the subspecies present. More recently Australian investigations of *P. graminis tritici* and *P. graminis avenae* have been carried out (Waterhouse, 1929). It has been shown that barley and rye are attacked by the former: *P. graminis secalis* is not present in Australia. A number of grasses were also found to be common hosts for one or other of these cereal rusts. But many other stem rusts occur on grasses and very little is known about them.

Of these a common type which is specially notable for its attack of *Lolium* spp. has been under observation since 1918. It quickly became apparent that it was not one of the cereal rusts: no lesions were produced on wheat, very occasional resistant reactions were shown on rye, tiny reactions occurred on a few varieties of oats at very favourable temperatures, and 260 barley varieties showed sharp resistance with the exception of two varieties in which a "2+" reaction was given. In no case were the reactions comparable with those caused by *P. graminis tritici* or *P. graminis avenae.* Detailed studies were therefore undertaken to determine its identity, host range and distribution.

Morphological Studies.

Large uredosori occur on stems and leaves, rupture of the epidermis being a noticeable feature. Lesions on glumes and rachises are not uncommon. Those on the stems frequently give place to black teleutosori late in the season, and sometimes these also occur on the leaves. The aecidial stage has not been found in nature but has been produced in the plant house on *Berberis vulgaris* L. from teleutospores on *Lolium perenne* L. that had been exposed to winter conditions on the tablelands at Glen Innes,

New South Wales. Inoculations with these aecidiospores produced uredosori on *L. perenne* and *Dactylis glomerata* L. but on none of the cereals. All spore forms show characteristics which agree with those described for *P. graminis*. It has been shown (Levine, 1923, and Waterhouse, 1930) that statistical examinations of the spore morphology may reveal significant differences between subspecies.

Measurements were made of 200 aecidiospores and 200 uredospores lightly shaken from leaves of the susceptible host, and of 200 teleutospores obtained by scraping sori on the stems. The standard methods previously described (Waterhouse, 1930) were used.

The results are set out in Table 1, in which the name *P. graminis lolii* is used for the new rust, and the measurements are grouped with those determined for the Australian subspecies *P. graminis tritici* and *P. graminis avenae* (Waterhouse, 1930), and the U.S.A. determinations for the remaining grass subspecies and *P. graminis secalis* (Levine, 1923).

TABLE 1.

Comparison of Measurements of Spore Forms of Several Subspecies of Puccinia graminis.

Rust Subspecies.	Length in μ.			Width in μ.		
	Mean.	Standard Deviation.	Range.	Mean.	Standard Deviation.	Range.
			Aecidiospores.			
P. graminis lolii	16·92	0·47	12·5–23·2	16·41	0·50	11·6–19·3
P. graminis avenae r.1 ..	21·18	2·29	14·9–27·9	16·53	1·91	11·6–20·46
P. graminis tritici r.46 ..	19·08	1·95	14·9–24·2	16·63	1·54	14·9–20·46
P. graminis secalis	17·10	2·0	12·0–22·0	13·46	1·17	11·0–16·0
P. graminis agrostidis ..	16·46	1·93	12·0–22·0	12·98	0·97	11·0–15·0
P. graminis poae	15·07	1·35	12·0–18·0	13·23	0·97	11·0–15·0
			Uredospores.			
P. graminis lolii	27·61	0·56	22·3–31·6	18·08	0·48	14·9–24·2
P. graminis avenae (all races)	29·99	3·14	20·5–39·1	18·33	1·59	13·1–22·3
P. graminis tritici (all races)	31·04	3·70	20·5–44·6	18·25	1·88	11·2–22·3
P. graminis secalis	27·14	2·91	21·0–36·0	17·19	1·26	14·0–21·0
P. graminis agrostidis ..	22·37	2·61	15·0–30·0	15·68	1·12	13·0–18·0
P. graminis phlei-pratensis ..	23·95	2·41	18·0–30·0	16·88	1·32	13·0–20·0
P. graminis poae	18·64	1·51	15·0–23·0	15·78	1·06	13·0–18·0
			Teleutospores.			
P. graminis lolii	48·75	1·78	32·8–63·7	16·93	0·56	11·6–21·2
P. graminis avenae r.1 ..	46·95	6·54	29·8–67·0	15·27	1·85	11·2–20·5
P. graminis tritici (3 races)	44·32	7·40	29·8–74·4	15·90	2·27	11·2–22·3
P. graminis secalis	47·35	6·65	35·0–65·0	14·77	1·83	10·0–19·0
P. graminis agrostidis ..	40·30	5·87	25·0–55·0	14·64	1·72	10·0–19·0
P. graminis phlei-pratensis ..	41·30	4·78	30·0–55·0	15·63	1·46	12·0–19·0
P. graminis poae	36·90	9·13	20·0–60·0	15·52	2·07	11·0–21·0

The aecidiospores resemble those of *P. graminis poae* in being sub-spherical, but are much larger. In making the measurements, the uniformity in outline was striking, together with the tendency for the spores to remain in chains.

The uredospores are quite unlike those of *P. graminis poae*, resembling most closely those of *P. graminis secalis*. They are much larger than those of any of the other grass rusts.

The teleutospores agree in general with those of *P. graminis avenae* and again are quite unlike those of any of the grass rusts, being much larger. In the course of making the measurements, teleutospores having either a single cell or a series of three cells were noted.

On these morphological grounds the rye grass rust is different from any of the described subspecies.

Cultural Studies.

The recognized subspecies on grasses gave reactions in side-by-side comparisons as shown in Table 2, in which the new rust is again listed under the name *P. graminis lolii*. The designations of the reactions are those proposed by Stakman and Levine (1922).

Table 2.

Comparison of Reactions of Grass Subspecies of P. graminis *on Grass Hosts.*

Rust.	Grass Hosts and Their Reactions.			
	Poa compressa.	*Agrostis alba.*	*Phleum pratense.*	*Lolium perenne.*
P. graminis poae	4	0	;	;
P. graminis agrostidis ..	0	4	;	;
P. graminis phlei-pratensis ..	0	0	4	0
P. graminis lolii	0	0	;	4

On the basis of these grass reactions, *P. graminis lolii* is different from the recognized subspecies.

Turning next to the subspecies on cereals, inoculation experiments gave the reactions described hereunder:

P. graminis tritici (10 physiologic races) gave no attack on *Lolium* spp., and *P. graminis lolii* produced no lesions on any of the very many varieties of all the *Triticum* spp. tested.

P. graminis avenae (three races) attacked some individual plants of *Lolium* spp., but with a low frequency: the usual reaction was a tiny fleck. *P. graminis lolii* gave flecks on more than 100 varieties of oats: in the case of a few varieties like "Victory" it gives a "2–" reaction at very favourable temperatures.

P. graminis secalis does not occur in Australia, but side-by-side comparisons using three isolates of this subspecies which comprised two physiologic races showed that it is quite different from *P. graminis lolii*. Inoculations of 120 varieties of barley with the *P. graminis secalis* cultures resulted in 17 of them giving large semi-susceptible reactions ("2+"), 41 gave semi-resistant ("2") reactions, whilst the remainder were resistant (";") and ("1"). With *P. graminis lolii*, all gave resistant (";" and "1") reactions. An extensive series of inbred ryes which have been selfed for 17 years and which were fully susceptible to the two races of *P. graminis secalis* gave resistant reactions when inoculated with *P. graminis lolii*.

The cultural comparisons with the six subspecies of *P. graminis* indicate that *P. graminis lolii* must be regarded as a different subspecies.

Distribution of the Rust.

Serious damage is done to rye grass and cocksfoot when conditions are favourable for rust development, and other grasses of lesser importance are also damaged. Stems and leaves are attacked and not infrequently sori occur on the rachis and glumes.

In the course of the investigations the rust was isolated with the stated frequency from the grasses set out in Table 3. Many of the specimens were sent in for study by co-operators in scattered areas, whilst others were collected as opportunities offered. But it has not been possible to make an exhaustive survey of its occurrence, which may well be larger than indicated herein.

The practice has been to test each grass rust isolate on the four cereals and *Lolium perenne*: whenever an infection of the latter is shown, it is used to inoculate the original grass host in order to check its pathogenicity.

It will be noted that a number of these grasses have already been recorded as natural hosts for *P. graminis avenae*. This rust was found together with *P. graminis lolii* many times on a number of the grasses listed above. Determinations showed that it was either race 2 (not separated from race 1) or race 7 (not separated from

TABLE 3.

Naturally-occurring Grass Hosts of P. graminis lolii *with the Number of Isolates Examined from Each.*

Tribe.	Grass.	Number of Isolates.
Phalarideae	*Phalaris tuberosa* L.	9
	P. minor Retz	4
	P. paradoxa L.	1
	P. aquatica L.	1
Agrostideae	*Agrostis avenacea* Gmel.	8
	Echinopogon caespitosus C. E. Hubbard	18
	Dichelachne spp.	17
	Amphibromus Neesii Steud.	2
	Alopecurus pratensis L.	2
	Gastridium ventricosum (Gouan) Schinz et Thall.	1
	Stipa variabilis Hughes	1
	Lagurus ovatus L.	1
Aveneae	*Holcus lanatus* L.	5
	Aira cupaniana Guss.	1
	Trisetum flavescens (L.) Beauv.	1
	Trisetum sp.	1
	Arrhenatherum elatius (L.) J. et C. Presl.	2
Festuceae	*Festuca elatior* var. *pratensis* (Huds.) A. Gray	12
	F. elatior var. *arundinacea* (Schreb.) Wimm.	2
	Scleropoa rigida (L.) Griseb.	1
	Vulpia bromoides (L.) S. F. Gray	43
	V. Myuros (L.) Gmel.	3
	Dactylis glomerata L.	78
	Spartina alterniflora Loisel	1
	Lamarckia aurea (L.) Moench.	5
	Koeleria phleoides (Vill.) Pers.	5
	Poa annua L.	3
	P. iridifolia Hauman.	1
	Bromus Gussonii Parl.	2
	B. Benekeni G. Beck.	1
	B. breviaristatus Buckl.	1
Hordeae	*Lolium perenne* L.	99
	L. multiflorum Lam.	4
	L. loliaceum (Bary et Chaub.) Maz.	3
	L. rigidum Gaud.	17
	L. temulentum L.	12
	Hordeum leporinum Link.	1

race 3), and in one instance *Lamarckia aurea* (L.) Moench was infected by both these oat rust races in addition to *P. graminis lolii*. The details of these occurrences are set out in Table 4.

Apart from the joint occurrence on the one host of these two stem rusts, there were numerous cases in which the grass host of *P. graminis lolii* was also attacked by its leaf rust: *Lolium* spp. carrying *P. coronata lolii* E., and *Bromus* spp. attacked by *P. bromina* E. were notable examples.

In addition to the natural occurrence of the rust on grass hosts, studies were made of the plant house behaviour of many other grasses when inoculated under controlled conditions. These have shown that there are susceptible members within the following species, although in certain cases resistant members predominate.

Lolium remotum Schrank, *Briza maxima* L., *Bromus racemosus* L., *B. hordeaceus* L., *B. madritensis* L., *Ehrharta longiflora* Sm., *Phleum pratense* L., *Aegilops ovata* L., *Elymus paboanus* Claus., *E. canadensis* L., *E. junceus* Fisch., *Arrhenatherum elatius* (L.) J. et C. Presl., *Hordeum marinum* Huds., *Poa annua* L.

These plant house tests brought to light two important happenings, viz., that physiologic specialization occurs within *P. graminis lolii*, and that there are striking differences in the resistance and susceptibility of individuals within a species when inoculated with the same rust isolate.

TABLE 4.

Frequency Occurrence of the Two Races of P. graminis avenae *in Addition to* P. graminis lolii *on Various Grasses.*

Grass Host.	Frequency of Occurrence of Oat Stem Rust.	
	Race 2.	Race 7.
Lolium perenne	8	
L. multiflorum	1	
L. loliaceum	2	
L. rigidum	3	
Dactylis glomerata	29	2
Vulpia bromoides	30	2
V. Myuros	1	1
Echinopogon caespitosus	3	
Dichelachne spp.	1	
Festuca elatior var. *pratensis*	2	
Phalaris tuberosa	4	2
P. minor	2	
Agrostis avenacea	5	
Koeleria phleoides	3	
Lamarckia aurea	2	1

PHYSIOLOGIC SPECIALIZATION IN P. GRAMINIS LOLII.

Ten clumps of *Lolium perenne* growing in the University grounds were potted and tested with the stock culture of the rust. One gave sharp flecks (resistance), whilst all the others gave "4" reactions (susceptibility). The resistant plant and two of the susceptibles were retained. Later the plants were inoculated with a different isolate: the "resistant" clone produced "4" reactions in a side-by-side comparison in which the stock culture still gave flecks. A further interesting observation was that whilst the "resistant" clone was heavily attacked by *P. coronata lolii*, one of the two "susceptibles" was quite resistant to this leaf rust. It is thus clear that the breeding of a type with the combined resistance to stem and leaf rusts should not be difficult.

Further evidence of specialization came from *L. rigidum*. In a stand of rusted Wimmera rye grass at Tichborne, New South Wales, Dr. I. A. Watson collected a plant which was resistant. Seedlings from it segregated for resistance (fleck reactions) and susceptibility ("3" reactions) when inoculated with the stock culture. Typical plants of each sort were grown to maturity without bagging, and seed saved for further testing. These seedlings again segregated for resistance. Ten of these resistant ones were inoculated with the different isolate of *P. graminis lolii* and proved to be susceptible, thus giving proof of specialization of the fungus.

In yet another case, 16 seedlings of *Arrhenatherum elatius* were grown to maturity and each plant divided into separate entities for inoculation tests. Two of them, which gave susceptible "3" reactions with the stock culture, produced resistant "1" reactions with the second isolate.

Differential Resistance of Individuals within Species of Grasses.

In addition to the occurrence of resistance in *Lolium* spp., other cases of individual plants showing resistance were found in the following: *Agrostis avenacea* Gmel, *Hordeum leporinum* Link, *H. marinum* Huds., *Briza maxima* L., *Phalaris tuberosa* L., *P. minor* Retz., *Bromus racemosus* L., *B. Gussonii* Parl., *B. hordeaceus* L., *B. madritensis* L., *Lagurus ovatus* L., *Lamarckia aurea* (L.) Moench., *Ehrharta longiflora* Sm., *Phleum pratense* L., *Arrhenatherum elatius* var. *bulbosum* (Willd.) Spenner., *Dactylis glomerata* L., *Poa annua* L., *Lolium rigidum* Gaud., *L. multiflorum* Lam.

These inoculations showed that in some of the cases, a pot of 30 to 40 seedlings would give 3 or 4 resistant and the remainder susceptible plants, whereas the reverse was found in other cases. As a safeguard, seedlings showing the unusual reaction were grown to maturity in order to check their identity.

Inheritance studies were made in a few cases. In one, a collection was made of typical heads, nearing maturity, of *Bromus madritensis* growing in the Sydney University grounds. Pots of seedlings inoculated with the stock culture gave varying reactions: some were "X=", others a mixture of "X=" to "X+" and others "X‡". Eleven of the "X=" and 10 of the "X‡" were grown to maturity in the open.

In the next generation about 40 seedlings from each plant were tested. Of the 11 resistant ("X=") plants, one gave "X‡" (susceptible) reactions, five gave reactions varying from "X=" to "X‡" (heterozygous), and five gave "X=" (resistant) reactions. Of the 10 original susceptible ("X‡") plants, five produced seedlings giving "X=" to "X‡" reactions and five gave "X=" to "X" reactions—notably lower than the preceding.

For the next generation testing, representative resistant and susceptible plants from each group—72 in all—were grown on. Seedling tests of their progenies showed that three gave "X‡" (susceptible) reactions, nine gave "X=" to "X" (resistant) and the remainder "X=" to "X‡" (heterozygous).

Pure-lining of the grass was not carried out, and observations at flowering time indicate that natural crossing is to be expected. A genetical interpretation of the foregoing results was not possible, but the evidence shows that within a species there are marked differences between individuals in their resistance and susceptibility.

In the course of these seedling tests, the occurrence of albino seedlings was noted in the following grasses: *Lolium perenne*, *L. multiflorum*, *Agrostis avenacea*, *Hordeum marinum*, *Phalaris minor*, *Vulpia bromoides*, *Koeleria phleoides*, *Dactylis glomerata*, *Phleum pratense*, and *Agropyron trichophorum*.

Variegation was found in seedlings of *Lolium perenne* and *L. multiflorum*. These seedlings produced normal green leaves in later stages of growth, and their seedling progenies in no case showed inheritance of chlorophyll deficiency.

Resistant Grasses.

Apart from the occurrence of resistant and susceptible individuals within the species mentioned, resistance only was found in many species. This was of two sorts.

In the first, small hypersensitive flecks were produced. The grasses concerned are *Aegilops ovata* L. (some strains), *Phleum pratense* (some strains), *Briza maxima* (some strains), *Poa annua* (some strains).

In the second, resistance was complete, since inoculation produced no reaction whatever. These grasses were *Briza maxima* (some strains), *B. minor*, *Phleum pratense* (some strains), *Secale montanum* Guss., *Agrostis gigantica* Roth, *Poa compressa* L., *Agropyron scabrum* (Labill.) Beauv. (long and short glumes), *A. repens* (L.) Beauv.

Distribution of P. graminis lolii.

In respect of time, the isolates examined were distributed as follows: 1918 (2), 1921 (11), 1922 (2), 1923 (3), 1924 (7), 1925 (4), 1926 (13), 1927 (21), 1928 (8), 1929 (20), 1930 (24), 1931 (19), 1932 (18), 1933 (9), 1934 (45), 1935 (22), 1936 (21), 1937 (11), 1938 (19), 1939 (16), 1940 (9), 1941 (10), 1942 (2), 1943 (3), 1944 (2), 1945 (4), 1946 (4), 1947 (17), 1948 (9), 1949 (8), 1950 (6).

The source of the isolates was as follows: New South Wales, 249; Victoria, 4; South Australia, 25; Queensland, 2; Tasmania, 30; Western Australia, 1; Australian Capital Territory, 27; New Zealand, 31.

Discussion.

Delimitation of the units of classification of living things is necessarily difficult. It is particularly so in the organism under consideration because of the very wide variations it shows. The characteristics of *Puccinia graminis* Pers. as a species are clear as to general morphology and life history. Detailed studies, however, bring to light differences which have led to the setting up of groups which are called "subspecies" or "varieties". Statistical studies of the spore morphology reveal differences between them. Certain of them, e.g., *P. graminis phlei-pratensis*, may differ from others in their capacity to attack the barberry. The parasitic behaviour shown on certain hosts further emphasizes the differences between the subspecies and is, indeed, the main basis for their determination.

Within these subspecies further separation is made into physiologic races. These are characterized by the differential reactions they show upon groups of selected varieties of the host plant. Thus *P. graminis tritici* is split into more than 200 physiologic races which differ in the reactions produced on 12 particular varieties of wheat. The initial choice of these differential varieties is an empirical one based upon numerous "trial and error" tests. By more detailed study, as, for example, by using additional differential host varieties, isolates which appear to be the same physiologic race are separable further on the basis of the resistant or susceptible reactions now shown. These entities have been styled "biotypes" and may be regarded as individuals or groups of individuals which have the same genetic constitution.

In the present study no problem arises as to distinctions between biotypes and physiologic races. The question has to be considered, however, whether the stem rust on rye grass can rightly be considered as a physiologic race of one of the established subspecies (or varieties) of *P. graminis*, or whether it should be regarded as a new subspecies.

In his early work, Eriksson (1918) records as hosts of *P. graminis avenae* in Europe a number of grasses including *Dactylis glomerata*, *Lamarckia aurea*, *Vulpia bromoides*, and *Briza maxima*. These all have been found in Australia infected by *P. graminis*. In many of the cases the infection has been shown to be caused by one or other of the recognized physiologic races of *P. graminis avenae*, e.g., race 2 and race 7, of which the chief feature is their capacity to attack oats, even if some varieties are resistant. In many other cases the stem rust present has been unable to infect oats, or to do so very weakly in the case of only a few varieties in which a resistant reaction is shown. In yet other instances both these rusts were present on the grass host: one attacks oats and not *Lolium perenne*, and the other attacks *L. perenne* but not oats. A detailed examination has shown that both types can infect the barberry. Differences in the size of the spore forms is revealed by statistical examination of the measurements. In itself this would not be sufficient to warrant establishing a new subspecies, since significant differences are known to occur between certain well-recognized physiologic races within a subspecies. But when, in addition, the grass rust is unable to attack the cereal, then, instead of being regarded as a physiologic race of that cereal rust, it must be considered to be more widely divergent and to belong to a different subspecies.

The question then arises whether it is one of the recognized subspecies of grass stem rusts. Here again the rye grass rust is morphologically different when spore measurements are examined, and it differs also in its capacity to infect the normal hosts of these subspecies. Hence it must be regarded as a different subspecies.

Because of its frequent occurrence on *Lolium* spp. and the economic importance of these grasses, the name *P. graminis lolii* is proposed for this rust.

Acknowledgements.

Valuable help has been given by Dr. I. A. Watson and Dr. E. P. Baker, and is gratefully acknowledged. Thanks are due to workers in many places who have

forwarded specimens for study, and to Miss Joyce W. Vickery of the National Herbarium, for grass determinations. Financial assistance from the Commonwealth Research Grant has been of the utmost value.

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CELAENOPSOIDES GUNTHER, 1942: A SYNONYM OF *OPHIOMEGISTUS* BANKS, 1914 (ACARINA:PARASITIDAE).

By Carl E. M. Gunther, M.D., B.S., D.T.M. (Sydney), D.T.M. & H. (England), Field Medical Officer, Bulolo Gold Dredging Limited, Bulolo, Territory of Papua–New Guinea.

[Read 25th July, 1951.]

Synopsis.

Celaenopsoides buloloensis Gunther 1942, taken from rats at Bulolo, is congeneric with *Ophiomegistus luzonensis* Banks 1914, from a snake in the Philippine Islands. This paper records the consequent changes in nomenclature.

Mr. K. P. Lamb, of the New Zealand Department of Scientific and Industrial Research, has very kindly pointed out (personal communication) that *Celaenopsoides buloloensis* Gunther, 1942, is congeneric with *Ohphiomegistus luzonensis* Banks, 1914.

Banks's original specimens were taken on a snake in the Philippine Islands; in 1947 Grant reported and redescribed the same species from a snake at Hollandia in Dutch New Guinea. My specimens were taken from rats at Bulolo in the Mandated Territory of New Guinea. Apart from the host-difference and certain specific differences, there is one important distinction between *O. luzonensis* and *C. buloloensis*: the former shows no parapodal plates, while the latter has long thin parapodal plates running back to the tip of the abdomen. Banks's key to the Parasitinae (1915) gives, in part:

"4. Venter with lateral chitinous plates, separate from the ventral plate, and extending to posterior margin of the body 5
Venter without separate lateral plates reaching to the tip of the body 6
5. Anal aperture in the ventral plate ..... *Caelenopsis* [*sic*]
Anal aperture in the post-ventral plate ..... *Euzercon*
6. Body nearly circular, legs short, first pair with quite long hairs at tip; hind legs without teeth on the femora; male mandibles with a brush of long hair; male aperture in the sternal plate ..... Tribe Antennophorini."

Later in the same publication Banks refers, in passing, to *Ophiomegistus* as belonging to the Antennophorini. Now *Ophiomegistus* was erected as a monotypical genus, and *O. luzonensis* has no parapodal plates, but *C. buloloensis* is so clearly congeneric with *O. luzonensis* that the presence or absence of parapodal plates is obviously of no significance, and therefore Banks's key is inadequate. However, that is not for consideration here. The systematics of the genus are as follows:

Genus Ophiomegistus Banks, 1914.

Ophiomegistus Banks, N., 1914: *J. Entom. and Zool.*, Pomona College, VI, 58; 1915: U.S. Dept. Agric., Report 108, 87; Grant, C. D., 1947, *Microentomology*, xii, i, 22.

Celaenopsoides Gunther, 1942: Proc. Linn. Soc. N.S.W., lxvii, 87.

1. *O. luzonensis* Banks, 1914 [*loc. cit.*]; Grant, 1947 [*loc. cit.*]. Type genus.
2. *O. buloloensis* (Gunther, 1942 [*loc. cit.*]) *vice Celaenopsoides buloloensis* Gunther, 1942 [*loc. cit.*].

ON *TROMBICULA MINOR* BERLESE, 1905.

By Carl E. M. Gunther, M.D., B.S., D.T.M. (Sydney), D.T.M. & H. (England), Field Medical Officer, Bulolo Gold Dredging Limited, Bulolo, Territory of Papua–New Guinea.

(Three Text-figures.)

[Read 27th June, 1951.]

Synopsis.

Trombicula minor Berlese 1905 is the genotype of *Trombicula*, but unfortunately no specimens of *T. minor* are available. This paper records all that is known of the species; the synonymy is discussed and a full list of references is given.

I. The Genotype.

The genus *Trombicula* Berlese, 1905, is of considerable medical importance, since among its members are all the known vectors of tsutsugamushibyo (Japanese river fever, mite typhus, scrub typhus). *Trombicula minor* Berlese, 1905, is the genotype of *Trombicula*, and hence is of comparable acarological importance. But, unfortunately, there are no specimens of *T. minor* at present available, and it has been deemed advisable to assemble in one place all that is known of the species.

The original specimens were collected by Professor Kraepelin, then Director of the Hamburg Museum, among bat guano in caves at Tjompea, in Java (Willmann, 1941, p. 135: "Das Präparat von *Trombicula minor* ist mit folgender Fundortsangabe versehen: 'Tjompea, Java, 19.III.1904, aus Höhlenguano gesiebt.' "). They were described by Antonio Berlese (Berlese, 1905, p. 155: "*Trombicula minor* n. sp."); it is apparent that there were two complete specimens (Berlese, 1905, p. 156: "Duo vidi exempla collecta ad Tjompea", and Willmann, 1941, p. 133: "Im Präparat findet sich noch ein zweites Exemplar ohne Eier") and some fragments (Berlese, 1912, p. 94: ". . . io non possideo che alcuni frammenti di questo acaro, . . .").

The two complete specimens were lodged at the Hamburg Museum (Berlese, 1912, p. 94: "I tipici si trovano al museo di Amburgo; . . ."), and Berlese retained the fragments himself (*supra*).

In 1941, Herr Carl Willmann, of Bremen, examined the Hamburg specimens and redescribed them (Willmann, 1941, p. 132: ". . . habe ich eine Nachuntersuchung des Typenexemplares vorgenommen. Das Präparat wurde mir vom zoologischen Museum in Hamburg zu diesem Zwecke liebenswürdigerweise bereitwilligst zur Verfügung gestellt.").

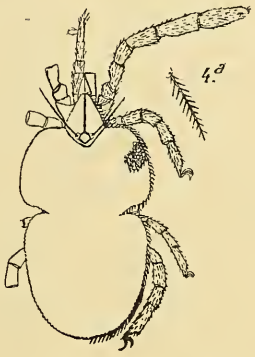
In 1950 I visited Hamburg, intending to study the genotype myself; Professor F. Weyer, Director of the Bernhard-Nocht-Institut für Schiffs- und Tropenkrankheiten, most kindly made inquiries for me at the Hamburg Museum and found that the two specimens of *T. minor* had been destroyed (Weyer, personal communication, 25th May, 1950: "Ich habe sofort mit dem Zoologischen Museum telephoniert und erfuhr, dass die Typen und Paratypen von *Trombicula minor* durch den Krieg zerstört sind.").

I then consulted Herr Carl Willmann, of Bremen. He reviewed the above facts and pointed out that *T. minor* is unalterably the genotype of *Trombicula*, according to Article 30c of the International Rules of Zoölogical Nomenclature (in Schenk and McMasters, 1936, p. 34: "c) A genus proposed with a single original species takes that species as its type."). He also pointed out that nothing but a suitable topotype would serve to replace the lost genotype (cf. Schenk and McMasters, 1936, p. 8: "When the original type material of a species is lost, the reviser of the species should choose a neotype. The neotype must be a specimen from the type-locality of the species and certainly must agree with the original figure and description.").

Later, I made inquiries at the Instituto Superiore de Sanita in Rome, but could secure no information about the fragments retained by Berlese.

Dr. Cornelius B. Philip, of the Rocky Mountain Laboratory in Montana, very kindly allowed me to see the correspondence he has had with Dr. A. Diakonoff, of the Zoological Museum at Buitenzorg. Dr. Diakonoff, at Dr. Philip's request, had secured some material from the caves at Tjompea, and this was examined at the laboratory; unfortunately there were no Trombiculae found. It is hoped that further attempts will be made.

There the matter rests until such time as a suitable topotype is found and accepted. Its acceptance must be based on its agreement with Berlese's original description and illustration (1905); but Berlese's 1912 work, and especially the additional details reported by Willmann in 1941, must also be given full consideration. Berlese's fragments, if they can be located, may be of some help, even though in 1912 he said of them: ". . . ho potuto rilevare solo i caratteri accenati, ma non si trova la base del capotorace



Text-figure 1.—*Trombicula minor* Berl. (Prona; 4*a*, corporis seta.). (After Berlese, 1905, Pl. xv, figs. 4, 4*a*.)

coll'area sensilligera per potere vedere se esistono o meno gli occhi". For completeness, and for the convenience of future workers, I include here the relevant quotations and the illustrations from both these writers:

Berlese, A., 1905: *Redia*, II, ii, 155: "Acari di Giava: *Trombicula minor* n. sp.: Albida (?), elongata, in medio circiter corpore valde coarctata. Crista metopica posterius in arcam subrhombicam desineno, utrinque longe unipilam (pili isti curte barbatuli). Pedes antici caeteris longiores et robustiores, tarso longe conico. Palpi longiores, ungue valido et longo, interne ad unguem spinis longis et robustis duabus, tentaculo autem sat longo cylindrico. Derma corporis crasse et aeque granuloso-verruculosum ex verruca quaque pilus exoritur qui sat brevis est, utrinque barbatulus. Pedes pilis conformibus dense obtecti (Fig. 4). Ad 680μ long."

Berlese, A., 1912: *Redia*, VIII, i, 94: "*Trombicula minor* Berl. 1905. Albida. Pili trunci curtiores (20–25μ). Tarsi antici bene conici, acuti, tibiae vix curtiores, duplo et dimidio longiores quam lati. Palpi graciles, longi, ungue exili et bene longo, falcato, spinis internis duabus. Ad. 680μ long."

"Inoltre anche il palpo é diverso [from *T. mediocris*]. Esso é piú smilzo, con unghia molto piú lunga e sottile, e con due sole spine alla sua radice, dal lato interno."

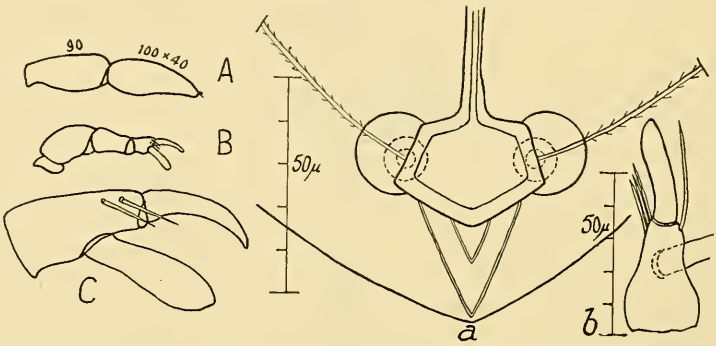
"I tarsi anteriori, . . . sono conici e molto stretti nella parte apicale; misurano 100μ di lunghezza per 40μ di larghezza. Inoltre piccola é la differenza di lunghezza tra i tarsi anteriori e le tibie, poiché queste sono lunghe 90μ cioé piú corte (della decima parte) del tarso."

Willmann, C., 1941: "Zool. Anzeiger, CXXXIII, v/vi, 131: "Nach BERLESE (1905) hat die Palptibia innen neben der Endkralle 2 starke Dornen."

"Ich konnte an dem Typenexemplar die Palpen leider nur in Dorsalansicht untersuchen, habe aber feststellen können, dass BERLESE sich augenscheinlich geirrt hat, . . .

An dem Typenexemplar ist trotz der ungünstigen Lage deutlich zu erkennen, dass an der Innenseiten 3 'Dornen' . .. vorhanden sind. Sie stehen aber so dicht nebeneinander, dass es von oben aussieht, als wenn sie aus einem gemeinsamen Grundteil herauskämen. Es ist aber anzunehmen, dass es sich in Wirklichkeit um 3 einzelne, starke Borsten handelt, die so dicht neben- und etwas untereinander stehen, dass sie den Eindruck einer dreifach gegabelten Borste hervorrufen. Eine dreizinkige Gabel an dieser Stelle wäre für die gesamte Familie der Trombidiidae etwas ganz Absonderliches. An der Aussenseite der Endkralle steht eine lange, einfache Borst (Abb. 1b)."

"BERLESE war also selbst im Zweifel, ob die Spezies Augen habe oder nicht. Zu einem einwandfreien Ergebnis hat die Untersuchung des Typenexemplares auch nicht geführt. Ich habe die Area sensilligera mit Immersionssystem untersucht und konnte folgendes feststellen: Die lange, gerade Crista hat in der Mitte eine Längsrinne. Sie erweitert sich hinten zu einer sechseckingen Area sensilligera (Abb. 1a). Die Haargruben, Trichobothrien nach GRANDJEAN, liegen direkt am Aussenrande der Areole. Aus ihnen



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Text-fig. 2.—*Trombicula minor* Berl. (A : B :: 100 : 1). A, tarso e tibia 1° paio; B, palpo; C, apice del palpo molto più ingrandito (lato interno). After Berlese, 1912, p. 94.

Text-fig. 3.—*Trombicula minor*. *a*, area sensilligera; *b*, palptibia, dorsal. After Willmann, 1941, p. 134.

regen die langen, steifen, feinbewimperten Sinneshaare heraus. Sie sind 107µ lang, während die ganze Criste 127µ lang ist. Diese deutlich zu erkennenden, von einem Kreis umschlossenen, vertieften Haargruben sind nach aussen umgeben von einem stark gewölbten, vollig glatten Wall, der etwa zwei Drittel eines Kreisumfanges einnimmt. BERLESE zeichnet es 1905 so, als wenn neben dem schräg nach vorn gerichteten Seitenrande der Area eine starke, kreisformige Trichobothrie vorhanden sei, aus deren Mitte die Sinneshaare hervortreten. Das ist aber nicht der Fall. Man sieht die Haargruben erst bei tieferer Einstellung des Mikroskoptubus. Sie liegen exzentrisch zu der Umwallung und sind halb unter die Areole und den stark gewölbten äusseren Wall geschoben. Dieser Wall jederseites des Seitenrandes der Area macht den Eindruck, als ob es sich wohl um ein Auge handeln könne. Mit Bestimmheit möchte ich das aber nicht behaupten. Die Lage der Augen direkt am Seitenrande der Sinnesareole wäre nicht besonders auffällig, findet sich doch eine ähnliche Bildung bei der Gattung Trombiculoides JACOT, bei der die als Augen angesprochenen Organe nur in einer starken Vorwölbung des Seitenrandes der Sinnesarea bestehen, also noch weniger hervortreten als hier. Das Eigenartige ist aber die Lage der Trichobothrien zu den 'Augen'. Die Sinnesborsten kommen genau auf der Grenze der Areole und der 'Augen' heraus, und die kreisförmigen Umgrenzungen der Haargruben schieben sich, wie schon gesagt, sowohl unter den Seitenrand der Areole als auch unter die vermeintlichen 'Augen' hinunter."

Lest there be any doubt about the status of Berlese's original specimens, Berlese himself first started this hare (1912: ". . . e non é certo il caso di pensare ad individui giovani."), and Ewing followed him (1920 and 1938)—I include here Willmann's state-

ment (1941): "Es handelt sich bei dem Typenexemplar von *Trombicula minor* BERL. auf keinen Fall um eine Nymphe, es ist ein adultes Tier, in dessen Körper deutlich ein vollausgebildetes Ei zu erkennen ist."

II. The Synonymy of Trombicula minor.

I have been largely responsible for creating considerable confusion concerning the taxonomy of *T. minor* and certain other Trombiculae, and it is now necessary for me to explain and clear up the situation as far as I can.

In 1939 I described a larval mite from New Guinea, *Trombicula hirsti* var. *buloloensis*, and stated that it was probably only a local variant of *T. hirsti* Sambon, 1927. In the same year I bred nymphs of this species and published (1939*a*) the statement: ". . . as far as can be determined, these nymphs are identical with *Trombicula minor* Berlese, 1904 [sic]."

Womersley (1939) considered certain collateral evidence from Queensland mites and approved the above identification. He also discounted the slight differences between *T. hirsti* Sambon and *T. hirsti* var. *buloloensis*, and pronounced them to be synonymous.

In 1940 I reviewed the literature and reached the following conclusions:

1. That *T. pseudoakamushi* Hatori, 1919 (*nec* Tanaka, 1916), was synonymous with *T. mediocris* Berlese, 1912.

2. That *T. pseudoakamushi* Hatori was also synonymous with *T. hirsti*.

3. And therefore that, because of the assumption that *T. hirsti* was a synonym of *T. minor*, both *T. pseudoakamushi* Hatori and *T. mediocris* were also synonyms of *T. minor*.

I used this synonymy in several subsequent papers (1939*b*, 1940*a*, 1940*b*, and 1941). It was adopted by many writers, but others did not accept it as proved, and Ewing (1944), reviewing Willmann's paper on the genotypes of *T. minor*, concluded that *T. hirsti* var. *buloloensis* was distinct from *T. minor*.

In 1950 I took some nymphs of *T. hirsti* var. *buloloensis* to Herr Carl Willmann in Bremen. He examined them, and from comparison with his notes, sketches, and recollections of *T. minor* he was able to state authoritatively that the two species were quite distinct. This being so, the argument that *T. mediocris* is synonymous with *T. minor* falls down—there is no other evidence beyond Miyajima's very vague suggestion (1920). Thus *T. minor* Berlese, 1905, stands alone, without any synonyms.

It is obviously necessary also at this stage to dispose of all those names which have formerly been regarded as synonyms of *T. minor*. That *T. pseudoakamushi* Hatori is synonymous with *T. hirsti* can hardly be doubted; Hirst (1929) and Gater (1932) provide overwhelming evidence in support. That Radford (1942) listed *T. pseudoakamushi* Hatori, 1919, as a valid species, without any reference whatever to *T. pseudoakamushi* Tanaka, 1916, means nothing; Womersley and Heaslip (1943) list "*T. hatorii* sp. nov.", with *T. pseudoakamushi* Hatori as its synonym, but their discussion is not convincing.

But that *T. pseudoakamushi* Hatori is synonymous with *T. mediocris* is probably not so. The suggestion first came from Kawamura and Yamaguchi (1921), but there is no supporting evidence available. Walch (1925) stated that his nymph of "*T. pseudoakamushi* (variatio *deliensis* ?)" resembled *T. mediocris*, but his illustration of the crista is clearly different from Berlese's (1912). Thus it would seem that *T. mediocris* Berlese, 1912, must also be regarded as standing alone, without synonyms.

This leaves *T. hirsti*. The situation here has become complicated because of the work of Wharton (1946), Philip and Woodward (1946), and Philip and Kohls (1948). They regard *T. hirsti* var. *buloloensis* as synonymous with *T. wichmanni* (Oudemans, 1905) Hirst, 1917. This may well be—but the corollary would be that *T. hirsti* is therefore also synonymous with *T. wichmanni*, for there is as little variation on the one side as on the other. Moreover, Philip (1947) mentions that *T. hatorii* (= *T. pseudoakamushi* Hatori, *non* Tanaka) is likely to prove a synonym of *T. wichmanni*, which would complete the circle. However, I feel that this can wait until actual specimens

from all areas have been properly compared, and with the reservation that perhaps *T. hirsti* and its synonyms will ultimately become in turn synonyms of *T. wichmanni*. I offer the following synonymy for *T. hirsti*:

TROMBICULA HIRSTI Sambon, 1927.

(Sambon, L. W., 1927: *Ann. Mag. Nat. Hist.*, IX, xx, 157.)
T. pseudoakamushi Hatori, 1919 (*nec* Tanaka, 1916).
T. pseudoakamushi (variatio *deliensis*) Walch, 1924.
T. pseudoakamushi (variatio *deliensis* ?) Walch, 1925.
T. hirsti var. *morobensis* (*nom. nud.*) Gunther, 1938.
T. hirsti var. *buloloensis* Gunther, 1939.
T. hatorii Womersley and Heaslip, 1943.
T. minor var. *deliensis* Walch, 1923, in Womersley and Heaslip, 1943.
T. hirsti var. *boloensis* [*laps. cal.*] Farner and Katsampes, 1944.
T. buloloensis Gunther, 1939, in Blake *et al.*, 1945.
Eutrombicula buloloensis (Gunther, 1939) Wharton, 1946.

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My very grateful thanks are due to the many acarologists who have discussed these matters with me and given me advice and help—in particular, Herr Carl Willmann, who gave me so much of his time, and so courteously pronounced his opinions, and gave me permission to quote him and use his illustrations; the late Dr. H. E. Ewing, who, though very sick, still exerted himself to offer advice; and Dr. C. B. Philip, who so kindly read this paper, checked references, and gave much-appreciated advice.

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THE EVOLUTION OF THE RADIO-MEDIAL AREA IN THE WINGS OF THE MUSCOIDEA ACALYPTRATA (DIPTERA).

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(Thirty Text-figures.)

[Read 27th June, 1951.]

Synopsis.

The writer attempts to homologize the venation of the Muscoidea Acalyptrata with that of the Nematocera and Orthorrhapha. As a basis for discussion of the changes involved, the wings of two generalized Nematocera are considered in some detail. The medial field is then traced through the higher Nematocera and Orthorrhapha to demonstrate that, in its essentials, this field has remained unaltered since its first appearance in the Dolichopodidae, and evidence in support of this view is presented. An essay is made to place the *vena spuria* and the vein in the wings of the Syrphoidea and Muscoidea, usually referred to as M_1, in their correct relation to other parts of the venation, and to show that the *vena spuria* has exercised a profound influence, even in the wings of the most advanced Diptera. Finally, in a series of hypothetical figures, are set out the possible changes that have been necessary to evolve, from the wing of an asilid-bombyliid-like ancestor, the wing of the Muscoidea Acalyptrata.

Introduction.

During the past hundred years the venation of the dipterous wing has claimed the attention of many students. The need for a venational system early made itself felt in that period of entomology when descriptive work was practically its sole function. Through the efforts of Bates, Wallace, and others, great collections were being built up, and the rapid naming of hosts of newly discovered insects was of prime importance. In answer to this demand, the first venational systems were developed. Two of these appeared in 1862, Loew's system and Schiner's. Both had one feature in common: each was artificial, having as its object the supplying of a rapid and convenient method of notation for descriptive purposes.

The first attempt at a study of wing venation, as contrasted with the mere giving of names or numbers to the veins, was made in 1886, when Josef Redtenbacher propounded his system of venational nomenclature. He realized that the six venational fields were a common inheritance in the wings of all insects. To the principal vein in each of these fields he gave the names accepted today, namely, Costa, Sub-costa, Radius, Media, Cubitus, and the Anal group, and further, he adopted Adolph's conception of the alternation of convex and concave veins, a suggestion which then fell into abeyance until its importance was again recognized by Lameere in 1922.

Using Redtenbacher's ideas as a foundation, Comstock and Needham began their work in 1898, but it was not till 1918 that Comstock, in his book "The Wings of Insects", gave a complete account of the now well-known Comstock-Needham system. Based on morphology and homology, this system, modified as new evidence has become available, has been universally accepted as the only scientific one. Some of the more important modifications have resulted from the work of Tillyard, Alexander and, more recently, Vignon. Tillyard's researches have greatly clarified our ideas of the cubital and anal fields; our present conception of the radial field is the result of Alexander's work. Vignon has made a new study of the dipterous wing as a whole, and while all his conclusions are not yet accepted, there is much in his work that has real value. In Australia, considerable research on the dipterous wing has been done by several workers, but the outstanding contributions to our knowledge of the brachycerous venation have come from Hardy.

If evolution is to have any meaning for us we must regard the higher Diptera as having developed from a more generalized ancestor having many features in common with those of living Nematocera and Orthorrhapha, and it is to these that we must look for aid in the interpretation of the venation of the wing in higher forms. This paper makes no pretence to being a general study of the dipterous wing. I suggest some modification of our concepts of the venation of the medial field and of the area where that field and the radial are contiguous. The examples chosen for discussion are those which appear to me to be our best guides to the interpretation of the venation of this area of the wing in the Muscoidea Acalyptrata.

Evolutionary Trends in the Dipterous Wing.

The general trends of evolution have been to change the contour of the wing and to dispose the venation more effectively. From a long, narrow, petiolate wing, characteristic of the Tipulidae (see Text-figure 1), a shorter, broader one has been developed (see Text-figures 12, 14 and 15). Changes in venation have accompanied those in shape. Whereas, in the primitive wing, numerous veins were disposed over the whole wing area, in the higher Diptera their number is much reduced and they tend to be arranged nearer the costal margin, where their strengthening has given to the wing the reinforcement needed for sustained and rapid movement. To understand clearly these changes and the stages through which they have passed, it will be necessary to discuss the wing venation of some generalized types and then to follow the reduction through forms of increasing complexity until the higher Diptera are met. By this means it will be possible to homologize the veins of specialized forms with those of more generalized types, so giving an insight as to what the veins, present in the wings of the Muscoidea Acalyptrata, really are.

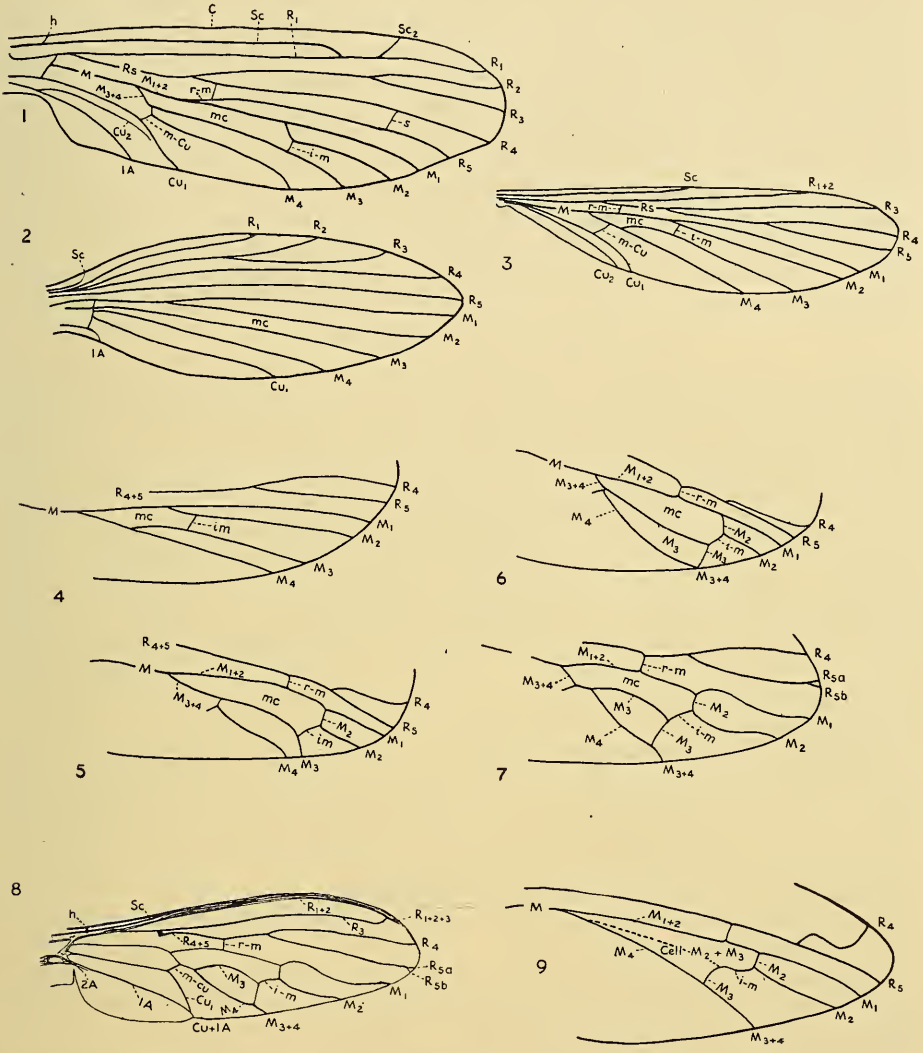
Venation of Two Primitive Living Nematocera.

The most generalized types of venation, in living Diptera, are to be found in the two nematocerous families, the Tanyderidae and the Psychodidae. As representative of these, the wing of *Nothoderus* (Tanyderidae) and that of an undetermined psychodid will serve to illustrate the archaic features of these wings. From the point of view of venation, the Tanyderidae are the most primitive known living Diptera. The wing of *Nothoderus* (Text-figure 1) is long and narrow, the veins being disposed evenly over its whole area. Although considerable reduction has already occurred, it still shows a very full venation. The subcosta still retains its primitive two-branched form, though Sc_2 is already in process of reduction. A complete radial field is present, R_1 and the four branches of Rs all reaching the wing margin as independent veins. The medial field, with its four independent branches, is complete, and the median cell, between M_2 and M_3, is small, elongate, sub-rectangular in outline, and closed by i-m. It is in the cubital and anal fields that most departure from the wing of the archetype has occurred, since considerable reduction in these fields is obvious. Cu_{1a} and Cu_{1b} have already coalesced to form the single vein Cu_1, while Cu_2 no longer reaches the anal margin. The first anal vein alone is present, the second and third having been completely suppressed.

The wing of *Psychoda* (Text-figure 2) shows features which indicate an advance on that of *Nothoderus*. The venation is still of a generalized nature and is evenly disposed over the whole wing area, but the length of the wing, relative to its width, is much less. The subcosta is now represented by a single vein only, there being no trace of Sc_2. The radial field is complete, as is the medial. The median cell is open, the crossvein i-m having been lost. The cubital field has been further reduced by the complete loss of Cu_2, while a single anal vein, IA (and that short and weak) has been retained.

In both these wings the characters to which I wish to draw attention are the complete five-branched radial field, the complete four-branched medial field, and the small median cell between M_2 and M_3, in *Nothoderus*, closed by the cross vein i-m. This is the primitive pattern of this part of the wing, a pattern shown in the wings of a very

small number of the older Nematocera only, and one which never reappears later. It is the reduction which these fields undergo in the course of evolution that is the object of this study.



Text-figures 1-9.

1, 2.—Generalized venation in the older Nematocera. 1, Wing of *Nothoderus australiensis* Alexander (Tanyderidae); 2, Wing of *Psychoda* sp. (Psychodidae).

3.—Generalized venation in the older Asilidae; the wing of *Leptogaster* sp.

4-7.—Development of the medial field in the Asilidae. 4, Medial field of *Leptogaster* sp. The small median cell closed by i-m, and the four free branches of the media are primitive characters; 5, Medial field of *Saropogon luteus*. The anal turning of the termination of M_3 is the first stage in the specialization of the medial field; 6, Medial field of *Senobasis mendax*. Basad movement of the termination of M_3 has closed cell M_3. Veins M_3 and M_4 have united at the wing margin to form one vein, M_{3+4}. Two closed cells in medial field; 7, Medial field of *Laphria* sp. Basad movement along M_4 of point of union of M_3 and M_4 results in vein M_{3+4} becoming of considerable length.

8.—Wing of *Laphria* sp. (Asilidae).

9.—Medial field of *Sphenoidoptera varipennis* (Bombyliidae). The loss of the basal free part of M_3 causes the first appearance of the cell M_2+M_3. The dotted line in the cell represents the part of M_3 which has been suppressed.

Venation of the Higher Nematocera.

Throughout the sub-order the above general disposition of the medial field is retained, but great changes in the radial field, foreshadowing those by which this field has been produced in the higher Diptera, have occurred in its more advanced members. Alexander (1927 and 1928) demonstrated, in the Tipulidae, the manner in which evolution has brought about the coalescence of R_1 and R_2 to form a single vein reaching the wing margin as R_{1+2}. He further showed that the changes applied not only to the Tipulidae, but equally to all higher members of the order. R_{1+2} is, therefore, a constant in the wings of all Diptera except those few primitive species which still retain both veins as separate entities. Where the union has occurred, R_3, left as a separate prong of the original R_{2+3} fork, reaches the wing margin as an independent vein, and it, too, occurs in all dipterous wings. In some of the higher Nematocera the R_{4+5} fork, by moving distad, has produced a single compound vein R_{4+5}, but in many, R_4 and R_5 retain their separate identities so that a radial field of four veins, a disposition common in the Orthorrhapha, is formed. The veins are R_{1+2}, R_3, R_4 and R_5 (see Text-figures 3 and 8).

Venation of the Orthorrhapha.

Just as the more generalized examples of venation are to be found in the lower Nematocera, so it is in the lower Orthorrhapha that is found what may be regarded as the generalized venation of this division. From here onwards there is a strong tendency towards the retention of a four-branched radial field, and it is the medial field that becomes the focal point of reduction. The lower members of the Asilidae form a good point of departure for a consideration of those changes which ultimately lead to the type of medial field characteristic of the higher Diptera. The wing of *Leptogaster* (Text-figure 3) illustrates those features of the venation common to many of the lower Orthorrhapha: the subcosta is a single vein. The radial field is four-branched, R_{1+2}, R_3, R_4 and R_5 all reaching the wing margin independently. Two cubital branches, Cu_1 and Cu_2, are present and reach the wing margin. There are no anal veins. The medial field (Text-figure 4) is of the primitive type, consisting of four independent veins, M_1, M_2, M_3 and M_4, all of which reach the wing margin. There is a small, elongate, median cell, closed by i-m.

Specialization of the medial field begins in the Asilidae. An early stage of this is shown in the medial field of *Saropogon* (Text-figure 5), where M_3, instead of proceeding directly to the wing margin, has its termination diverted towards the anal margin. This tendency in M_3 becomes more pronounced in higher members of the family.

In *Senobasis* (Text-figure 6) further basad movement of the termination of M_3 brings its tip into contact with that of M_4 at the wing margin, thereby closing cell M_3. The medial field now includes two closed cells—mc and cell M_3. The combination of veins at the wing margin is M_{3+4}.

The highest of the Asilidae advance a stage further. The point of union of M_3 and M_4 begins to move basad along M_4, finally attaining the position shown in the medial field of the wing of *Laphria* (Text-figure 7). There is thus brought about a coalescence of the two veins for a considerable part of their length.

Reduction of this field goes no further in the Asilidae, so that consideration of the wing as a whole (Text-figure 8) will illustrate the highest type of venation occurring in the family. The subcosta is a single vein and has considerably shortened. The radial field consists of four branches, R_{1+2}, R_3, R_4 and R_5. The union of R_{1+2} with R_3 occurs in the sub-families Laphriinae and Asilinae but, in the Dasypoginae, R_{1+2} and R_3 both end normally in the wing margin. R_4 and R_5 (the two small branches of R_5 are aberrant) each attains the wing margin and shows a tendency to turn anteriorly towards the wing apex. Of the medial field, three branches reach the wing margin. These are M_1, M_2 and M_{3+4}. The median cell is small and elongate. Posterior to it lies the closed triangular cell M_3. The median cell and cell M_3 are closed by three veins or parts of veins. Cell M_3 is closed by part of the vein M_3 while the median cell is closed by i-m and part of M_2. There are then, lying between M_{1+2} and M_4, two closed cells. In the cubital field is seen the first stage of the reduction which gives rise later to the small

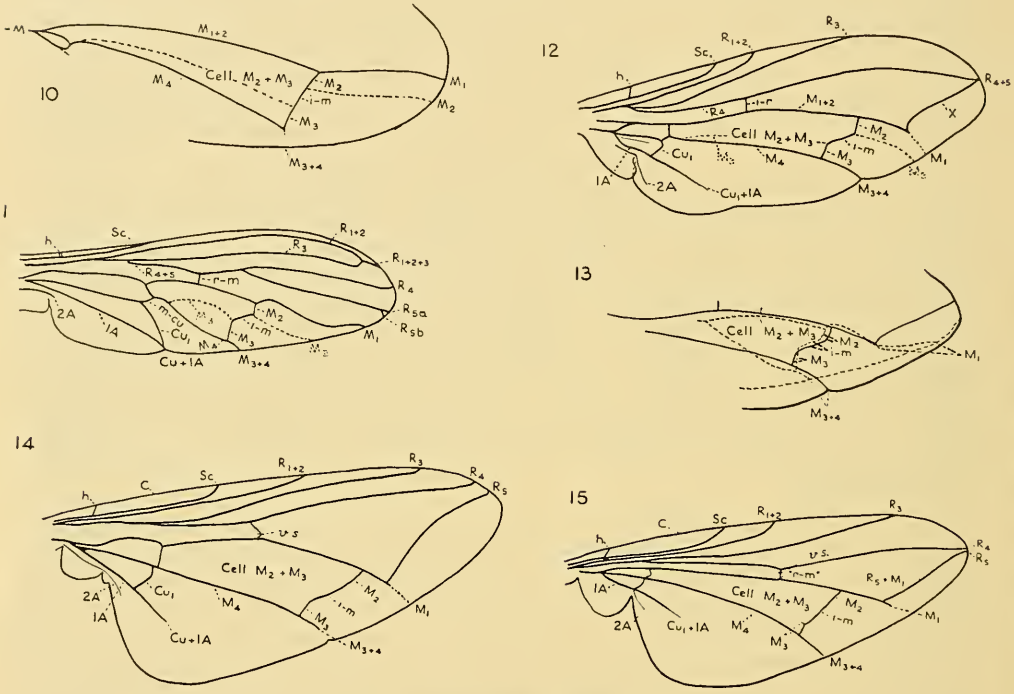
closed cubital cell of the higher Diptera; Cu_1, by turning basad, has united with 1A, thereby closing cell Cu_1. Cu_2 is vestigial, as also is 2A.

It is in the Bombyliidae that further stages in reduction are to be found. The radial field remains relatively unchanged. It still retains its four branches but there is a tendency for R_4 to turn apically, and, in the higher members of the family, this tendency, in both R_4 and R_5, is accentuated. In the medial field, however, very significant reduction has occurred. That of *Sphenoidoptera* (Text-figure 9) has lost the free basal part of M_3, though three medial branches, M_1, M_2 and M_{3+4} still reach the wing margin. The loss of the free basal part of M_3 results in the formation of a single, large, closed, sub-triangular cell within the medial field. Anteriorly this cell is bounded by M_{1+2}, and posteriorly by M_4. This large cell is not homologous with the median cell of lower Diptera and should not be so referred to. It is a compound cell, M_2+M_3. The identity of the median cell is merged in that of the combined cell, and from here onwards ceases to exist as an independent unit of the venation. Similarly, the "cross vein" closing it is not the i-m of the lower Diptera. It is a serial vein composed of three parts: one of these is the free basal part of M_2, the second is the free terminal part of M_3, and these are linked in the middle by the true cross vein, i-m. The "cross vein" so formed I propose to call the serial vein to indicate its true nature and to notate as *se*. Hardy (1947) has shown that a similar course of events has produced the compound cell in the wing of *Lepidostola* (Syrphidae). He is undecided as to whether or not M_2 forms part of the "cross vein" since he states that "the apparent cross vein may include the free basal part of M_2". All the evidence, however, supports my contention that the "cross vein" does include part of M_2. A study of large numbers of dipterous wings has convinced me that its inclusion, together with part of M_3, is certain in the wings of all Diptera which contain the cell M_2+M_3, that is, in all Diptera above the Bombyliidae. It is largely due to the failure to recognize M_2 in its correct position that has made impossible a satisfactory interpretation of the medial field in the higher Diptera.

The three-branched medial field, enclosing cell M_2+M_3, is maintained throughout the Orthorrhapha until the Dolichopodidae are reached, where a highly specialized field is developed. In the higher dolichopodids and in all Diptera higher than this family the terminal part of M_2 between the "cross vein" and the wing margin is suppressed and the medial field characteristic of the Cyclorrhapha makes its first appearance. In *Hydrophorus* (Text-figure 10) the medial field is so disposed. Two branches only of the media are evident; the anterior branch which reaches the wing margin is M_1, the posterior is M_4. All that now remains of M_2, as a separate entity, is that part of it which enters into the formation of the vein, *se*. The only remnant of M_3 is that part incorporated in the "cross vein" and the stub united with the end of M_4 as M_{3+4}.

This advanced type of medial field is so important that some consideration of it in detail is essential. If Text-figure 8 be again referred to, it will be obvious that, if the basal part of M_3 and the distal part of M_2 be eliminated, a similar type of medial field is the result. This has been done in Text-figure 11. The M_{1+2} branch still persists, but, of it, M_1 alone reaches the wing margin; M_{3+4} reaches the wing margin, but the free parts of M_2 and M_3 have lost their identities in linking with i-m to form the serial vein. The important fact to note here is that both branches of M_{1+2} are accounted for, M_1 terminating in the wing margin and M_2 in the anterior part of *se*. This is the disposition of these two veins in all the higher Diptera. If such be correct, we should expect to find, in the higher Diptera, "cross veins" of very irregular shape, indicative of their mode of formation. This is exactly what *does* occur. This angular type of "cross vein" is paralleled, time after time, in the wings of many Tachinidae which have retained evidence of its origin more definitely than have other families of the higher Diptera. It was this fact which, some years ago, caused me to begin the research, the results of which are given in this paper. Such a cross vein is shown in the wing of *Prosenina* (Tachinidae, Text-figure 12). The medial field of this wing is merely a repetition of the hypothetical field of Text-figure 11. This is made even more evident

if the two fields are superimposed, as has been done in Text-figure 13. The "cross vein" and cell M_2+M_3 have the same shape because they have been brought about in an identical manner. Throughout the Muscoidea Calyptrata every variation from the highly angular (*Prosenina*, Tachinidae, see Text-figure 12), through the sinuous (*Cylindromyia*, Tachinidae, Text-figure 14), to the almost straight (*Microtropeza*, Tachinidae, Text-figure 15), cross vein exists. Even in the Muscoidea Acalyptrata (for example, in the families Otitidae and Trypetidae) the sinuous *se* is not uncommon, though in this group it is usually straight. This straightening of the "cross vein" has hitherto tended to conceal its composite nature in those families in which it occurs.



Text-figures 10-15.

10.—Medial field of *Hydrophorus* sp. (Dolichopodidae).

The suppression of the free basal part of M_3 and the free terminal part of M_2 (shown by dotted lines) has given rise to the earliest appearance of the medial field, typical of that of the higher Diptera. The free parts of M_2 and M_3 are incorporated in the "cross vein".

11.—The wing of *Laphria* sp. (as in Text-figure 8) with the free basal part of M_3 and the free terminal part of M_2 (both shown dotted) eliminated to show how the medial field characteristic of the Tachinidae has been developed.

12.—The wing of *Prosenina* sp. (Tachinidae) showing the serial nature of the angular "cross vein" *se*. It is composed of the free basal part of M_2, the free terminal part of M_3, and the true cross vein i-m. Dotted lines represent the former courses of the suppressed parts of M_2 and M_3. X is the vein discussed later. (The cross vein notated as i-r should be r-m.)

13.—The medial field of *Prosenina* sp. (Tachinidae—solid lines) superimposed on that of *Laphria* sp. (Asilidae—dotted lines) to show how the medial field of the higher Diptera has evolved from one having asilid-like characteristics.

14.—Wing of *Cylindromyia* sp. (Tachinidae) showing sinuous form of vein *se*. Note stub of M_1 directed towards wing margin.

15.—Wing of *Microtropeza* sp. (Tachinidae) showing straight form of vein *se* and the stub of the suppressed free basal part of M_3.

Venation of the Syrphoidea and Muscoidea Calyptrata.

The location of M_1 and M_2 in their true positions is essential to a correct interpretation of the medial field in the higher Diptera. Because this has not hitherto been clearly understood needless confusion has arisen. A good illustration of this is the

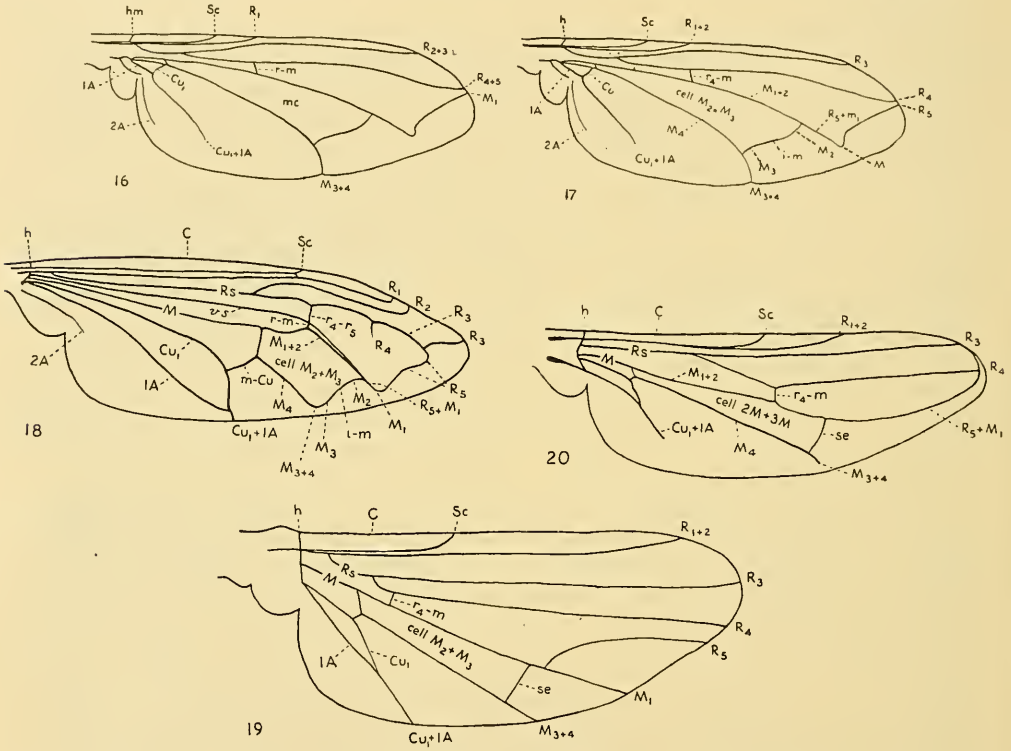
vein which, branching from M_1, is directed towards the wing apex (see X, Text-figure 12). It is usually notated as M_1, while M_1 itself is referred to as M_2; the actual M_2 in the serial vein is omitted altogether. Whatever this vein may be, it is certainly not M_1. Text-figures 12, 14 and 15 represent the wings of three species of Tachinidae. In these the termination of M_1 is clearly visible as a stub vein projected towards the wing margin. A fold in the wing membrane connects this stub vein with the margin, and suitable staining defines its former course even more clearly. What has occurred in the muscoid wing is that the termination of M_1 has been suppressed, its remnant being that section of it lying between the serial vein and the end of the stub vein. M_2, forming as it does part of *se*, cannot possibly occur in the position in which it is represented.

A further fact which militates against vein X as being M_1 is that of its direction and position. The occurrence of M_1 directed apically is highly exceptional, being found in those families only whose venation is complex. These families are the Mydaidae, Apioceridae and Nemestrinidae, and in the wings of each the presence of a four-branched radial field leaves no doubt that the vein posterior to R_5 must be M_1, or at least a medial branch incorporating it. It would certainly conflict with the principles of evolution of the insect wing if, in all the families of the Nematocera and the Orthorrhapha, M_1 should tend to continue straight to the wing margin or be directed anally, only suddenly to assume a completely new and abnormal position in the Syrphoidea and Muscoidea Calyptrata, and then, equally suddenly, to revert to its normal position in the Muscoidea Acalyptrata and the Hippoboscoidea. Yet this violence to homology has been accepted despite the fact that in both the Syrphoidea and the Muscoidea Calyptrata M_1 is clearly present in its normal position. The truth is that, in the Diptera as a whole, M_1 is remarkably constant in both its position and direction. Text-figures 16 and 17 represent the wing of *Calliphora stygia* Fabr. (Calliphoridae). Text-figure 16 is notated from Tillyard (1926); Text-figure 17 is notated to show the correct positions of M_1 and M_2.

Vein X, then, not being M_1 as usually understood, there appear to be two possibilities only as to its nature. It is either part of the anterior media, MA, or it is part of the radial field. In the dipterous wing the balance of evidence at present appears to favour the presence of MA, though Tillyard in 1926 (quoted from Hardy, 1947) stated that MA "appears to be entirely missing in most recent orders", thereby contradicting the opinion he had expressed in the previous year. Vignon (1932) claimed MA to be present, stating that the vein usually referred to as R_{1+5} was in reality MA_1; in the Syrphidae it is the *vena spuria* which he believes to be MA_1. Hardy (1947) considers that MA may be present in the Syrphidae, possibly incorporated in the *vena spuria*. The matter is so important, however, that the presence of MA must be demonstrated beyond all reasonable doubt before we can embody it in our scheme of venation, since our so doing will mean an entire recasting of the venation of the dipterous wing, a course which, at this stage of our knowledge, I do not feel to be warranted. Should MA be proven to be present, and Vignon's suggestion that the *vena spuria* is MA_1 be accepted, then I consider vein X to be the vestige of MA_1, as I believe it to be the functional part of the *vena spuria*. This would align my views with those of Vignon, at least in so far as this part of the wing is concerned. Subject to what has been said above, I shall regard MA as being absent from the dipterous wing and consider the present medial field to have been derived from the original posterior media, MP.

Provisionally rejecting the presence of MA, I believe vein X to be part of the radial field and considerable evidence exists to support this view. The vein makes its appearance in the wings of the Syrphoidea and the Muscoidea Calyptrata only, that is, in those families which have the *vena spuria* either actually present or which retain obvious vestiges of it. These two facts, considered together, suggest that there is some relation between them. Examination of large numbers of syrphid wings shows that the development of the *vena spuria* varies within wide limits among the species and

even among individuals. Sometimes little more than the vestiges where it crosses the so-called r-m can be observed. In other instances it attains a considerable length. In some few examples it is present almost as a complete functional vein. In these latter it appears to have its origin in Rs, and to be directed towards the termination of M_1, with which it may or may not coalesce. Even when incomplete, the stained wing often shows connections with Rs and M_1. In *Microdon* (Text-figure 18) it is practically complete, its distal end making contact with M_1 near the termination of the latter. From here it continues towards the wing apex as a functional vein. My interpretation, therefore, is that the *vena spuria* is R_5 and hence vein X is R_5 (Text-figure 18, and see Text-figures 14, 15 and 17). This means that in existing syrphids



Text-figures 16-20.

16, 17.—Wing of *Calliphora stygia* Fabr. (Calliphoridae). 16, Notated from Tillyard (1926); 17, Notated to show correct positions of M_1 and M_2. Rest of notation as explained in text. (R_5+m_1 should be R_5+M_1.)

18.—Wing of *Microdon fulgens* (Syrphidae) showing the venational pattern from which developed that of the higher Diptera. Note the very complete *vena spuria* (*v.s.*) and its connections. The terminal part of the *vena spuria* turns apically after coming in contact with M_1.

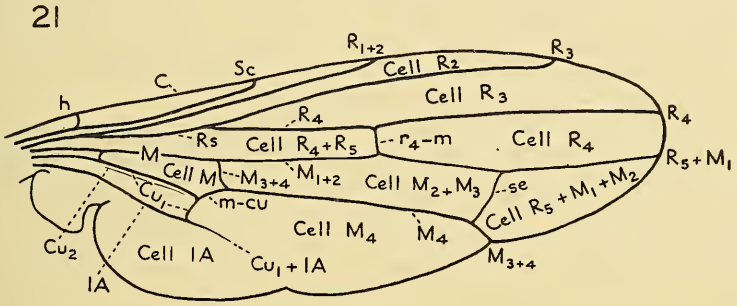
19.—Wing of *Platypezoides diversa* (Platypezidae) showing fusion of R_5 with M_1.

20.—Wing of *Chrysomyza aenea* (Otitidae) showing the apical trend of R_5+M_1, an example of the influence exerted on the combination by R_5.

the functional part of the *vena spuria* is R_5. Hardy (1947) questions the presence of R_5 in the wings of Syrphidae without denying the possibility of its occurrence. I believe that, when the *vena spuria* has been more widely studied, my contention that it is R_5 will be upheld. If the higher Diptera have developed from simpler forms allied to the lower, it seems difficult to deny to the Syrphidae the presence of R_5, which is a constant in the wings of the Nematocera and the Orthorrhapha. This would mean that the three radial branches in cyclorrhaphous wings are R_{1+2}, R_3 and R_4, with the vestiges of R_5 still retained as an independent vein in Syrphoidea and the Muscoidea Calyptrata. The cross vein, usually referred to as r-m, therefore connects not R_{4+5} with M_{1+2}, but R_4

with M_{1+2}, passing across R_5 as it does so. The true r-m is the posterior section of this vein.

The Muscoidea Calyptrata retain vestiges only of the *vena spuria*, but its former course across "r-m" is often defined by a noticeable angularity in "r-m" with short stubs of the original vein on either side (see Text-figures 14 and 15). When these are present, folds in the wing membrane connect them with Rs basally and with the tip of M_1 distally. In such cases the only part of R_5 that remains is the vein X (see Text-figure 12). The course of events, from the fully developed *vena spuria* to the final result as above, may have been brought about in the following manner: R_5 originally left Rs as a separate vein directed towards the tip of M_1, near where it turned sharply in an apical direction as other branches of the radius tend to do. Ultimately, union occurred between R_5 and M_1, and since M_1 now took over the functions previously performed by that section of R_5 between Rs and M_1, disintegration of this section began. An early stage of the reduction is represented in the wings of those Syrphidae in which the *vena spuria* is most complete (see Text-figure 18). With the passage of time the whole section was eliminated, its only vestige occurring where the vein crossed



Text-figure 21.

Wing of *Sapromyza ocellaris* Malloch (Lauxaniidae) to show the system of notation used in this paper for the wing of the Muscoidea Acalyptrata.

"r-m" (see Text-figures 14 and 15). In a later stage of development M_1 ceased to reach the wing margin (see Text-figure 15) and the distad movement of the point of union of R_5 and M_1 resulted in the coalescence of the two veins as R_5+M_1 (see Text-figure 20). The tendency for fusion to occur between R_5 and M_1 is early shown in the course of evolution. In varying degrees of completeness it is found in the wings of many Orthorrhapha. In the Tabanidae coalescence occurs, in most cases at the distal ends of the two veins, near the wing margin. More advanced examples of fusion occur in the Dolichopodidae, but it can best be seen in the wings of Platypezidae (Text-figure 19, *Platypezoides*) and Pipunculidae.

Venation of the Muscoidea Acalyptrata and Hippoboscoidea.

The culmination of the process of reduction is attained in these groups, and the preceding discussion has been a necessary introduction to a satisfactory interpretation of the venation, more particularly of the Muscoidea Acalyptrata. Further specialization eliminates even the vestiges of R_5 as a separate vein, its identity being merged in that of M_1. Nevertheless, the influence of R_5 is still noticeable in certain of the Otitidae, Tanypezidae and Calobatidae, in which a strong tendency is shown for R_5+M_1 still to be directed apically, as in *Chrysomyza* (Otitidae, Text-figure 20). In the higher families, such as the Lauxaniidae, this tendency is lost, R_5+M_1 continuing more or less directly to the wing margin. There is thus produced the venational plan which is characteristic of the most advanced Diptera.

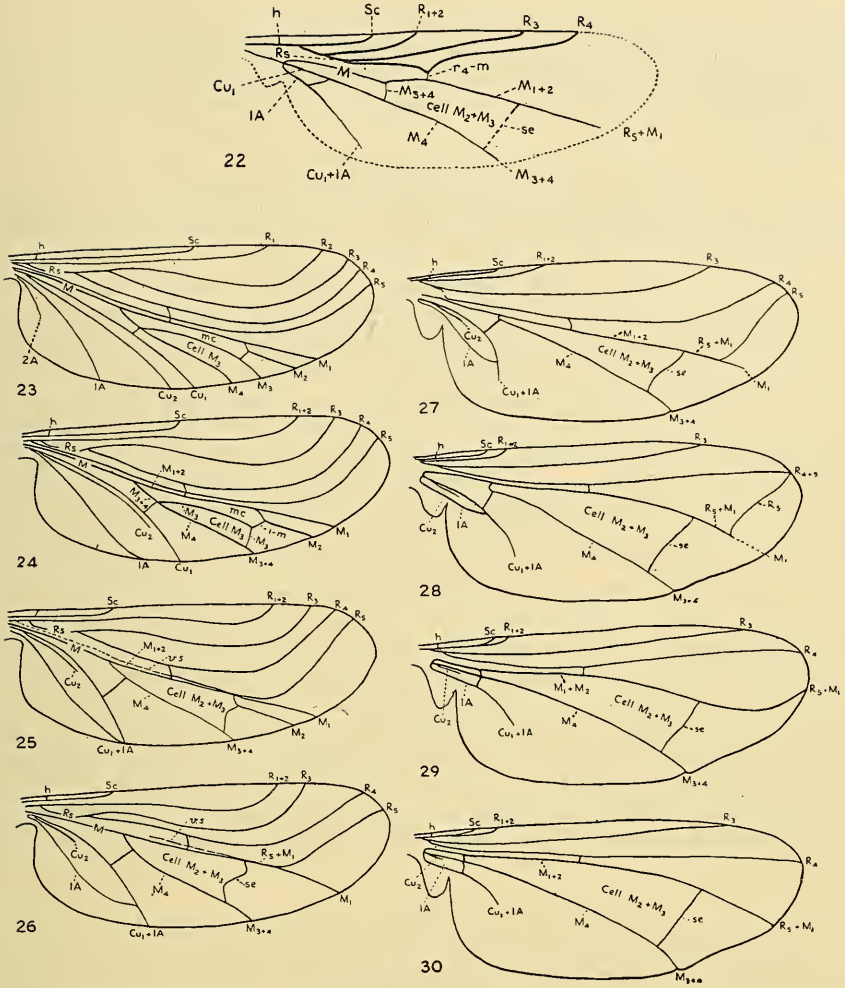
Sapromyza ocellaris Malloch (Lauxaniidae, Text-figure 21) exemplifies this type of venation. The number of veins has been greatly reduced, they tend to be reinforced in the anterior part of the wing, while large open cells occupy much of its posterior

region. A noticeable feature is the small number of closed cells, the result of the loss of cross veins, of which three only, "r-m", i-m incorporated in *se*, and m-cu remain. To indicate the true nature of "r-m" which bridges not R_{1+5} and M_{1+2}, but R_1 and M_{1+2}, I notate it as r_1–m. The subcosta is always short, making contact with the costa less than half-way along the margin. R_{1+2} is also short, and in many families its tip occupies the position formerly occupied by that of Sc. This results in the elimination of Sc, of which only a vestige remains near the wing base. If present, the sub-costal cell is small, but the basad movement of the termination of R_{1+2} often results in its obliteration. Cell R_2 is attenuated. Rs gives rise to two branches. The anterior of these is R_3, a long vein, more or less parallel to R_{1+2}, and terminating in the wing margin. The posterior branch is R_1, which continues independently to the wing margin. Of R_5 the distal part only remains, fused with M_1. The medial field consists of two branches. The anterior branch is M_{1+2} as far as the serial vein, where M_2 turns anally to form part of that vein. M_1 united with the vestiges of R_5 reaches the wing margin as R_5+M_1. The posterior branch of the media is M_4, which unites with the vestige of M_3 in the serial vein and reaches the wing margin as M_{3+4}. The large cell, bounded anteriorly by M_{1+2} and posteriorly by M_4, is cell M_2+M_3. This is closed by the serial vein *se*, composed of i-m, joined to parts of M_2 and M_3. Cell M_4 is very large. Cu_1, after forming the posterior boundary of cell M, turns anally and unites with 1A. The vein Cu_1+1A, so produced, is always short, never reaching the wing margin. Vestiges of Cu_2 and 2A sometimes occur near the wing base.

The venation of the Hippoboscoidea (Text-figure 22) is difficult of interpretation in the medial field by reason of further reduction. The serial vein, *se*, appears to have been eliminated, leaving cell M_2+M_3 open, but until I have a large collection of this superfamily available for study my suggestions can only remain tentative. It is often the exceptional individual which provides the key to difficulties, otherwise insuperable, and such are more likely to occur when there is ample material for examination. The effects of reduction have been to strengthen the veins of the radial field at the expense of those of the medial, and in these circumstances the loss of *se* would be a not unexpected result. Whether this has or has not happened will not affect the rest of the venation, which is modelled on that of the Diptera Acalyptrata.

Conclusions and Discussion.

As pointed out earlier, discussion of the venation of the lower Diptera was not an end in itself. I have used it in the elucidation of some difficulties of interpretation in the radial and medial fields of the Muscoidea Acalyptrata, and my conclusions are those stated above. I believe this venational type to have been derived from one having affinities with those of both the Asilidae and Bombyliidae. Such a wing may have been not unlike that of Text-figure 23. Text-figures 24–30 represent possible changes that occurred, culminating in the wing of *Sapromyza* (see Text-figure 21). The wing in Text-figure 23 combines a complete bombyliid-like radial field with a complete asilid-like medial field. In Text-figure 24 reduction has already resulted in the coalescence of R_1 and R_2 and the closure of cell M_3. Text-figure 25 shows the formation of the combined cell M_2+M_3 by the loss of the free basal part of M_3, while R_5 is degenerating into the *vena spuria*. In Text-figure 26 the loss of the terminal part of M_2 gives rise to the final development of cell M_2+M_3, which is closed by *se*. The basal part of R_5 is almost suppressed. In Text-figure 27 *se* is tending to straighten while only the free terminal part of R_5 remains. M_1 is being reduced and no longer reaches the wing margin. Text-figure 28 represents a further stage of Text-figure 27. In Text-figure 29, M_1 has lost its identity by its coalescence with R_5, the influence of which is still shown by the direction taken by R_5+M_1. Text-figure 30 is the typical wing of the Muscoidea Acalyptrata. A comparison with Text-figure 23 shows the very great reduction which has occurred. These changes may be summarized as follows. Throughout the series there has been a great reduction in the number of veins and their disposition has been completely changed. Their general costad movement has produced large areas in the posterior part of the wing membrane where venation is absent. The veins towards the



Text-figures 22-30.

22. Wing of *Ornithomyia* sp. (Hippoboscidae) to show the maximum of reduction in the dipterous wing. Note strengthening of anterior veins and corresponding weakening of the veins in the posterior region of the wing. The dotted line shows the position of the suppressed *se*.

23-30.—Possible stages in the evolution of the wing of the Muscoidea Acalyptrata. 23, Wing of hypothetical orthorrhaphous ancestor. A five-branched bombyliid-like radial field and a four-branched asilid-like medial field are present. The median cell is small and elongate. 24, R_1 and R_2 have fused to form R_{1+2}. A four-branched radial field, R_{1+2}, R_3, R_4 and R_5, is produced. Basad movement of the termination of M_3 has closed cell M_3 and the combined vein M_{3+4} has been developed. This results in the reduction of the medial field to three branches reaching the wing margin M_1, M_2 and M_{3+4}. 25, Following the coalescence of its distal part with M_1, the base of R_5 is disintegrating to form the *vena spuria*. Cell M_2+M_3 has been formed by the suppression of the free basal part of M_3; the medial field still has three branches reaching the wing margin. 26, Further disintegration of the *vena spuria* occurs; the radial field still remains four-branched. The medial field has completed its development by losing the free terminal part of M_2. Two branches only of the media now reach the wing margin M_1 and M_{3+4}. The angular "cross vein" *se*, by its shape, still shows its components. 27, R_{1+2} is shortening. M_1 now fails to reach the wing margin. The "cross vein" *se* is straightening. All trace of the *vena spuria* is lost except for the angularity in r_4-m, where it previously crossed. The fusion of R_5 and M_1 is proceeding. 28, R_{1+2} is very short. Most of the free terminal part of M_1 has been lost. Cell Cu_1 almost complete. 29, Influence of R_5 still shown by apical turn in R_5+M_1. All trace of M_1 as an independent vein lost. Cell Cu_1 complete. 30, The wing of the Muscoidea Acalyptrata. For complete notation see Text-figure 21.

costal margin are strengthened; those nearer the anal margin are weakened. I have attempted to explain these changes logically, using as evidence in support of my contentions the information available in the wings of living Diptera. With the exception of the hypothetical development series (Text-figures 23–30), all wings figured are those of actual insects.

Acknowledgements.

My thanks are due to Miss Helen M. Brookes, who assisted with the lettering of the Text-figures, and to Miss Margaret E. Morphett, who also helped with the lettering and drew Text-figure 8.

Note on Staining Methods.

In clarifying doubtful parts of the venation, such as unions between veins, and the courses previously taken by veins now suppressed, I have found suitable staining invaluable. Various stains, and methods of using them, were tried before the following method was adopted as being the most satisfactory. The stain used consists of one gramme of basic fuchsin dissolved in 100 c.c. of 95% alcohol. Wings, removed from freshly killed insects, were dropped into 95% alcohol, in which they were allowed to stand for half an hour before transferring to the stain. Wings from dried insects were put directly into the stain. Staining occurs very slowly, a desirable feature, since the process is at all times completely under control. The bases of the long veins first take up the dye, which then moves slowly along them until they are completely stained. Very prolonged immersion is necessary before absorption by the wing membrane begins, though areas in which veins have been recently suppressed absorb the dye more easily than those which have not been veined or in which venation has long been lost. Determined by what the operator is aiming at, staining, even for periods of four to six weeks, may not be too long. Every few days the wings are removed, washed in 95% alcohol, and examined under the microscope to note the extent of the staining. When this is sufficient for the purpose in view, they are immersed in absolute alcohol for half an hour, then in xylol for the same length of time, and mounted. Since basic fuchsin is sensitive to even the slightest trace of acid, some neutral mountant must be used. For permanence and best retention of colour "Sira" was found to give the best results.

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STUDIES ON AUSTRALIAN MARINE ALGAE.

VI. NEW GEOGRAPHICAL RECORDS OF CERTAIN SPECIES.

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National Herbarium of N.S.W., Sydney, Australia.

[Read 27th June, 1951.]

Synopsis.

In this paper it is shown that Australian records of *Neomeris dumetosa* refer to both that species and *N. van Bosseae.*

Further, for the first time, *Galaxaura fasciculata, G. glabriuscula* and *G. angustifrons* are recorded from Australia; *Sargassum fallax* and *S. flavicans* from New South Wales; *Sargassum cristatum* and *Hypnea cenomyce* from both north and east Australia; and *Hormophysa triquetra* and *Hypnea cervicornis* from Western Australia.

In addition, a list of Myxophyceae, determined by Dr. F. Drouet, and including algae new to Australia, is presented.

Introduction.

This paper continues a series recording the occurrence of algae not previously known from Australia, and extending the known geographic range here of other species.

The specimens cited are in the following herbaria: National Herbarium of N.S.W., Sydney (quoted as N.S.W.), the Lucas Collection now held at the above Herbarium (quoted as A.H.S.L.), the herbarium of the Botany School, University of Sydney (quoted as SYD.), the herbarium of the Sydney University Biological Society, held at the Botany School, University of Sydney (quoted as S.U.B.S.), the herbarium of the North Queensland Naturalists' Club, Cairns, Queensland (quoted as N.Q. Nats.) and my own herbarium (quoted as V.M.).

Chlorophyceae.

Neomeris Species in Australia.

Neomeris dumetosa Lamx. has been recorded from Australia. The specimens cited include both *Neomeris dumetosa* Lamx. and *Neomeris van Bosseae* Howe and are as follows:

Neomeris van Bosseae Howe. Collected at Bowen, Qld., by Rainford, in Sept. 1927, May 1928, and again in Jan. 1929 (all in Herb. A.H.S.L.). The first two collections are recorded by Lucas (1927) as *N. dumetosa* Lamx. The specimens agree with Harvey's Exsicc. Alg. Friendly Islands No. 81 from Tonga, cited by Howe (1909) as being *N. van Bosseae.*

N. dumetosa Lamx. Collected at Low Island, Qld., by Perrin and Lucas in May 1931 (in Herb. A.H.S.L.). Recorded by Lucas (1934) as *N.* (?) *dumetosa* Lamx. The specimens are broken, but the bands of lime formed by cohering primary branches are quite definite.

Phaeophyceae.

Sargassum fallax Sond.

New Record for New South Wales.

This species is described and illustrated by J. Agardh (1889); in Australia it is already known from Western Australia and from Queensland.

Locality.	Date.	Herbarium.	Notes.
Collaroy, nr. Sydney, N.S.W.	24,viii.1948	V.M. No. 377	Fertile. Drift.

SARGASSUM FLAVICANS (MERT.) J. AG.

New Record for New South Wales.

This species is known from Queensland and Western Australia and it is now recorded from New South Wales. All specimens quoted were kindly checked by Dr. Tore Levring against original Agardh collections now at Lund, Sweden.

Locality.	Date.	Herbarium.	Notes.
Near Boom, Botany Bay, N.S.W.	14.xii.1944	V.M. No. 235	Trawled.
Mouth of Gunnamatta Bay, Port Hacking, N.S.W.	8.vi.1945	V.M. No. 811	„
Port Hacking, N.S.W.	—.v.1944	V.M. No. 1007	Coll. by R. Bouchier.

SARGASSUM CRISTATUM J. AG.

New Record for New South Wales and Queensland.

Previously known from the west and south coasts of Australia, this species is now recorded, though only as drift, from New South Wales and from Queensland. Specimens quoted were kindly checked by Dr. Tore Levring against original specimens in the Agardh Herbarium now at Lund, Sweden.

Locality.	Date.	Herbarium.	Notes.
Collaroy, nr. Sydney, N.S.W.	7.vii.1944	V.M. No. 274	Drift.
Mooloolabah, Qld.	24.i.1944	V.M. No. 1012	„

HORMOPHYSA TRIQUETRA (L.) KUETZ.

New Record for Western Australia.

In the National Herbarium of New South Wales is a specimen collected by A. H. S. Lucas at Port Stephens, N.S.W., in June, 1909, and identified as *Hormosira ? articulata* (Forsk.) Zan. The label bears the additional information that this identification was confirmed by Mrs. Gepp. This species was recorded from New South Wales by Lucas in 1913 (p. 51). The species is now known from the northern and eastern coasts of Australia.

Osborn (1947) has recorded that the Australian plant known as *Hormosira ? articulata* (Forsk.) Zan. is in fact *Hormophysa triquetra* (L.) Kuetz.

The present is the first record of this species from Western Australia.

Locality.	Date.	Herbarium.
Dongara, W.A.	15.xi.1942	V.M. No. 2689, 2698, 2699, 2700.

MYXOPHYCEAE.

Dr. Francis Drouet, of the Chicago Natural History Museum, has kindly identified a number of specimens of Myxophyceae for me. These include algae new to Australia. As our blue-green flora is particularly poorly studied, and their records often unreliable, it seems wise to publish all of these identifications by Dr. Drouet, which are therefore listed below. An additional list will be included in a forthcoming publication on the Marine Algae of Brampton Island, Qld.

ANACYSTIS AERUGINOSA (ZAN.) DR. & DAILY.

Locality.	Date.	Herbarium.	Notes.
Curl Curl, nr. Sydney, N.S.W.	1.xii.1945	V.M. No. 1158	Black slime on rocks nr. beach.

CALOTHRIX CRUSTACEA BORN. & FLAH.

Corrimal Headland, N.S.W.	26.iii.1945	V.M. No. 648	

ENTOPHYSALIS CONFERTA (KUETZ.) DR. & DAILY.

Wattamolla, nr. Sydney, N.S.W.	26.viii.1944	V.M. No. 214	On *Lyngbya confervoides* Gom. Growing in rock pool.

HORMOTHAMNION ENTEROMORPHOIDES GRUN. EX BORN. & FLAH.

Heron Island, Great Barrier Reef, Qld.	—.i.1948	V.M. and S.U.B.S.	No. A18
„ „ „ „ „ „ „ „			No. A22
„ „ „ „ „ „ „ „			No. 37

HORMOTHAMNION SOLUTUM BORN. & GRUN.

Floating, 25 miles E. of Bedout Is., W.A.	23.x.1945	V.M. No. 2087	From surface scoopnet from C.S.I.R. Fisheries Investigation ship "Isobel". Previously recorded (May, 1946) as *Nodularia* prob. *spumigena* Mert.

HYDROCOLEUM LYNGBYACEUM GOM.

Heron Island, Great Barrier Reef, Qld.	—.i.1948	V.M. and S.U.B.S.	No. 36

LYNGBYA CONFERVOIDES GOM.

Wattamolla, nr. Sydney, N.S.W.	26.viii.1944	V.M. No. 214	Growing in rock pool.

LYNGBYA LUTEA GOM.

Corrimal Headland, N.S.W.	26.iii.1945	V.M. No. 648	

LYNGBYA MAJUSCULA GOM.

Adams Beach, Stradbroke Is., Moreton Bay, Qld.	15.i.1944	V.M. No. 930	

LYNGBYA SEMIPLENA GOM.

North Curl Curl, nr. Sydney, N.S.W.	21.vii.1947	V.M. No. 2392	On rocks near beach. Prevalent.
Curl Curl, nr. Sydney, N.S.W.	1.xii.1945	V.M. No. 1158	Black slime on rocks nr. beach.

LYNGBYA SORDIDA GOM.

Headland, Palm Beach, nr. Sydney, N.S.W.	26.xi.1947	V.M. No. 2470	Small form.

RIVULARIA FIRMA WOMERSL.

Twofold Bay, Eden, N.S.W.	24.i.1946	V.M. No. 2031	Coll. by E. Pope.

SKUJAELLA HILDEBRANDTII (GOM.) J. DE TONI.

Joseph Bonaparte Gulf, W.A.	13.ix.1949	V.M. No. 2817	Surface trawl.

RHODOPHYCEAE.

GALAXAURA SPECIES.

The recent appearance of Chou's two papers (1944, 1945) on Pacific species of *Galaxaura*, containing keys to the species, assists greatly the identification of specimens belonging to this difficult genus.

Chou, dealing with the Pacific species, records only five species as from Australia, viz., *G. spathulata*, *G. arborea*, *G. umbellata*, *G. oblongata* and *G. elongata*. Svedelius (1945) gives important descriptions and comparisons of species, and records also from here *G. fastigiata* and *G. obtusata*, if indeed the latter differs from *G. umbellata*.

The following three species are now also recorded from Australia, while the additional occurrence of one of these species, and of one other species, are to be recorded in a forthcoming paper on the Marine Algae of Brampton Island, Qld.

GALAXAURA FASCICULATA KJELLM. EMEND CHOU.

Known from the Celebes and Philippine Islands, Tonga, Japan, Malayan Archipelago, etc.

Locality.	Date.	Herbarium.	Notes.
Whitsunday Reef, Hayman Island, Qld.	—.viii.1946	V.M. No. 2284 also SYD.	Coll. Mrs. Bingham.
Low Island, N. Qld.	—.v.1931	N.S.W.	Coll. F. Perrin and A. H. S. Lucas.
,, ,, ,,	—vi.1931	,,	

GALAXAURA GLABRIUSCULA KJELLM. EMEND CHOU.

Known from Tahiti, Hawaiian Islands, Java and the Bonin Islands.

Locality.	Date.	Herbarium.	Notes.
Coral Reef, Green Is., off Cairns, N. Qld.	30.viii.1936	V.M. & N.Q. Nats. No. 3519	Coll. by H. Flecker.
Arkhurst Reef, Hayman Is., Qld.	—.viii.1946	V.M. No. 2283 also SYD.	
Cape Tribulation, 30 m. south of Cooktown, Qld.	18.xi.1947	V.M. & N.Q. Nats. No. 12117	

GALAXAURA ANGUSTIFRONS KJELLM. EMEND CHOU.

This species is known from Brazil and Java, but the present is the first record of it from Australia. The species has most likely been treated in Australia as *Brachycladia marginata*, under which name *G. arborea* and *G. spathulata* also have been included. Chou has illustrated and described these three species, and suggests that *G. intermedia* and *G. spathulata* may be the corresponding sexual and non-sexual phases of the same plant. It seems likely that *G. angustifrons* and *G. arborea* likewise correspond.

Locality.	Date.	Herbarium.	Notes.
Collaroy, nr. Sydney, N.S.W.	19.xii.1944	V.M. No. 460	Drift.
,, ,, ,,	7.vii.1944	V.M. No. 271	,,
Newport ,, ,,	16.xi.1944	V.M. No. 459	Growing in pool under overhanging rock.
Barrenjoey Hd., Palm Beach, N.S.W.	25.ii.1945	V.M. No. 513	Below L.T.L.

HYPNEA CENOMYCE J. AG.

New Record for North and East Australia.

Previously known from Western Australia and Tasmania in Australia and from Lord Howe Island, the present is the first record of this species from N.S.W. or Queensland.

Dr. Tore Levring kindly checked my specimens No. 918 and 674 with original Agardh material at Lund, Sweden, and he reports the identification as correct.

This species has a more compact habit than other local species of this genus; it is relatively coarse, much branched towards its apices and it occurs on ocean headlands, while our common Hypneas are estuarine in habitat.

This is the species of *Hypnea* referred to (May, 1948, p. 35) as having been confused sometimes with a species of *Gracilaria* (see below).

Locality.	Date.	Herbarium.	Notes.
Rock Island, Long Reef, nr. Sydney, N.S.W.	8.xii.1944	V.M. No. 493	Sheet B is tetrasporic.
Far out rocks, Newport to Bilgola Headland, nr. Sydney, N.S.W.	3.xi.1945	V.M. No. 918	
Little Beach, Narrabeen, nr. Sydney, N.S.W.	13.xii.1947	V.M. No. 2484	
Extra L.T. Level, Whale Beach Headland, nr. Sydney, N.S.W.	29.xii.1947	V.M. No. 2501	Few tetraspores.

Locality.	Date.	Herbarium.	Notes.
Amity Beach, Stradbroke Is., Moreton Bay, Qld.	1.xii.1943	V.M. No. 674	Tetrasporic.
Green Is., N. Qld.	23.viii.1936	V.M. & N.Q. Nats. No. 2191	Coll. by A. B. Cumings. Tetrasporic.
Double Island Reef, N. Qld.	14.ix.1947	V.M. & N.Q. Nats. No. 11448	Coll. by H. Flecker. Tetrasporic.
Low Island, N. Qld.	—.vi.1931	A.H.S.L.	Coll. by F. Perrin and A. H. S. Lucas. Specimen labelled "*Gracilaria*".
Michaelmas Cay, off Cairns, Qld.	—.vi.1926	A.H.S.L.	Coll. by T. Iredale and G. Whitley. Specimen recorded (Lucas, 1927, p. 155) as *Gracilaria taenioides* J. Ag.

Hypnea cervicornis J. Ag.

New Record for Western Australia.

This species is described and illustrated by Tanaka (1941, p. 240–2, fig. 13); it differs from our common *H. Valentiae* (Turn.) Mont. in the absence of a persistent main axis and in the great density of the lateral spinous branches. This species is widespread in the warm Pacific and is already recorded from Queensland; the present records extend its known range in Australia to Western Australia also.

Locality.	Date.	Herbarium.	Notes.
Geraldton, W.A.	—.vii.1928	N.S.W.	Coll. by A. H. S. Lucas.
Rottnest Is., W.A.	—.viii.1928	N.S.W.	„
On beach, North Is., Abrolhos Group, W.A.	6.xii.1945	V.M. No. 2230	Coll. by G. P. Whitley. Tetrasporic.

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THE MARINE ALGAE OF BRAMPTON ISLAND, GREAT BARRIER REEF, OFF MACKAY, QUEENSLAND.

By Valerie May, M.Sc.,

National Herbarium of New South Wales, Sydney, N.S.W.

[Read 27th June, 1951.]

Synopsis.

This paper describes the marine algal flora of Brampton Island. This flora was found to be very rich and to include a number of species new to Queensland, and some new to Australia.

A comparison is made between the results obtained and other algal records from N.E. Australia and also between the floras of the various areas of the island.

Introduction.

There are relatively few collections of, or studies on, the marine algae of any part of the Great Barrier Reef of Australia. We have the records of the Great Barrier Reef Expedition of 1928–1929, which include Lucas's summary of algal species hitherto recorded from N.E. Australia (1931) and the report by Stephenson and others (1931) which includes a study of the ecology of the algae of the Low Islands. We have also the detailed lists given by Lucas (1934) of the algae of the Low Islands. Other than these the records are more fragmentary, the most detailed being by Sonder (1871).

The present paper presents the results of a collection made at Brampton Island, in the Great Barrier Reef, off Mackay, Queensland, by the author during June, 1948 (specimens numbered 2660–2815), and also of a second collection from the same locality made by members of the Sydney University Biological Society in January, 1949 (specimens No. A–H). This second collection yielded two additional species (*Sargassum carpophyllum* and *Goniolithon* ? *Fosliei*), while one other species (*Sargassum flavicans*), which had been found by the author only as drift material, was found growing attached. Obviously further collections at other seasons of the year are likely to increase the number of species known from Brampton Island.

The marine algal flora of Brampton Island appears to be exceptionally varied. It includes 85 species, as compared with 74 from the Low Islands (Lucas, 1934), and 205 hitherto recorded (Lucas, 1931) from N.E. Australia. This list from N.E. Australia, however, does not include the Myxophyceae, and is anyway not complete; for instance, records by Grunow (1874) and even by Lucas himself (1927) are omitted. Recent additions to the records of species occurring in Queensland have been made by the present author (1946, 1948, 1949, 1951).

It is of interest to note that while the Low Islands are richer than is Brampton Island in the number of species of Chlorophyceae recorded, they are poorer in the number of species of Rhodophyceae recorded.

In the algae of Brampton Island the following species appear to be recorded from Australia for the first time: *Cladophoropsis* ? *membranacea*, *Vaughaniella rupicola*, *Brachytrichia Quoyi*, *Calothrix pilosa*, *Sirocoleum guyanense*, *Galaxaura subfruticulosa*, *Dasya pacifica*, *Endosiphonia spinuligera*, *Amphiroa* prob. *foliacea*.

The following species have been recorded from other parts of Australia but are not previously known from Queensland: *Caulerpa papillosa*, *Entophysalis conferta*, *Ceramium gracillimum*, *Polysiphonia implexa*, *Polysiphonia zostericola*.

Brampton Island is a continental island with a tide range of about 15 feet. For ecological comparison the sand and mud flats extending about the island have been treated in this paper collectively as "Flats", while the main reef developed of one side of the island is designated "Reef". One rocky headland—Pelican Island—appears detached from the main island at high tide, but is linked by rock-strewn flats at low

tide; algae from this general location have been treated in this paper as from the "Pelican Island Flats". Carlyle Island also becomes land-linked to Brampton at extremely low tides, and since a coral reef from this adjoining island was particularly well developed, the collection from it has also been included in the present paper; algae from this location are marked as from "Coral Reef".

Apart from these four above described areas, two species were collected encrusting rocks at high-tide level, and some drift material was also collected. These collections are so labelled in the paper.

For a comparison of the floras of the various ecological areas the accompanying table (Table 1) of species found in each location is presented. However, it is emphasized

TABLE 1.

The Species Collected from the Different Areas.

Flats.	Reef.	Coral Reef.	Pelican Is. Flats.	Encrusting Rocks at H.T.L.	Found Only as Drift.
CHLOROPHYCEAE.					
Ulva lactuca.					
Enteromorpha sp.	*Anadyomene brownii.*	*Valoniopsis pachynema.*			
Dictyosphaeria Versluysi.	*D. favulosa.*		*D. favulosa.*		
Struvea delicatula.	*S. delicatula.*	*S. delicatula.*			
	Boergesenia Forbesii.				
	Cladophoropsis ? membranacea.		*Bornetella oligospora.*		
Spongocladia vaucheriaeformis.	*S. vaucheriaeformis.*				
Udotea flabellum.	*U. flabellum.*				
	U. orientalis.		*U. orientalis.*		
Halimeda macroloba.	*H. macroloba.*				
H. incrassata.	*H. incrassata.*				
	H. opuntia.				
	Codium spongiosum.				
Caulerpa sertularioides.					
C. serrulata.	*C. serrulata.*				
C. racemosa.		*C. racemosa.*			
		C. papillosa.			
No. of species : 11	13	4	3	0	0
PHAEOPHYCEAE.					
	Ectocarpus confervoides.	*E. confervoides.*	*E. confervoides.*		
			Sphacelaria tribuloides.		
			Pocockiella nigrescens.		
	Stypopodium zonale.				
			Dictyota dichotoma.		
Dictyopteris pardalis.			*D. pardalis.*		
Padina Commersonii.	*P. Commersonii.*		*P. Commersonii.*		
Vaughaniella rupicola.					
Hydroclathrus clathratus.	*H. clathratus.*				
	Chnoospora obtusangula.				
Cystophyllum muricatum.					
	Hormophysa triquetra.				
	Sargassum scabripes.		*S. carpophyllum.*		*S. lophocarpum.*
			S. flavicans.		
	Turbinaria ornata.				
No. of species : 5	8	1	8	0	1

TABLE 1.—*Continued.*

The Species Collected from the Different Areas.—Continued.

Flats.	Reef.	Coral Reef.	Pelican Is. Flats.	Encrusting Rocks at H.T.L.	Found Only as Drift.
MYXOPHYCEAE.					
				Entophysalis conferta.	
Brachytrichia Quoyi.					
			Hormothamnion solutum.		
				Calothrix pilosa.	
	Hydrocoleum lyngbyaceum.				
	Sirocoleum guyanense.				
Lyngbya majuscula.			*L. majuscula.*		
No. of species: 2	2	0	2	2	0
RHODOPHYCEAE.					
Liagora ceranoides.	*L. ceranoides.*				
Galaxaura glabriuscula.		*G. subfruticulosa.*			
	Gelidiella acerosa.	*G. acerosa.*			
Desmia Kilneri.					
	Peyssonnelia Gunniana.		*P. Gunniana.*		
			Goniolithon ? Fosliei.		
			Fosliella farinosa.		
		Mastophora plana.			
		Amphiroa prob. *foliacea.*			
Metagonolithon graniferum.					
Jania rubens.	*J. rubens.*				
		Sebdenia ceylonica.			
	Sarconema filiforme.				
	Eucheuma muricatum.				
Hypnea Valentiae.	*H. Valentiae.*				
	H. cervicornis.	*Plocamium hamatum.*			
		Gracilaria lichenoides.	*G. lichenoides.*		
Corallopsis minor.					
C. Urvillei.					
Ceratodictyon spongiosum.					
Champia parvula.					
Ceramium gracillimum.					
Centroceras clavulatum.					
	Spyridia filamentosa.				
Dasya pacifica.			*D. pacifica.*		
	Dasya sp.	*Dasya* sp.			
		Dasya sp.			
Polysiphonia implexa.					
P. zostericola.					
Digenea simplex.	*D. simplex.*		*D. simplex.*		
Roschera glomerulata.			*R. glomerulata.*		
Endosiphonia spinuligera.	*E. spinuligera.*				
Leveillea jungermannioides.	*L. jungermannioides.*				
	Amansia glomerata.	*A. glomerata.*			
Laurencia rigida.					
L. obtusa.	*L. obtusa.*	*L. obtusa.*			
Acanthophora spicifera.					
Chondria sp.		*Chondria* sp.			
No. of species: 23	15	12	7	0	0
Total no. of species: 41	38	17	20	2	1

that these figures are only approximate, the main purpose during the collecting being to get a representative specimen of every species then growing at Brampton Island, and only secondarily of all species in each location. The outstanding observation from this table is the high percentage incidence of species of Chlorophyceae on the Reef (34% of species occurring there), of Phaeophyceae in the Pelican Island Flats area (40% of species occurring there) and of Rhodophyceae in the extreme Coral Reef region (71% of species occurring there).

My sincere thanks are due to Dr. F. Drouet, of the Chicago Natural History Museum, who kindly identified all the Myxophyceae recorded in the present paper.

CHLOROPHYCEAE.

Ulvales.

Family Ulvaceae.

Ulva Linnaeus.

Ulva lactuca L., 1753, p. 1163; Borgs., 1939, pp. 57–58.

No. 2755, Flats.

Geogr. Distr.: Widespread. N., S. and E. Australia.

Enteromorpha Link.

Enteromorpha sp.

Epiphytic on *Cystophyllum muricatum.*

No. 2723, Flats.

Siphonocladales.

Family Anadyomenaceae.

Anadyomene Lamouroux.

Anadyomene brownii (Gray) J. Ag., 1886, p. 127; De Toni, 1889, p. 370.—*Calonema Brownii* Gray, 1866, p. 46, t. 44, f. 3.

No. 2786, 2787, Reef.

Geogr. Distr.: Celebes. N.E. Australia.

Valoniopsis Borgesen.

Valoniopsis pachynema (Martens) Borgs., 1934, pp. 10–17.—*Bryopsis pachynema* Martens, 1866, p. 24, Pl. 4, fig. 2.—*Valonia confervoides* Harv. Alg. Ceyl. Exsicc. No. 73; Alg. Friendly Is. Exsicc. No. 101; in J. Ag., 1886, p. 100; De Toni, 1889, p. 378.

No. 2769, Coral Reef.

Geogr. Distr.: Warm Atlantic and Indian Oceans, Ceylon, Friendly Is., Hawaiian Archipelago. Lord Howe Is. N. and E. Australia.

Family Valoniaceae.

Dictyosphaeria Decaisne.

1. Dictyosphaeria favulosa Decne., 1842, p. 32; De Toni, 1889, p. 371.

No. 2790, Reef; D., Pelican Is. Flats.

Geogr. Distr.: Mexico, Red Sea, warm Indian and Pacific Oceans. N. Australia.

2. Dictyosphaeria Versluysi W.v.B., 1905, p. 114.

No. 2692, 2734, Flats.

Geogr. Distr.: Malayan Archipelago, Mexico. N.E. Australia.

Family Siphonocladaceae.

Struvea Sonder.

Struvea delicatula Kuetz., 1849–1869, t. 2, f. 2; De Toni, 1889, p. 366.

No. 2706, Flats; 2766, Coral Reef; 2793, Reef.

Geogr. Distr.: Ceylon, Island of Guadeloupe, Mexico. W. and N.E. Australia.

Boergesenia Feldmann.

Boergesenia Forbesii (Harv.) Feldm., 1938, p. 18, figs. 3–5; Borgs., 1948, p. 21–22.—*Valonia Forbesii* Harv., Alg. Ceylon Exsicc. No. 75; Friendly Islands Algae Exsicc. No. 102; in J. Ag., 1886, p. 96; De Toni, 1889, p. 374.

No. 2676, 2782, Reef.

Geogr. Distr.: Red Sea, Indian and Pacific Oceans. N.E. Australia.

Cladophoropsis Borgesen.

Cladophoropsis (?) membranacea (Ag.) Borgs., 1905, p. 288–289, figs. 8–13.—*Cladophora membranacea* (Ag.) Kuetz., 1849, p. 415.—*Siphonocladus membranaceus* (Ag.) Born. in Hariot, 1887, p. 56; De Toni, 1889, pp. 358–359.—*Conferva membranacea* Ag., 1824, p. 120.

No. 2797, Reef.

Geogr. Distr.: Antilles and Santa Cruz, New Zealand. Probable new record to Australia.

Spongocladia Areschoug.

Spongocladia vaucheriaeformis Aresch., 1853, p. 201; De Toni, 1889, p. 360.

No. 2675, Reef; 2724, Flats; 2777, Reef.

Geogr. Distr.: Mauritius, Malayan Archipelago, New Guinea, Lord Howe Is., etc. N.E. Australia.

Dasycladales.

Family Dasycladaceae.

Bornetella Munier-Chalmas.

Bornetella oligospora Solms-Laubach, 1893, p. 87, tab. 9, figs. 1–4, 6, 7.

No. 2800, Pelican Is. Flats.

Geogr. Distr.: Malayan Archipelago, New Guinea. N.E. Australia.

Siphonales.

Family Codiaceae.

Udotea Lamouroux.

1. Udotea orientalis A. and E. S. Gepp, 1911, pp. 119–120, Pl. 1, figs. 1, 4, Pl. 6, figs. 47–48.

No. 2679, 2788, Reef: 2811, Pelican Is. Flats.

Geogr. Distr.: Indian and Pacific Oceans. N.E. Australia.

2. Udotea flabellum (Ellis and Sol.) Lamour., 1812, p. 186; Pap., 1944, pp. 337–338.—*Corallina Flabellum* Ellis and Sol., 1786, p. 124, tab. 24, figs. A–C.

A. and E. S. Gepp (1911, pp. 131–133, Pl. 3, figs. 26–28) describe and figure this plant under the name *U. flabellum* (Ellis and Sol.) Howe.

No. 2678, Reef; 2728, Flats.

Geogr. Distr.: Atlantic Ocean, Red Sea, Madras, Ceylon, Friendly Islands. N.E. Australia.

Halimeda Lamouroux.

1. Halimeda Opuntia (L.) Lamour. emend. Bart., 1901, p. 18; Lamour., 1812, p. 186.—*Corallina Opuntia* L., 1765, p. 805 (in part).

No. 2677, Reef.

Geogr. Distr.: Widespread in warm seas. N. Australia.

2. Halimeda macroloba (Decne.) Bart., 1901, p. 24; Decne., 1841, p. 118.

No. 2693, Flats; 2776, Reef.

Geogr. Distr.: Warm Indian and Pacific Oceans, Red Sea. W. and N. Australia.

3. Halimeda incrassata (Ellis) Lamour. emend. Bart., 1901, p. 25; Lamour., 1812, p. 186.—*Corallina incrassata* Ellis, 1755, p. 53, tab. 25, f. A.

No. 2713, Reef; 2721, Flats.

Geogr. Distr.: Atlantic, Indian and Pacific Oceans, W. Indies, Madagascar, Malayan Archipelago, China Sea, Friendly Islands, etc. N.E. Australia.

Codium Stackhouse.

Codium spongiosum Harv., 1855, p. 565; De Toni, 1889, pp. 489–490.

No. 2667, drift; 2669, Reef.

Geogr. Distr.: W.N. and E. Australia.

Family Caulerpaceae.

Caulerpa Lamouroux.

1. Caulerpa sertularioides (Gmel.) Howe, 1905, p. 576.—*Fucus sertularioides* Gmelin, 1768, tab. 15, fig. 4.—*Caulerpa plumaris* (Forsk.) W.v.B., 1898, pp. 294–296.

No. 2727, Flats.

Geogr. Distr.: Tropical seas generally. N.E. and S. Australia.

2. Caulerpa serrulata (Forsk.) J. Ag. emend. Borgs., 1932; J. Ag. 1872, p. 19.—*Fucus serrulatus* Forsk., 1775, p. 188.—*Caulerpa freycineti* Ag., 1823–1828, p. 446; W.v.B., 1898, pp. 310–318, Pl. 25, figs. 4–11, Pl. 26, figs. 1–6.

Var. de Boryana (Ag.) W.v.B. (*loc. cit.*, pp. 315–316, Pl. 25, figs. 10–11).

No. 2703, Flats; 2711, Reef.

Geogr. Distr.: Red Sea, Gaudeloupe. N.E. Australia.

3. Caulerpa racemosa (Forsk.) J. Ag. emend. W.v.B., 1898, pp. 357–373, Pl. 31, figs. 5–8, Pl. 32, figs. 1–7, and Pl. 33; J. Ag., 1872, p. 35, n. 51.—*Fucus racemosus* Forsk., 1775, p. 191.

Var. laetevirens (Mont.) W.v.B. (*loc. cit.*, pp. 366–368, Pl. 33, fig. 8).

No. 2725, 2726, Flats.

Geogr. Distr.: Is. of Toud, Ceylon, Florida, Gaudeloupe. W. and N.E. Australia.

? var. nummularia (Harv.) W.v.B. (*loc. cit.*, p. 376). A very small specimen.

No. 2768, Coral Reef.

Geogr. Distr.: Friendly Islands, etc. N.E. Australia.

4. Caulerpa papillosa J. Ag., 1872, p. 42, n. 61; W.v.B., 1898, pp. 383–384, Pl. 34, fig. 8.—An unexpected species.

No. 2764, Coral Reef.

Geogr. Distr.: W. and S. Australia.

PHAEOPHYCEAE.

Isogeneratae.

Ectocarpales.

Family Ectocarpaceae.

Ectocarpus Lyngbye.

Ectocarpus confervoides (Roth.) Le Jol., 1863, p. 75; May, 1939, pp. 537–554.—*Ceramium confervoides* Roth., 1797, pp. 151–152, Pl. 8, fig. 3.

Plurilocular reproductive structures do not bear hairs at their apices in these specimens.

No. 2759, Coral Reef; 2779, Reef; F., Pelican Is. Flats.

Geogr. Distr.: Widespread. All around Australia.

Sphacelariales.

Family Sphacelariaceae.

Sphacelaria Lyngbye.

Sphacelaria tribuloides Menegh., 1840, p. 2, n. 1; De Toni, 1895, pp. 502–503.

No. 2809, Pelican Is. Flats.

Geogr. Distr.: Mediterranean, Adriatic and Red Sea, Atlantic Ocean, Hawaii, etc. W. and N. Australia.

Dictyotales.

Family Dictyotaceae.

Pocockiella Papenfuss.

Pocockiella nigrescens (Sond.) Pap., 1943, p. 467.—*Zonaria nigrescens* Sond., 1845, p. 50.—*Gymnosorus nigrescens* (Sond.) J. Ag., 1894, p. 12; De Toni, 1895, pp. 228–229.

No. 2665, drift; 2807, Pelican Is. Flats.

Geogr. Distr.: N., S., E. and W. Australia.

Stypopodium Kuetzing.

Stypopodium zonale (Lamour.) Pap., 1940, pp. 205–206.—*Fucus zonalis* Lamour., 1805, 38, Pl. 25, fig. 1.

My grateful thanks are due to Miss C. I. Dickinson, of Royal Botanic Gardens, Kew, England, who has kindly compared my material with other specimens of this species.

No. 2789, Reef.

Geogr. Distr.: W. Indies, S. Africa, Japan, N.E. Australia.

Dictyota Lamouroux.

Dictyota dichotoma (Huds.) Lamour., 1809, p. 42; De Toni, 1895, pp. 263–264.—*Ulva dichotoma* Huds., 1778, p. 476.

Var. intricata (Ag.) Grev., 1830, p. 58.

No. 2814, Pelican Is. Flats.

Geogr. Distr.: Widespread. N. and E. Australia and Tasmania.

Dictyopteris Lamouroux.

Dictyopteris pardalis (Harv.) May, 1947, p. 274.—*Haliseris pardalis* Harv. in Kuetz., 1849–1869 (Part 9'), p. 24, t. 59, f. 2; De Toni, 1895, p. 258.

No. 2729, Flats; 2802, Pelican Is. Flats.

Geogr. Distr.: W., N. and E. Australia.

Padina Adanson.

Padina Commersonii Bory, 1828, n. 41, t. 21, f. 2; De Toni, 1895, p. 244.—As Harvey's Alg. Ceylon Exsicc. No. 55 sub nomine *P. Pavoniae.*

No. 2715, Reef; 2750, Flats; C., Pelican Is. Flats.

Geogr. Distr.: Mauritius, Ceylon, Malaya, Japan, Friendly Is., etc. N., W. and S. Australia.

Vaughaniella Borgesen.

Vaughaniella rupicola Borgs., 1950, pp. 1–10, figs. 1–8.

No. 2751, Flats. On *Padina* sp.

Geogr. Distr.: Mauritius. New record to Australia.

Heterogeneratae.

Punctariales.

Family Encoeliaceae.

Hydroclathrus Bory.

Hydroclathrus clathratus (Bory) Howe, 1920, p. 590; Setchell and Gardner, 1925, p. 543.—*Fucus clathratus* Bory in Ag., 1823–1828.

Nos. 2683, 2722, Flats; 2778, Reef.

Geogr. Distr.: Widespread in tropical Atlantic and Pacific Oceans, Mediterranean and Red Seas. N., S., E. and W. Australia.

Chnoospora J. Agardh.

Chnoospora obtusangula (Harv.) Sond., 1871, p. 45; De Toni, 1895, p. 465.—*Dictyota obtusangula* Harv., 1859, p. 329, n. 14.

As Harvey's Friendly Island Algae Exsicc. No. 4.

Nos. 2714, 2795, Reef.

Geogr. Distr.: Atlantic Ocean, Japan, Friendly Islands. N.E. Australia.

Cyclosporeae.

Fucales.

Family Sargassaceae.

Cystophyllum J. Agardh.

Cystophyllum muricatum (Turn.) J. Ag., 1848, p. 231; De Toni, 1895, p. 154.—*Fucus muricatus* Turn., 1808–1819 (vol. 2), p. 108, tab. 112.

Prevalent, but by accident there remains only a poor specimen.

No. 2723, Flats.

Geogr. Distr.: India, Admiralty Islands, etc. All around Australia.

Hormophysa Kuetzing.

Hormophysa triquetra (L.) Kuetz., 1843, p. 359; Borgs., 1939, p. 96.—*Fucus triqueter* L., 1771, p. 312.—*Cystoseira triquetra* (L.) J. Ag., 1848, p. 215.

Osborn (1948, p. 48) records that the Australian plant known as *Hormosira ? articulata* (Forsk.) Zan. is in fact *Hormophysa triquetra.*

No. 2664, drift; 2712, Reef.

Geogr. Distr.: India, Red Sea. W., N. and E. Australia.

Sargassum Agardh.

1. Sargassum scabripes J. Ag., 1872, p. 52; 1889, p. 48, tab. 2.

No. 2660, Reef; 2661, drift.

Geogr. Distr.: N. Australia.

2. Sargassum carpophyllum J. Ag., 1848, p. 304; 1889, p. 82, tab. 25 (2).

No. A., Pelican Is. Flats.

Geogr. Distr.: Indian Ocean. N. and W. Australia.

3. Sargassum flavicans (Mert.) Ag., 1823–1828, p. 18; J. Ag., 1889, pp. 82–83, tab. 25 (3).—*Fucus flavicans* Mert., 1819, p. 8.

No. 2663, drift; B., Pelican Is. Flats.

Geogr. Distr.: W., N. and E. Australia.

4. Sargassum lophocarpum J. Ag., 1889, p. 93, tab. 27 (2).

No. 2662, drift.

Geogr. Distr.: N., S., E. and W. Australia.

Turbinaria Lamouroux.

Turbinaria ornata J. Ag., 1848, p. 266; De Toni, 1895, p. 128.—*Fucus turbinatus* var. *ornatus* Turn., 1809–1819 (vol. 1), p. 50, tab. 24, figs. c–h.

No. 2668, Reef.

Geogr. Distr.: Ceylon, New Zealand, Andaman Islands, Friendly Islands, Admiralty Islands, Samoa, etc. N. Australia.

MYXOPHYCEAE.

Family Chamaesiphonaceae.

Entophysalis Kuetzing.

Entophysalis conferta (Kuetz.) Dr. and Dailey, 1948, p. 79.—*Palmella conferta* Kuetz., 1845, p. 149.

No. 2701, encrusting rocks at high tide level.

Geogr. Distr.: Widespread. E. Australia.

Family Stigonemataceae.

Brachytrichia (Zanardini) Bornet and Flahault.

Brachytrichia Quoyi (Ag.) Born. and Flah., (Part 2) 1886–1888, p. 73.—*Nostoc Quoyi* Ag., 1824, p. 22.

Nos. 2736, 2757, Flats.

Geogr. Distr.: Widespread. New record to Australia.

Family Nostocaceae.

Hormothamnion (Grunow) Bornet and Flahault.

Hormothamnion solutum Born. and Grun. ex Born. and Flah., (Part 4) 1886–1888, p. 259.

Nos. 2803, 2813, Pelican Is. Flats.

Geogr. Distr.: Widespread. W. and N.E. Australia.

Family Rivulariaceae.

Calothrix (Agardh) Bornet and Flahault.

Calothrix pilosa Harv. ex Born. and Flah., (Part 1) 1886–1888, p. 363.

No. 2701, encrusting rocks at high tide level.

Geogr. Distr.: Red Sea, Mauritius, Friendly Is., Jamaica, Mexico, Brazil, etc. New record to Australia.

Family Oscillatoriaceae.

Hydrocoleum (Kuetzing) Gomont.

Hydrocoleum lyngbyaceum Kuetz. ex Gom., (Part 15) 1892, p. 337, Pl. 12, f. 8, 9, 10.

No. 2671, Reef.

Geogr. Distr.: Widespread. N.E. Australia.

Sirocoleum (Kuetzing) Gomont.

Sirocoleum guyanense Kuetz. ex Gom., (Part 15) 1892, p. 348.

No. 2671, Reef.

Geogr. Distr.: Widespread. New record to Australia.

Lyngbya (Agardh) Gomont.

Lyngbya majuscula Gom., (Part 16) 1892, p. 131, Pl. 3, figs. 3 and 4.

No. 2742, growing on *Digenea simplex*.

Nos. 2707, 2735, 2742, Flats; 2812, Pelican Is. Flats.

Geogr. Distr.: Widespread. N.E. Australia.

RHODOPHYCEAE.

FLORIDEAE.

Nemalionales.

Family Helminthocladiaceae.

Liagora Lamouroux.

Liagora ceranoides Lamour., 1816, p. 239; Borg., 1939, p. 104.—*Liagora leprosa* J. Ag. 1847, p. 8.

No. 2697, Flats; 2716, 2796, Reef.

Geogr. Distr.: West Indies, Red Sea, Mauritius, Indian Ocean, Malayan Archipelago, Japan, etc. N.E. Australia.

Family Chaetangiaceae.

Galaxaura Lamouroux.

1. Galaxaura subfruticulosa Chou, 1944, pp. 41–44, Pl. 2, fig. 6, Pl. 8, fig. 2.

In this specimen the tumid cell is very large, usually being half as wide again as the terminal cell; Chou reports the size of this cell is variable.

No. 2763, Coral Reef.

Geogr. Distr.: Mexico, prob. Japan and China. New record to Australia.

2. Galaxaura glabriuscula Kjellm. emend. Chou, 1945, pp. 11–13, Pl. 4, figs. 14–20, Pl. 10, fig. 1; Kjellm., 1900, pp. 56–77, Pl. 7, figs. 1–2, Pl. 20, fig. 26.

No. 2710, Flats.

Geogr. Distr.: Tahiti, Hawaii, Bonin Islands, Java. N.E. Australia.

Gelidiales.

Family Gelidiaceae.

Gelidiella Feldmann and Hamel.

Gelidiella acerosa (Forsk.) Feldm. and Hamel, 1934, t. 46, p. 533; Borg., 1939, p. 107.—*Fucus acerosus* Forsk., 1775, p. 190.

No. 2771, Coral Reef; 2780, Reef.

Geogr. Distr.: Warm seas generally. N.E. Australia.

Cryptonemiales.

Family Rhizophyllidaceae.

Desmia Lyngbye.

Desmia Kilneri J. Ag., 1876, p. 355.—*Chondrococcus Kilneri* (J. Ag.) De Toni, 1897–1905 (pt. 4), p. 1676.

Papenfuss (1940, p. 218) discusses the use of the generic name *Desmia* in preference to *Chondrococcus*.

No. 2704, Flats.

Geogr. Distr.: N. Australia.

Family Squamariaceae.

Peyssonnelia Decaisne.

Peyssonnelia Gunniana J. Ag., 1876, p. 387; De Toni, 1924, p. 591.

Adherent to undersides of rocks.

No. 2673, Reef; 2806, Pelican Is. Flats.

Geogr. Distr.: Malayan Archipelago. N., S. and E. Australia, Tasmania.

Family Corallinaceae.

Goniolithon Foslie.

Goniolithon ? Fosliei (Heydr.) Fosl., 1903, p. 470, t. 25, f. 3; W.v.B. and Foslie, 1904, pp. 46–48, fig. 19, Pl. 9, figs. 1–5.—*Lithothamnion Fosliei* Heydr., 1897, p. 58 ex parte.

Insufficient material for sure determination.

No. H., Pelican Is. Flats.

Geogr. Distr.: Maldive and Laccadive Islands, Red Sea, Zanzibar, Malayan Archipelago. Murray Island, N. Australia.

Fosliella Howe.

Fosliella farinosa (Lamour.) Howe, 1920.—*Melobesia farinosa* Lamour., 1816, p. 315, tab. 12, fig. 3.

Specimen epiphytic on *Sargassum* sp.

No. 2815, Pelican Is. Flats.

Geogr. Distr.: Widespread. N., S., E. and W. Australia.

Mastophora Decaisne.

Mastophora plana (Sond.) Harv., 1847, p. 108; De Toni, 1924, p. 695.—*Melobesia plana* Sond., 1845, p. 55.

No. 2758, Coral Reef.

Geogr. Distr.: Marianas Is. W. and N.E. Australia.

Amphiroa Lamouroux.

Amphiroa prob. foliacea Lamour., in Freyc., 1824–1826, p. 628, t. 93, f. 2–31; W.v.B. and Foslie, 1904, pp. 92–93, tab. 14, figs. 1–11.

A poor specimen, insufficient for definite determination. The plant bears a minute epiphyte, *Dasya* sp. (No. 2772).

No. 2773, Coral Reef.

Geogr. Distr.: India, Malaya, Marianas. Not previously recorded from Australia.

Metagoniolithon Weber van Bosse.

Metagoniolithon graniferum (Harv.) W.v.B. and Foslie, 1904, p. 103, tab. 15, figs. 10, 12; De Toni, 1924, p. 704.—*Amphiroa granifera* Harv. Syn. in 1858–1863, p. xxx, n. 362.

No. 2691, Flats.

Geogr. Distr.: Peru. W., N., S. and E. Australia.

Jania Lamouroux.

Jania rubens (L.) Lamour., 1816, p. 272; De Toni, 1924, p. 709.—*Corallina rubens* L., 1765, p. 1305.

As Harvey's Alg. Exsicc. Friendly Is. No. 30.

Nos. 2681, 2781, Reef; 2702, Flats; 2741, Flats as epiphyte on *Digenea simplex* (No. 2739).

Geogr. Distr.: Temperate and warm seas, Lord Howe Island. N., E. and S. Australia.

Gigartinales.

Family Sebdeniaceae.

Sebdenia Berthold.

Sebdenia ceylonica (Harv.) Heydr., 1892, p. 477, t. 26, f. 16–17; De Toni, 1924, p. 297.—*Halymena ceylonica* Harv., Alg. Ceyl. Exsicc. No. 39; in Kuetz. 1849–1869 (Part 16), t. 93.

No. 2760, Coral Reef.

Geogr. Distr.: Red Sea, Ceylon, New Guinea, Samoa. N.E. Australia.

Family Solieriaceae.

Sarconema Zanardini.

Sarconema filiforme (Sond.) Kylin, 1932, pp. 22–23.—*Dicranema filiforme* Sond., 1845, p. 56.

No. 2799, Reef.

Geogr. Distr.: All around Australia.

Eucheuma J. Agardh.

Eucheuma muricatum (Gmel.) W.v.B., 1913–1928 (part d.), pp. 413–415, Pl. 12, figs. 1–5 and fig. 164.—*Fucus muricatus* Gmel., 1768, p. 111, Pl. 6.—*Eucheuma spinosum* (L.) J. Ag., 1852–1863, p. 626; De Toni, 1897–1905 (Part 1), pp. 369–370.

No. 2794, Reef.

Geogr. Distr.: S. Africa, Indian Ocean, Sumatra, New Guinea, Lord Howe Is., Japan. N. and W. Australia.

Family Hypnaceae.

Hypnea Lamouroux.

1. Hypnea cervicornis J. Ag., 1852–1863, p. 451; Tanaka, 1941, pp. 240–242, fig. 13.

No. 2785, Reef.

Geogr. Distr.: Brazil, Mexico, W. Indies, Atlantic and Indian Oceans. W. and N.E. Australia.

2. Hypnea Valentiae (Turn.) Mont., 1840, p. 161; Hauck, 1887, p. 20; Borg., 1934*a*, pp. 17–18; 1943, pp. 58–59.—*Fucus Valentiae* Turn., 1808–1819, Pl. 78.—*Hypnea charoides* Lamour., 1813, p. 44, Pl. 10, figs. 1–3; Tanaka, 1941, pp. 243–244, fig. 16; Borg., 1943, pp. 56–58.—*Hypnea seticulosa* J. Ag., 1852–1863.

This species appears to be both prevalent and variable. No. 2680 is very hirsute, while No. 2696 is nearer *H. nidifica* J. Ag. Neither specimen bears stellate bulbils, but other Australian collections have led me to the opinion that the presence or absence of these bulbils is not of specific importance so I follow Hauck (1887, p. 20) and include *H. charoides* among the synonyms of *H. Valentiae*.

No. 2680, Reef; 2696, Flats, on *Cymodocea* sp.

Geogr. Distr.: Indian Ocean, Japan, S. Pacific. All around Australia.

Family Plocamiaceae.

Plocamium (Lamouroux) Lyngbye.

Plocamium hamatum J. Ag., 1876, p. 338; De Toni, 1897–1905 (Part 1), p. 589.

No. 2767, Coral Reef.

Geogr. Distr.: Norfolk Is. N. and E. Australia.

Family Gracilariaceae.

Gracilaria Greville.

Gracilaria lichenoides (L. in Turn.) Harv., 1844, p. 445; May, 1948, pp. 27–39.—*Fucus lichenoides* L. in Turn., 1808–1819, tab. 118A (excl. var. and synon.).

Specimens are very small, so are not treated in subspecific units.

No. 2775, Coral Reef; 2808, Pelican Is. Flats.

Geogr. Distr.: East Indian to Pacific Ocean. N. and E. Australia.

Corallopsis Greville.

1. Corallopsis minor (Sond.) J. Ag., 1876, p. 409; De Toni, 1897–1905 (part 1), p. 459.—*Corallopsis salicornia* var. *minor* Sond., 1871, p. 24, t. 3, f. 6–11.

Nos. 2666, 2748, Flats.

Geogr. Distr.: Marianas Islands. N. Australia.

2. Corallopsis Urvillei (Mont.) J. Ag., 1852–1863, p. 583; De Toni, 1924, p. 276.—*Hydropuntia Urvillei* Mont., 1842, p. 7.

No. 2731, Flats.

Geogr. Distr.: China Sea. N. Australia.

CERATODICTYON Zanardini.

CERATODICTYON SPONGIOSUM Zan., 1878, n. 8; De Toni, 1924, p. 243.

Attached to pebbles in mud.

Nos. 2670, 2682, Flats.

Geogr. Distr.: Warm Pacific and Indian Oceans. N.E. Australia.

RHODYMENIALES.

Family CHAMPIACEAE.

CHAMPIA Desveaux.

CHAMPIA PARVULA (Ag.) J. Ag., 1876, p. 303; De Toni, 1924, p. 307.—*Chondria parvula* Ag., 1824, p. 207.

No. 2732, Flats.

Geogr. Distr.: Common in warm seas. All around Australia.

CERAMIALES.

Family CERAMIACEAE.

CERAMIUM (Roth) Lyngbye.

CERAMIUM GRACILLIMUM Griff. and Harv. in Harv., 1846–1851, t. 206; De Toni, 1924, p. 515.

No. 2708 was growing on *Desmia Kilneri* J. Ag., No. 2704. The distribution of this species in Australia seems surprising.

Nos. 2694, 2708, 2737, 2744, Flats.

Geogr. Distr.: Atlantic Ocean, Mediterranean and Adriatic Seas, West Indian Ocean, Japan, etc. S. Australia and Tasmania.

CENTROCERAS Kuetzing.

CENTROCERAS CLAVULATUM Mont., 1840–1850, p. 140; Feldmann-Mazoyer, 1940, pp. 337–341, figs. 128–129.

No. 2695 growing on *Cymodocea* sp.; No. 2740 on *Digenea simplex.*

Nos. 2695, 2740, 2753, Flats.

Geogr. Distr.: Mediterranean and Adriatic Seas, Atlantic and Pacific Oceans. All around Australia.

SPYRIDIA Harvey.

SPYRIDIA FILAMENTOSA (Wulf.) Harv. in Hook., 1833, p. 336; Feldmann-Mazoyer, 1940, pp. 348–351, fig. 133.—*Fucus filamentosus* Wulf., 1803, p. 64.

No. 2720, Reef.

Geogr. Distr.: Atlantic coasts of Europe, Africa and America, Mediterranean and Red Seas, Indian Ocean, Japan. N., S. and E. Australia and Tasmania.

Family DASYACEAE.

DASYA Agardh.

1. DASYA PACIFICA Harv., Friendly Is. Alg. No. 12; in J. Ag., 1852–1863, p. 1223; De Toni, 1897–1905 (Part 3), p. 1207.

Nos. 2743, 2754, Flats; 2804, Pelican Is. Flats.

Geogr. Distr.: Friendly Islands. New record to Australia.

2. DASYA sp.

A prevalent and distinctive species, probably new. The plant is dendroid, about 3 cm. high, bears dichotomous monosiphonous hairs from near the apex, has five pericentral cells and is much corticated. It has not been found fertile.

Nos. 2718, 2783, 2784, Reef; 2770, Coral Reef.

Geogr. Distr.: I have also collected this species at Woolgoolga, northern N.S.W.

3. DASYA sp.

A small amount of a little epiphyte, No. 2772, was found growing on *Amphiroa* prob. *foliacea*, No. 2723, from the Coral Reef.

Family Rhodomelaceae.

Polysiphonia Greville.

1. Polysiphonia implexa H. and H., 1845, n. 59; De Toni, 1897–1905 (Part 3), pp. 889–890.

As Lucas's specimens from Lord Howe Is. (Lucas, 1935). A surprising distribution.

Nos. 2684, 2749, Flats.

Geogr. Distr.: Lord Howe Is. S.W. Australia.

2. Polysiphonia zostericola Lucas, 1919, p. 177.

Checked against type material in Lucas's Herbarium (housed at National Herbarium of N.S.W., Sydney, Aus.).

No. 2687, Flats.

Geogr. Distr.: E. Australia.

Digenea Agardh.

Digenea simplex (Wulf.) Ag., 1823-1828, p. 389; De Toni, 1924, p. 404.—*Conferva simplex* Wulf., 1803, p. 17, n. 16.

Specimens of this species were usually found bearing many epiphytes.

No. 2739, Flats; 2792, Reef; E., Pelican Is. Flats.

Geogr. Distr.: Most warm seas. N. and W. Australia.

Roschera Sonder.

Roschera glomerulata (Ag.) W.v.B., 1914, p. 289; De Toni, 1924, pp. 404–405.—*Tolypiocladia glomerulata* (Ag.) Schmitz. in Engl. and Prantl, 1897, p. 442.—*Hutchinsia glomerulata* Ag., 1823–1828, p. 102.

Plant size is variable.

Nos. 2685, 2686, 2733, Flats; 2805, Pelican Is. Flats.

Geogr. Distr.: E. Africa, W. India, Ceylon, Japan, Friendly and Philippine Islands, New Zealand, etc. N. Australia.

Endosiphonia Zanardini.

Endosiphonia spinuligera Zan., 1878, p. 34, n. 4; Falk., 1901, p. 571, t. 13, f. 12; W.v.B., 1913–1928 (Part c), p. 354.

A species but rarely collected previously.

Weber van Bosse (*loc. cit.*) points out that her specimen (Siboga material) differs from the type material in that there is only one layer of cells next to the pericentral cells of the same length as these pericentral cells, whereas on description there should be two or more such layers. She concludes, however, that both specimens represent the same species. The Australian material in L.S. of the thallus, shows two rows of cells external to, and of the same length as, the pericentral cells.

No. 2719, Reef; 2746, Flats.

Geogr. Distr.: New Guinea, E. Indian Ocean. New record to Australia.

Leveillea Decaisne.

Leveillea jungermannioides (Mart. and Hering) Harv., 1855, p. 539; Borg., 1939, p. 132.—*Amansia jungermannioides* Mart. and Hering in Mart., 1836, p. 485.

No. 2791 growing on *Digenea simplex*.

No. 2745, 2752, Flats; 2791, Reef.

Geogr. Distr.: Red Sea, Indian Ocean, Japan, Norfolk Island. W. and N.E. Australia.

Amansia Lamouroux.

Amansia glomerata Ag., 1824, p. 247; De Toni, 1924, p. 426.

No. 2674, Pool in Reef; 2765, Coral Reef.

Geogr. Distr.: Warm Pacific and Indian Oceans. N.E. Australia.

Laurencia Lamouroux.

1. Laurencia rigida J. Ag., 1876, p. 651; De Toni, 1897–1905 (Part 3), p. 789.

No. 2747, Flats.

Geogr. Distr.: Warm Indian Ocean, Java, Korea. N. and S. Australia.

2. Laurencia obtusa (Huds.) Lamour., 1813, p. 42; De Toni, 1924, p. 371.—*Fucus obtusus* Huds., 1778, p. 586.

This seems to be a prevalent species of rather varying habit.

No. 2688, Flats; 2717, Reef; 2762, Coral Reef.

Geogr. Distr.: Widespread in warm seas. All around Australia.

Acanthophora Lamouroux.

Acanthophora spicifera (Vahl) Borg., 1910, p. 201, figs. 18–19; 1945, p. 61.—*Fucus spiciferus* Vahl, 1802, p. 44.

No. 2730 is a poor specimen.

Nos. 2730, 2738, Flats.

Geogr. Distr.: Widespread in tropical seas. N.E. Australia.

Chondria Harvey.

Chondria sp.

I have insufficient comparative material to determine the species.

No. 2709, Flats; 2761, Coral Reef.

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An alphabetical list and index of the species recorded in the present paper.

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THE DEVELOPMENT OF BRYOZOAN FAUNAS IN THE UPPER PALAEOZOIC OF AUSTRALIA.

By Joan Crockford, D.Sc. (Mrs. Beattie).*

(Four Text-figures.)

[Read 25th July, 1951.]

Synopsis.

The development, sequence, and stratigraphic significance of bryozoan faunas in Australia during the Carboniferous and Permian are described in as much detail as is possible from the research so far carried out on this group. The distribution of bryozoan faunas during each period is first summarized; then the occurrence of any forms of stratigraphic significance in each area and the correlations which they suggest are considered; in conclusion, the evolution of the broad faunal provinces found in the late Palaeozoic of Australia, and the probable sources and relationships of the bryozoan faunas of these provinces are discussed.

Lower Carboniferous Bryozoan Faunas.

Lower Carboniferous strata extend from the Hunter River in New South Wales to beyond Rockhampton in Queensland; small collections of Bryozoa from several localities within this area (Text-fig. 1) have yielded a comparatively large and varied fauna. The early Carboniferous saw the influx of new families and subfamilies of Bryozoa, and the disappearance of some of the older families or, where these families persisted, new genera of a distinctly Carboniferous type were evolved at this time; many of these new and specialized genera rapidly appeared in the faunas here (Tables 1 and 2). Correlation of Australian Lower Carboniferous horizons has been made by comparison of goniatite, coral, and brachiopod faunas with those of the Tournaisian and Viséan of Belgium or of England and Scotland; as few published descriptions of Bryozoa from western European faunas of this age are available, comparison of the bryozoan faunas is best made with those of the United States and Russia, and the Tournaisian-Viséan boundary of Europe is here regarded as approximating to the Osage-Meramac boundary of the United States, and the Viséan-Namurian boundary as lying at or near the top of the Chester Series (Cheyney et al., 1945).

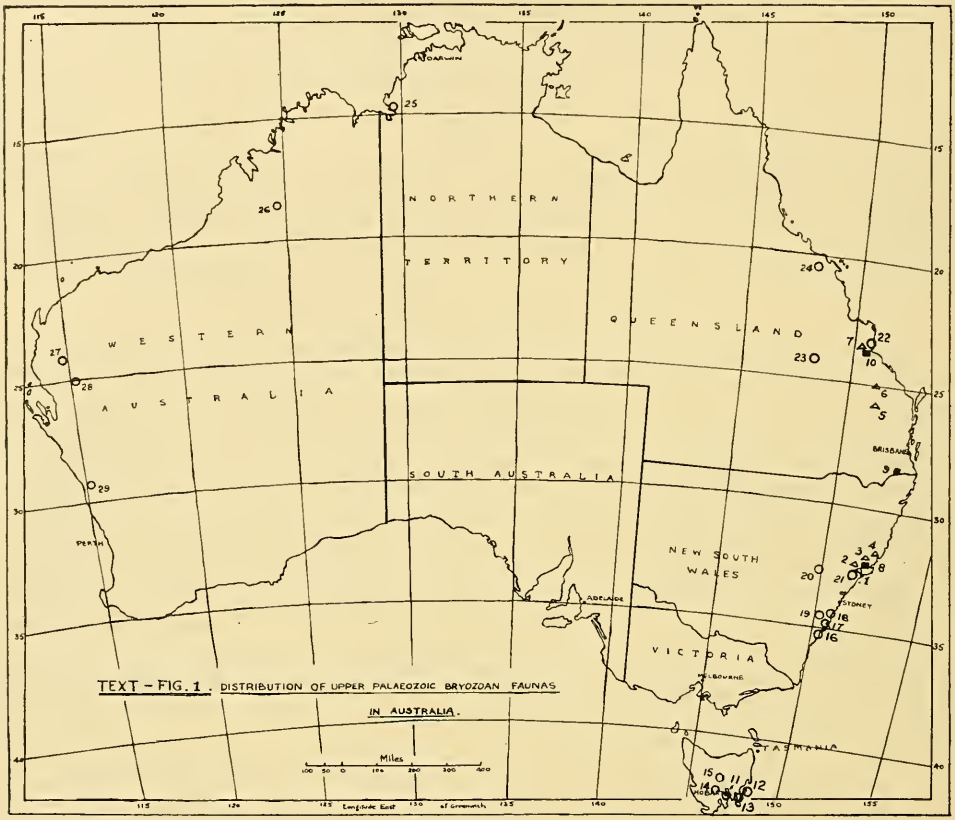
The Age of Bryozoan Faunas from the Burindi and Lower Kuttung Series.

The marine Burindi Series ranges from the base of the Tournaisian to the top of the Viséan, and is partly contemporaneous with the predominantly freshwater Lower Kuttung Series; the freshwater glacial beds of the Upper Kuttung are Upper Carboniferous (Text-fig. 2).

The main bryozoan horizon in the Burindi is that found at Glen William and Hilldale, and is some 200 to 400 feet below the top of the Lower Burindi Series at these localities. The occurrence of *Evactinopora*, *Fistulamina*, *Goniocladia*, and *Streblotrypa* all indicate an early Mississippian age for this fauna. *Evactinopora* first occurs in the Burlington and Keokuk Limestones in the United States; *E. trifoliata* is a distinctly more primitive form than any described from these Limestones and fixes the probable upward limit to the age of this fauna. *Fistulamina* (as *Meekopora ? aperta* Ulrich, 1890) also occurs in the Keokuk; typical species of *Streblotrypa* readily distinguished from the more primitive Devonian species appear in abundance in the early part of the Osage group; *Goniocladia* appears at the base of the Viséan in Russia and in the Lower Carboniferous of Scotland; and *Hemitrypa* is particularly abundant in the Keokuk, and *H. clarkei* closely resembles two Keokuk and Warsaw species. The fenestrate and pinnate Bryozoa from this horizon also bear a strong general resemblance to those described by McCoy in 1845 from the Lower Carboniferous limestone of Ireland, and several Burindi species, though now considered distinct, were originally identified by de Koninck (1878) with these Irish species. The occurrence of this group of genera in

* This work was commenced during the tenure of a Linnean Macleay Fellowship and continued under a Commonwealth Research Fellowship at the University of Sydney.

the top beds of the Lower Burindi Series, and the stage of development reached by species representing each of them, suggests an age equivalent to an early part of the Osage Series of the United States, and so to an horizon within the upper part of the Tournaisian.



TEXT – FIG. 1. DISTRIBUTION OF UPPER PALAEOZOIC BRYOZOAN FAUNAS IN AUSTRALIA.

Text-figure 1.—Distribution of Upper Palaeozoic Bryozoan Faunas in Australia. The principal localities to which reference is made in the text are indicated as follows:

Lower Carboniferous (△): 1, Glen William and Hilldale; 2, Rouchel Brook; 3, Barrington; 4, Taree; 5, Mundubbera and Mundowran; 6, Cannindah; 7, Stanwell and Rockhampton.

Upper Carboniferous (■): 8, Stroud; 9, Mt. Barney; 10, Stanwell and Rockhampton.

Permian (○): 11, Hobart district; 12, Maria Island; 13, Eaglehawk Neck; 14, Fitzgerald; 15, Marlborough; 16, Ulladulla; 17, Gerringong; 18, Wollongong; 19, Bundanoon; 20, Rylstone; 21, Hunter River Coalfield; 22, Lake's Creek; 23, Springsure; 24, Bowen River Coalfield; 25, Port Keats; 26, Nooncanbah, West Kimberley; 27, Minilya River, North-West Basin; 28, Lyons and Gascoyne Rivers, North-West Basin; 29, Irwin River.

The fauna of the marine intercalation near the base of the Lower Kuttung at Rouchel Brook and Back Creek is not far separated (by coarse marine and volcanic sediments) from this Lower Burindi horizon; its fauna, though less varied, shows no distinctive differences from the Lower Burindi fauna and is assumed to be of closely similar age.

The bryozoan fauna occurring in the Burindi Series (undivided) at Barrington includes species of "*Batostomella*" and *Dichotrypa*. "*Batostomella*", congeneric with *B. spinulosa* Ulrich, 1890, is first recorded from the Ste. Genevieve Limestone of the Meramac Group in the United States, and in Russia this genus is listed (Nikiforova, 1933) from the Viséan, but is not known to occur in definitely Tournaisian localities. *Dichotrypa*, though one species occurs in the Middle Devonian, is particularly abundant in the St. Louis Limestone of the Meramac, and occurs also in the Viséan in Russia.

TABLE 1.

Distribution of Species in the Lower Carboniferous of N.S.W.

(The forms listed were described as new species by de Koninck, 1878, and Crockford, 1947.)

Species.	Lower Burindi.		Lower Kuttung.		Upper Burindi (?).	Upper Burindi.
	Glen William.	Hilldale.	Rouchel Brook.	Back Creek.	Barrington.	Taree.
Fistulipora mirari	×	×				
Dybowskiella rhomboidea						×
Evactinopora trifoliata	×					
Fistulamina inornata	×	×		×		
Goniocladia laxa		× (1)				
G. parva			×			
Ramipora (Ramiporalia) bifurcata	×					
"Batostomella" lineata					×	
Fenestella propinqua*	×	×		×	×	
F. acarinata	×	×				
F. cribriformis			×			
F. roucheli			×			
F. barringtonensis					×	
F. cellulosa					×	
Hemitrypa clarkei	×	×				
Ptilopora koninckí	×		×			
Dendricopora hardyi	(2)					
Pennniretepora osbornei	×					
Streblotrypa parallela	×	×	×		×	
Dichotrypa fragilis					×	

(1) Original locality Burragood and Colo Colo.

(2) Original locality Burragood.

* The generic name *Fenestella* Lonsdale, 1839, is here used in preference to *Fenestrellina* d'Orbigny, 1849 : an application for suspension of the Rules of Zoological Nomenclature for the generic name *Fenestella* has been submitted to the International Commission on Zoological Nomenclature by G. E. Condra and M. K. Elias (*J. Paleont.*, 15, 1941, 565–6).

TABLE 2.

Distribution of Species in the Lower Carboniferous of Queensland.

(The forms listed were described as new species by Crockford, 1947.)

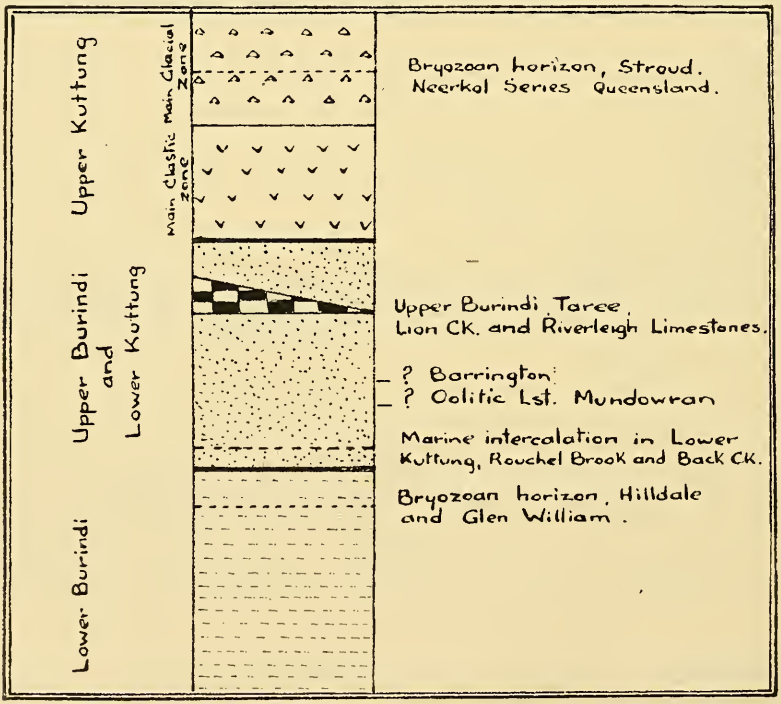
Species.	Oolitic Lst. Mundowran.	Lion Creek Lst.	Riverleigh Lst.	Cannindah Lst.
Fistulipora etheridgei		×		
Dybowskiella crescentica				×
Evactinopora irregularis	×			
Fistulamina malmoensis			×	
Ramipora (Ramiporella) flexuosa			×	
Leioclema porosa		×		
Stenodiscus stanwellensis		×		
Fenestella yarrolensis	×			
F., sp. indet.			×	
Polypora sulcifera			×	
Archimedes regina			×	
A. spiralis			×	
Pennniretepora fragilis			×	
Rhabdomeson, sp. indet.	×			
Streblotrypa, sp. indet.				×

There is no direct field evidence of the stratigraphic position of this fauna; the presence of these two genera at Barrington, and their absence from the Hilldale–Glen William horizon, suggest that the Barrington fauna is slightly younger and should be correlated with part of the Meramac, rather than the Osage, Group of the United States, and is therefore of early Viséan age.

Dybowskiella, associated with *Fistulamina* and *Fistulipora*, occurs in the Upper Burindi Limestone at Taree; the coral fauna of this limestone is Upper Viséan in age.

The Age of Bryozoan Faunas from the Lower Carboniferous of Queensland.

Bryozoa have been described from the Lower Carboniferous at four localities in Queensland (Text-fig. 1; Table 2). The earliest of these faunas seems to be that of the oolitic limestone at Mundowran in the same district as the Riverleigh Limestone; the field and stratigraphic relationships of these limestones to each other are not known (Hill, 1934, 105). As well as *Evactinopora*, *Fenestella*, and *Rhabdomeson*, this oolitic limestone contains abundant fragments of specifically indeterminate Bryozoa, *Fistulamina*, *Fistulipora*, and batostomellids having been recorded from it. *Evactinopora irregularis* is more advanced than *E. trifoliata* of the Lower Burindi, and more closely approaches North American Burlington and Keokuk species; its zoarium was probably attached and its growth form is slightly irregular, so that it is probably no younger a species than the Burlington-Keokuk forms, in which the zoaria are free and their



Text-fig. 2.—The Carboniferous Sequence of the Northern Hunter Valley area of New South Wales, and the relative positions of the principal Bryozoan horizons.

growth form more stabilized. The presence of this form thus suggests that this horizon is of earlier age than the Riverleigh Limestone, and is equivalent to some part of the Osage Series and so to the topmost beds of the Tournaisian; but equivalent to a slightly higher horizon than the top part of the Lower Burindi, in which the more primitive *E. trifoliata* occurs.

The coral faunas of the Riverleigh and Lion Creek Limestones are Upper Viséan (Zone D2) in age or very slightly younger (Hill, 1943, 62). Two species of *Archimedes*

occur in the Riverleigh Limestone; though this genus first occurs in the earlier Keokuk-Warsaw beds in the United States, the greatest number of species occurs in the Chester Series, equivalent in age to the top of the Viséan; *Archimedes* first occurs in the western United States and Russia in the Lower Pennsylvanian. *Ramiporella flexuosa* is a more primitive form than the species of this subgenus described from the Upper Carboniferous of Russia. *Polypora* also first occurs in Australia in this limestone, and *Stenodiscus* appears in the Lion Creek Limestone, but each of these genera appears in an earlier part of the Lower Carboniferous in Europe and the United States.

Upper Carboniferous Bryozoan Faunas.

Bryozoa are abundant in the Neerkol Series at Stanwell, Rockhampton and Mt. Barney, and in a thin marine intercalation in the Upper Kuttung at Stroud (Table 3).

Table 3.

Distribution of Species in the Upper Carboniferous of Queensland and New South Wales.
(The forms listed were described as new species by Crockford, 1949.)

Species.	Neerkol Series.					Marine Intercalation in Upper Kuttung Series, Stroud.
	Ridge above Lion Creek.	Malchi Creek, Rock-hampton.	Par. 2v, Par. Stanwell.	Mt. Barney, Pors. 193–4, Par. Palen.	Mt. Barney, Pors. 127v and 202, Par. Palen.	
Fistulamina frondescens ..						×
F. dispersa	×			×		
Leioclema ? sp.	×					
Fenestella malchi		×		×	×	×
F. osbornei	×	×	×	×		×
F. micropora	×					
F. barneyi			×	×		
F. cincta		×				
Polypora pustulosa			×			
P. neerkolensis			×	×	×	
P. palenensis					×	
P. tenuirama		×				
Penniretepora spp.		×	×			

Fenestellids have been recorded from the Kullatine Series in the Manning River district and the Emu Creek Series at Drake, but no specimens suitable for description have been collected. These Upper Carboniferous faunas (Crockford, 1949, 419) are characterized by the association of *Fistulamina* with abundant *Fenestella* and *Polypora*; they lack the variety found in Lower Carboniferous faunas, especially in the absence of fistuliporoids other than *Fistulamina*, and are distinguished from succeeding Permian faunas by the virtual absence of batostomellids and also the absence of *Protoretepora* and *Minilya*; while it is possible that faunas described so far have come only from zones in which fenestrate forms predominate and that other facies have been passed over in collecting, the collections have been made from many widely scattered localities and at present are regarded as representative.

Stratigraphic Use of the Bryozoan Faunas.

Generalized correlation between the Neerkol Series at the type locality near Rockhampton and at Mt. Barney and the Upper Kuttung is indicated by the bryozoan faunas (Crockford, 1949, 428). No species described from the Upper Carboniferous here is known to occur elsewhere, and all the genera present are known earlier as well as in the Upper Carboniferous; thus there is, unfortunately, no possibility at present of using these faunas for wider correlations. The Pennsylvanian of the United States and the Upper Carboniferous of Europe saw the introduction of many new forms with

TABLE 4.

Distribution of Species in the Permian of Eastern Australia.

Species.	New South Wales.							Tasmania.					Queensland.			
	Hunter Valley.						South Coast.									
	Lower Marine.		Upper Marine Series.													
	Allandale Stage.	Rutherford Stage.	Fenestella Shales.	Muree Stage.	Mulbring Stage.	Tlladulla Mudstones.	Wollongong & Gerringong.	Maria Island and Porter's Hill.	Marlborough.	Berriedale Lst.	Grange Quarry.	Eaglehawk Neck and Fitzgerald.	Dilly Stage, Springsure.	Lake's Creek Quarry.	Middle Bowen Series.	Gympie Beds.
Batostomella cylindrica Crockford						×										
Dyscritella porosa Crockford ..	×															
D. restis Crockford		×														
Stenopora johnstoni Etheridge ..	×	×						×								
S. etheridgei Crockford		×														
S. spiculata Crockford ..	×															
S. rugosa Crockford			×													
S. contigua Crockford ..				×												
S. crinita Lonsdale				×	×		×					×				
S. gracilis (Dana)							×									
S. nigris Crockford							×									
S. frondescens Crockford ..							×									
S. tasmaniensis Lonsdale ..										(1)						
S. ovata Lonsdale										(1)						
S. pustulosa Crockford										×						
S. hirsuta Crockford										×						
S. parallela Crockford										×						
S. grantonensis Crockford ..										×						
S. australis Nicholson and Etheridge															×	
S. jackii Nicholson and Etheridge															×	
S. leichardtii Nicholson and Etheridge															×	
S. gimpiensis Etheridge ..																×
Stenodiscus moniliformis Crockford										×						
Fenestella fossula Lonsdale ..	×	×	×			×			×	×	×		×			
F. dispersa (Crockford) ..	×	×	×			×			×	×	×		×			
F. exserta Laseron			×			×										
F. granulifera (Crockford) ..			×							×				×		
F. altacarinata (Crockford) ..			×			×										
F. quinquecella (Crockford) ..						×			×							
F. canthariformis (Crockford)			×										×	×		
F. horologia Bretnall													×			
F. aspratilis Bassler														×		
F. simulatrix (Crockford) ..														×		
F. sparsinodata (Crockford) ..														×		
F. rockhamptonensis (Crockford)														×		
F. sparsa (Crockford)														×		
F. spinifera (Crockford) ..														×		
F. expansa (Crockford) ..														×		
F. expansa var. *nodulifera* (Crockford)														×		
Hemitrypa sexangula Lonsdale..										(2)						
Minilya duplaris (Crockford)														×		
M. bituberculata (Crockford) ..			×													
Polypora pertinax Laseron ..	×	×														
P. virga Laseron	?		×			×			×							

TABLE 4.—*Continued.*

Distribution of Species in the Permian of Eastern Australia.—Continued.

Species.	New South Wales.							Tasmania.					Queensland.			
	Hunter Valley.					South Coast.										
	Lower Marine.		Upper Marine Series.													
	Allandale Stage.	Rutherford Stage.	Fenestella Shales.	Muree Stage.	Mulbring Stage.	Ulladulla Mudstones.	Wollongong & Gerringong.	Maria Island and Porter's Hill.	Marlborough.	Berriedale Lst.	Grange Quarry.	Eaglehawk Neek and Fitzgerald.	Dilly Stage, Springsure.	Lake's Creek Quarry.	Middle Bowen Series.	Gympie Beds.
P. woodsi (Etheridge) ..			×			×			×	×	×			×		
P. montuosa (Laseron) ..			×													
P. dichotoma Crockford ..						×										
P. triseriata Crockford						×										
P. multinodata Crockford ..			×													
P. magnafenestrata Crockford	×		×			×				×						
P. linea Crockford			×													
P. minuta Crockford														×		
P. smithii Etheridge																×
Protoretepora ampla (Lonsdale)				×						(2)						
P. koninckí Etheridge															×	
Ptilopora carinata Crockford ..							(3)									
Rhombopora filiformis Crockford						×										
R. laxa (Etheridge)																×

(1) Mt. Wellington, Mt. Dromedary, and Norfolk Plains (Strzelecki).
(2) Originally described from an unknown horizon, Tasmania.
(3) Described from Crinoidal Stage, Shoalhaven Heads.

Permian affinities which existed under varied climatic conditions over a large part of the world; the absence of any of these new forms from the Upper Carboniferous here suggests that the eastern Australian geosyncline was already cut off by the beginning of the Upper Carboniferous from the free communication with other areas of Carboniferous sedimentation which was so evident in the Lower Carboniferous.

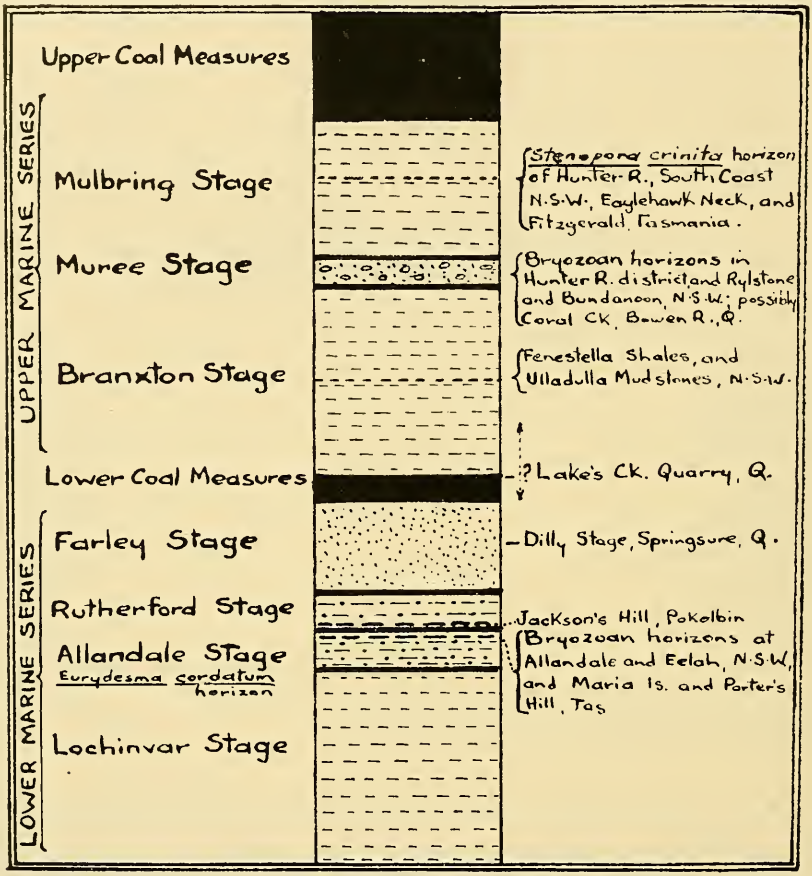
Permian Bryozoan Faunas.

Permian marine sediments containing abundant bryozoan faunas are widespread in Australia; their occurrences fall into two distinct provinces in Eastern and Western Australia. Within these two broad provinces the faunas in the various basins of deposition show individual characteristics, but there are comparatively minor differences; some slight mingling of the two types of fauna occurs, mainly in northern Queensland.

The Eastern Australian Permian Faunas.

Bryozoan faunas have been described from Hobart and Marlborough in Tasmania, the South Coast, Western, and Hunter River coalfields in New South Wales, and Rockhampton, Springsure, and the Bowen River in Queensland; faunas of the same general type occur in many other parts of these three States, but their faunas are less well known and are given only passing reference here. These Permian sediments extend for more than a thousand miles, but in spite of this and their great thickness and varied facies, the generic composition of the bryozoan faunas is remarkably uniform, and most genera present are long-ranged forms (Table 4); a small collection

of Bryozoa from the Permian of New Zealand in the Australian Museum collections belongs to the same general faunal type; no Bryozoa have been described from the Permian of New Zealand. The sequence in the Hunter River coalfield and the relative positions of bryozoan horizons in other districts are summarized in Text-figure 3.



Text-fig. 3.—Sequence in the Hunter River district, and the approximate relative positions of Bryozoan horizons in Eastern Australia.

Stratigraphic Use of the Bryozoan Faunas.

(*a*) *Correlation within Eastern Australia.*

Distinct bryozoan faunas from several horizons within two areas, the Hunter River-Western Coalfield-South Coast basin in New South Wales and the Hobart district in Tasmania, are recognizable and their faunas can to some extent be correlated.

In the Hunter River district the Lower Marine contains few Bryozoa below the base of the Allandale; specimens in the Lochinvar Stage, all fenestellids, are unfortunately specifically unrecognizable. The *Pecten* horizon at the top of the Allandale Stage contains abundant fenestellids, a few large stenoporids and fine ramose batostomellids; at the base of the overlying Rutherford Stage these fine batostomellids locally form bryozoal limestones. The stenoporids and other batostomellids of these horizons are distinct from those found in higher stages (Table 4); *Polypora pertinax* is also a common form in both horizons and several associated fenestellids as yet undescribed also appear to be of limited vertical range. *Stenopora johnstoni* and *Polypora pertinax* should be of value as index fossils for this section of the Lower Marine Series. The sandy sediments of the overlying Farley Stage are a facies unsuitable for Bryozoa;

their virtual absence is unfortunate, as important bryozoan horizons in other States occur in beds correlated with this stage.

Near the base of the Upper Marine, the Fenestella Shales contain an abundant bryozoan fauna; several species are restricted to this one band within the Branxton Stage (Table 4) and should be useful and easily identified zone fossils; on the South Coast this horizon and its characteristic fauna occur at Ulladulla, some two hundred miles distant. Stenoporids and other batostomellids are typically very rare throughout this stage. The Muree Stage contains many fenestellids, coarse species of *Polypora* being especially characteristic, but their preservation is usually too poor for description; *Protoretepora ampla* occurs in this horizon in the Western and Southern coalfields, and small zoaria of *Stenopora crinita*, in contrast to the very large zoaria developed later, first appear in the Muree. The Mulbring Stage is characterized by abundant large zoaria of *S. crinita* and of coarse ramose stenoporids, and by the extreme rarity of fenestellids and of the tiny ramose batostomellids found in earlier horizons; the large zoaria of *S. crinita* are distinctive and easily identified, and should be useful index fossils for this stage.

Bryozoan faunas from five localities in Tasmania can be closely correlated with these horizons. At Porter's Hill and Maria Is. the occurrence of *Stenopora johnstoni* indicates a horizon near the top of the Allandale, and at Maria Is. there is a *Eurydesma* zone just below the beds in which *S. johnstoni* occurs. The fenestellids at Marlborough suggest a horizon close to the Fenestella Shales. Large zoaria of *Stenopora crinita* occurring at Eaglehawk Neck and Fitzgerald show that these horizons are equivalent to the Mulbring Stage, and this agrees with the position of the beds at Eaglehawk Neck near the top of the marine Permian sequence there.

In the Hobart district the Permian is heavily faulted; faunas from Granton, Collinsvale, and Rathbone's Quarries (all in the Berriedale Limestone), and Glenorchy, Newtown, and Mt. Wellington have common features which suggest they are on the same

TABLE 5.

Distribution of Species in the Hobart District.

Species.	Berriedale Limestone.			Telosa Road, Glenorchy.	Newtown.	Huon Rd., Mt. Wellington, 1000 ft. above Sea Level.	"Mt. Wellington" of Strzelecki, Strickland Ave. Track, 1 m. W. of Cascade.
	Granton Quarry.	Collinsvale Quarry.	Rathbone's Quarry.				
Stenopora tasmaniensis ..							×
S. ovata							×
S. pustulosa		×	×	×	×	×	
S. hirsuta	×	×	×				
S. parallela						×	×
S. grantonensis	×						
Stenodiscus moniliformis ..		×					
Fenestella fossula						×	
F. dispersa						×	
F. granulifera						×	
Polypora magnafenestrata ..				×			

horizon (Table 5); the Berriedale Limestone has been considered to belong to the Lower Marine Series; of Bryozoa occurring both in this horizon and in New South Wales, only one is short ranged, and this form, *Fenestella granulifera*, though restricted to the Fenestella Shales in the Hunter district, occurs also at the top of the Dilly

Stage (correlated with the Farley Stage) in Queensland; its occurrence suggests a horizon either within the topmost beds of the Lower Marine or the basal beds of the Upper Marine Series. The rich fenestellid horizon of the Grange Quarry contains three species which occur in New South Wales; of these, *Polypora woodsi* is found only in the Fenestella Shales here, but is longer ranged in Queensland and Western Australia.

The Lake's Creek Quarry fauna in Queensland is Artinskian in age (Crockford, 1945, 125) but cannot at present be correlated with any one horizon in New South Wales. The top of the Dilly Stage at Springsure contains numerous stenoporids as well as the recorded fenestellids; this horizon has been correlated from other forms with the Farley Stage; the bryozoan fauna resembles that of the slightly younger Fenestella Shales, but the coarse sediments of the Farley Stage itself contain no recognizable Bryozoa. Species of *Protoretepora* and *Stenopora* were described by Nicholson and Etheridge from the Middle Bowen Series (Reid, 1930, 74; and Table 4); the stenoporids differ from those found elsewhere in eastern Australia in the small diameter of their tubes, only about half that generally found in eastern Australian species, irrespective of the size or shape of the zoarium itself; in this respect the Middle Bowen stenoporids strongly resemble those of the Permian of Western Australia. The presence of *Protoretepora* upon this horizon suggests correlation with the Muree Series and with the Nooncanbah Series in Western Australia.

(b) Correlation with other Permian Faunas.

The bryozoan faunas from the base of the Allandale Stage to the top of the Upper Marine Series are of Artinskian age, possibly ranging into the base of the Kungurian; there is no evidence from bryozoan faunas regarding the age of the Lochinvar Stage. The general type of fauna which appeared well developed in the Allandale and in rocks of equivalent age in Tasmania persisted without great change through almost all of the Permian sequence; the stenoporids in particular of the Allandale Stage are of a well-marked Permian type. *Polypora woodsi* indicates a Lower Permian age for the Branxton Stage and equivalent horizons; *P. woodsi* is the Artinskian representative of the *P. elliptica* gens (Elias, 1937, 327), which shows well-marked progressive variation from the base of the Carboniferous into the Permian. The occurrence of *Minilya* in the Branxton Stage and of *M. duplaris* at Lake's Creek also indicates a Lower Permian age; *Minilya* first appears at the top of the Pennsylvanian, and *M. duplaris* is a widespread Artinskian species. *Fenestella horologia*, which occurs in the Dilly Stage, is also an Artinskian form. The occurrence of *Protoretepora ampla* in the Muree and in the Nooncanbah Series of Western Australia supports correlations of these horizons; the Nooncanbah Series probably lies at the top of the Lower Permian, and the Muree is also probably upon or very near this horizon. Thus the Mulbring Stage and the Eaglehawk Neck beds may be basal Kungurian; it is notable that in these beds fenestellids are virtually absent and giant batostomellids such as *Stenopora crinita* have become abundant; fenestellids rapidly disappear at about the top of the Artinskian throughout the world and the stenoporids also disappear early in the Kungurian, the development of giant forms being a typical final development of an evolutionary line before extinction.

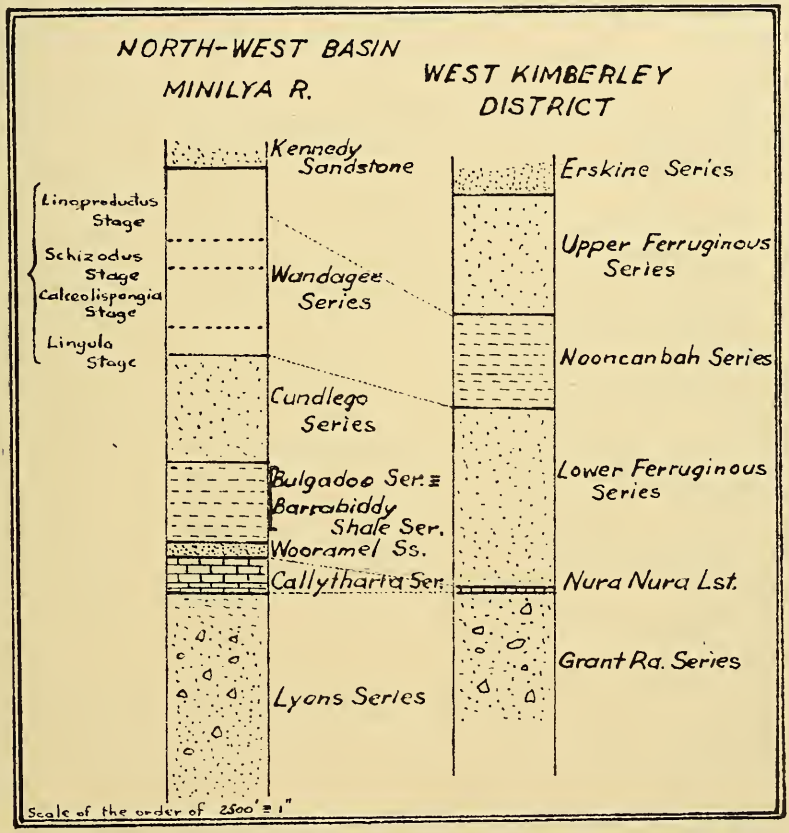
Many attempts have been made to correlate eastern Australian and Indian late Palaeozoic sequences; in these attempts the occurrence of several Bryozoa has been widely quoted, particularly the occurrence of forms described from Tasmania by Lonsdale (1844, 1845). These identifications have been discussed in detail in the revisions of each species described by Lonsdale; while none of the figured specimens from India seem to be conspecific with the eastern Australian types, there is a marked general similarity in the groups of genera present in the Anthracolithic Series of Kashmir particularly and the eastern Australian Permian, and the stage of development reached by several genera common in both areas, and especially of the stenoporids, *Fenestella* and *Protoretepora*, suggests a generally similar time range for the sediments in which they occur; but beyond this the bryozoan faunas do not at present give any evidence for precise correlation between the various stages of the eastern Australian

sequence and the Indian late Palaeozoic; closer comparison is at present possible between the more varied faunas of the Western Australian province and the Salt Range faunas of India.

The Western Australian Permian Faunas.

Bryozoa are abundant in the Permian sediments of the Irwin River, North-West Basin, and West Kimberley districts; the generalized sequence in each of these areas is shown in Text-figure 4; the stratigraphy has been summarized by Teichert (1946). Marine strata containing similar Bryozoa were cut in bores at Port Keats, on the west coast of the Northern Territory; this fauna also is discussed here. These areas of Permian deposition extend for some 1,000 miles from Port Keats south-west to the Irwin River.

The Bryozoa so far described from the Western Australian Permian are listed and their stratigraphic distribution summarized in Table 6; a number of specialized Permian genera, as well as long-ranged forms, occur, and though only a small proportion of the species present are known elsewhere (Table 7), many of those described from Western



Text-fig. 4.—Generalized section of the Permian sequence in Western Australia (after Teichert, 1941, 390).

Australia show clear affinity with Permian forms from other areas; the relationships of individual species have been discussed previously in descriptive papers. The fauna of the Fossil Cliff horizon in the Irwin River district is not listed separately, since descriptions of the main collections from this horizon, sent to the United States for study by Moore and Bassler, are not yet published and only small collections at present remain in Australia; in these the fauna appears generally similar to that found in the Callytharra. Another group in the Western Australian faunas which has as yet

TABLE 6.

Distribution of Species in the Permian of Western Australia and the Northern Territory.

Species.	Callytharra.	Barrabiddy Shale Series.	Cundlego.	Calceolispongia Stage, Wandagee.	Linoproductus Stage, Wandagee.	Nooncanbah.	Port Keats.
Fistulipora vacuolata Crockford						×	
F. wadei Crockford						×	
F. compacta Crockford				×			
F. conica Crockford				×			
F. gigantea					×		
Dybowskiella geei Etheridge							×
D. crescens (Crockford)						×	
Hexagonella australe (Bretnall)	×						
H. dendroidea (Hudleston)	×						
H. densa Crockford		×					
H. nalbia Crockford					×		
H. undulata Crockford					×		
H. bifida Crockford						×	
H. lineata Crockford						×	
H. plana Crockford						×	
Evactinopora crucialis Hudleston	×						
Goinocladia timorensis Bassler						×	
Ramipora ambrosoides (Bretnall)	×			×	×	×	
"*Sulcoretepora*" *meridianus* (Etheridge)						×	
Stenopora sp. "A" Etheridge						×	
S. sp. "B" Etheridge		×					
S. sp. "C" Etheridge						×	
Fenestella horologia Bretnall	×			×	×	×	×
F. affluensa Bretnall	×						
F. chapmani (Crockford)	×						
F. sparsigemmata (Crockford)	×						
F. alia (Crockford)	×						
F. disjecta (Crockford)					×	×	
F. columnaris (Crockford)	×						
F. ruidacarinata (Crockford)						×	
F. valentis (Crockford)						×	
F. lennardi (Crockford)						×	
F. cacuminatis (Crockford)						×	
Minilya duplaris (Crockford)				×		×	
M. princeps (Crockford)						×	
M. amplia (Crockford)	×						
Protoretepora ampla (Lonsdale)						×	
P. australis (Hinde)	×						
Lyropora erkosoides Etheridge	×						
Polypora fovea Crockford				×			
P. retificis Crockford				×			
P. woodsi (Etheridge)	×					×	
P. multiporifera Crockford				×		×	
Penniretepora triporosa Crockford	×						
P. granulata Crockford	×						
P. fossata Crockford	×						
Septopora ornata Crockford	×						
Synocladia spinosa Crockford			×				
Rhabdomeson mammilata (Bretnall)						×	
Rhombopora tenuis (Hinde)	×						
R. hindei Etheridge							×
Streblotrypa browni Etheridge							×
S. marmionensis Etheridge	×	×	×	×	×	×	
S. etheridgei Crockford						×	
Rhombocladia minor Crockford	×						
R. spinulifera Crockford						×	
Streblocladia excavata Crockford	×						

received little attention is the Batostomellidae, which are abundantly represented by *Stenopora, Batostomella,* and closely related forms; the wide distribution of batostomellids in collections from most areas in Western Australia has been shown by the numerous records of their occurrence in faunal lists in stratigraphic papers, but so far this group has received little attention in descriptive work.

Stratigraphic Use of the Bryozoan Faunas.

(a) Correlation within Western Australia.

The occurrence in the Western Australian sequence of *Penniretepora, Lyropora, Septopora* and *Streblocladia* is restricted to the Callytharra Series; not a single specimen of any of these genera has been found in large collections from other horizons. The Callytharra is also characterized by the presence of numerous ribbon-like zoaria of *Hexagonella,* and by a group of fenestellids which, though some are long-ranged, contains a large proportion of species quite distinct from those found on higher horizons. The apparent absence of *Goniocladia, Stenopora,* and *Synocladia,* and the comparative rarity of *Fistulipora,* in the Callytharra is also notable.

Synocladia is common in and characteristic of the Cundlego Series and is not known on any other horizon in Western Australia.

Table 7.

Distribution of Species Common to the Permian of Western Australia and Localities Elsewhere.

Species.	Distribution in W.A.	Occurrences Elsewhere.
Goniocladia timorensis ..	Nooncanbah.	Basleo Beds, Timor.
Ramipora ambrosoides ..	Callytharra to Wandagee and Nooncanbah.	Basleo Beds, Timor (as *Acanthocladia acuticostata* Bassler.
Fenestella horologia	,, ,, ,,	Bitaoeni to Basleo Beds, Timor, and Permian, Vancouver Is. (as *F. parviuscula* (Bassler)); Dilly Stage, Qld.
Minilya duplaris	,, ,, ,,	? Middle Productus Lst., Salt Ra. (as *F. perelegans* Meek); Dilly Stage, and Lake's Ck., Qld.
Polypora woodsi	Callytharra and Nooncanbah.	Bitaoeni Beds, Timor (as *P. tripliseriata* Bassler); Dilly Stage and Lakes Ck., Q'ld.; Upper Marine, N.S.W.; Granton, Tas.
Protoretepora ampla ..	Nooncanbah.	Muree Stage, N.S.W.
Rhabdomeson mammillata ..	,,	Anthracolithic Series, Southern Shan States (as *R. shanse* Reed).
Streblotrypa marmionensis	Callytharra to Wandagee and Nooncanbah.	? Basleo and Amarassi Beds, Timor (?=*S. germana* Bassler).

The Wandagee and Nooncanbah Series are characterized by abundant massive and coarse ramose *Fistulipora;* by broad frond-like species of *Hexagonella* which, although they do occur on other horizons, are particularly characteristic of the higher beds of the Permian sequence; by the common occurrence of *Goniocladia* and the presence of *Protoretepora;* and by the distinct species of other genera such as *Fenestella, Polypora, Minilya, Rhombopora* and *Rhabdomeson,* in all of which, though they include some long-ranged forms, there are several species which are restricted to these higher beds. Massive and coarse ramose stenoporids are also very common in both series. These faunas of the Wandagee Series of the North-West Basin and the Nooncanbah Series of the West Kimberley district bear a strong general resemblance to each other, and as more research is done the number of species common to both will be greatly increased. The fact that, excluding long-ranged forms, only three species have been recorded as common to both series does not give a true picture of their relationship, and reference to published descriptions will show the similarity between several other species from these two areas. Four stages within the Wandagee Series have been differentiated by

Teichert (1946, 99); several described fenestellids and fistuliporoids are restricted to a single stage within this series (Crockford, 1944, Table 1; 1946, 145–154).

The fauna described from Port Keats contains only two long-ranged species in common with other localities in this province; no precise correlation of the Port Keats horizon is possible at present, but in its general aspect this small fauna resembles the Callytharra fauna much more closely than those of higher series.

(*b*) *Correlation with Eastern Australia.*

The occurrences of several species common to both provinces (Table 7) and the close similarity already noted between stenoporids from the Middle Bowen and Western Australian species indicate that the faunas of these two provinces, despite the fundamental differences in their aspect, are of similar time range within the Permian. Only one species appears to be of definite value in closer correlation: *Protoretepora ampla*, the occurrence of which supports correlation of the Nooncanbah with the Muree Stage of the Upper Marine Series.

(*c*) *Correlation with other Permian Faunas.*

Only seven species occurring in the Western Australian Permian are known from localities outside Australia (Table 7), but the stage of development reached by many of the genera present in the fauna and the occurrence of several rare and specialized forms give information of stratigraphic value. The Western Australian faunas show most affinity with those described by Bassler (1929) from Timor and with the Middle and Upper Productus Limestone faunas of the Salt Range; in addition, several Callytharra species, and the fistuliporoids throughout the sequence, are similar to late Pennsylvanian and Permian forms from midcontinental North America.

The Callytharra fauna shows a strong general resemblance to the fauna of the Graham Formation of the Cisco Group at the top of the Pennsylvanian of Texas described by Moore (1929), and of the Upper Pennsylvanian of Oklahoma described by Warthin (1930); Raggatt and Fletcher (1936) have previously suggested correlation between these horizons; they were probably deposited in very similar facies and at not widely differing times, but no species are now considered common to these two areas. On the other hand, the Callytharra contains at least five species (Table 6) in common with the higher beds of the Western Australian sequence, and each of these five species occurs in Artinskian but not in older strata elsewhere (Table 7). In addition, *Hexagonella australe* and other ribbon-like species of this genus common in the Callytharra represent a similar stage of development to *H. turgida* Bassler, 1929, from the Basleo and Amarassi Beds of Timor, and to the genotype from the Middle and Upper Productus Limestones of India, and *Hexagonella* is not known from pre-Artinskian strata in any part of the world; *Septopora ornata* is more closely related to species described from the Somohole and Bitaoeni Beds of Timor than to Russian and North American late Carboniferous species; *Streblotrypa marmionensis*, which first appears in the Callytharra, possesses the central bundle of small tubes characteristic of Permian species of this genus, and is probably identical with a species described from the Basleo and Amarassi Beds of Timor; and *Polypora woodsi* is a widespread Artinskian species and is the Lower Permian representative of the *P. elliptica* genus of Elias (1937, 327). *Evactinopora* and *Lyropora*, both of which have not elsewhere been recorded from post-Mississippian horizons, occur in the Callytharra, and *Evactinopora* also in higher beds of the Permian sequence; while the described species of *Lyropora* is a typical form of this genus, *Evactinopora crucialis* (Hudleston, 1883, 593; Etheridge, 1903, 9) is more advanced in zoarial form than any Mississippian species, and the presence of these two genera does not suggest any correlation of the Callytharra with Carboniferous horizons. The bryozoan faunas indicate that the Callytharra should be correlated with the early part of the Artinskian, and probably, therefore, with the Bitaoeni Beds of Timor (cf. Teichert, 1941, 399). Teichert also correlates the Callytharra with the Lower Productus Limestone of the Salt Range; Bryozoa are apparently uncommon in the Lower Productus Limestone; the Callytharra faunas show some resemblance to those of the Middle and Upper Productus Limestones, but this

resemblance is not so strong as that between the Wandagee and Nooncanbah faunas and those of the Middle and Upper Productus Limestones.

Synocladia is restricted to the Cundlego Series; similar species of this genus also appear in abundance in the Middle Productus Limestone and continue into the Upper Productus Limestone, and other similar species have been described from the Permian of England and Germany. The Cundlego fauna is of definite Artinskian age and should probably be correlated with an early part of the Middle Productus Limestone.

The Wandagee and Nooncanbah faunas show their closest resemblance to those of the Timor Permian; the resemblance is rather more marked in comparing the Wandagee and Nooncanbah with the higher stages, the Basleo and Amarassi Beds, than with the Bitaoeni Beds. This is particularly noticeable in comparing the abundance of massive and coarse ramose species of *Fistulipora* in the Wandagee and Nooncanbah with the sudden abundance of similar forms with comparable internal structure in the Basleo and Amarassi Beds, and it is also noticeable that *Sphragiopora*, which occurs only in the Amarassi, and *Goniocladia*, which occurs only in the Basleo Beds, are both quite abundant in the higher beds in Western Australia, but do not occur in the earlier stages. Five species are known to be common to these higher beds in Western Australia and the Timor Permian sequence (Table 7); but only one, *Goniocladia timorensis*, is of restricted range in both areas, occurring only in the Nooncanbah and in the Basleo Beds. Species of *Hexagonella* occurring in the Wandagee and Nooncanbah Series, and also *Streblotrypa etheridgei* from the Nooncanbah, are distinctly more advanced species than any described so far from Timor, and this is true also of coarse specimens of *Goniocladia* which occur frequently in collections from the Wandagee and Nooncanbah. The Bryozoa, therefore, suggest correlation of these two series with a slightly higher horizon than that indicated by Teichert (1941, 399), and to be possibly slightly younger, and at least no older, than the Basleo Beds.

Teichert (*loc. cit.*) also correlates the Wandagee and Nooncanbah with the top part of the Lower Productus Limestone of India. The bryozoan faunas suggest that the Western Australian sequence from at least the Cundlego Series upwards is younger than the Lower Productus Limestone; the general aspect of the bryozoan fauna which appeared in the Middle and persisted into the Upper Productus Limestone is closely similar to that of the Wandagee and Nooncanbah. The similar stage of development of internal structure in species of *Fistulipora* and *Dybowskiella* present in both areas, and the affinity of species of *Goniocladia* is again noticeable, while the zoarial form in species of *Hexagonella* from these higher beds in Western Australia seems to be of later development than that of any described Salt Range species; and among the fenestellids, though so far only one species is probably common to both areas (Table 7), there is distinct similarity between other species, especially in the occurrence in both areas of *Protoretepora* s. str. It does not appear possible that the Wandagee and Nooncanbah Series could represent a horizon earlier than one within the Middle Productus Limestone. The bryozoan faunas of these two series therefore suggest either a late Artinskian or an early Kungurian age for the horizons on which they occur.

The Development of Faunal Provinces during the Upper Palaeozoic.

The bryozoan fauna of the Lower Carboniferous in eastern Australia migrated freely and rapidly between this and other areas of early Carboniferous deposition. This migration was from the north, the fauna being of the same general type as that found contemporaneously in central North America and Europe. The mild, cold, temperate climate during the Tournaisian favoured the development of the varied fauna found; the seas commenced to withdraw to the north during the early Viséan and the climate became sub-glacial, but rapid migration of faunas from this same Tethyan source remained possible until the close of the Viséan, and this fauna quickly re-established itself in the brief warmer intervals represented by the Upper Viséan reef limestones.

The Upper Carboniferous was a period of intense glaciation in New South Wales, where the freshwater facies of the Hunter River passes northwards into predominantly

marine sediments in northern New South Wales and Queensland. The bryozoan faunas appear to be the remnant, restricted by adverse climatic conditions, of the earlier Carboniferous faunas; they appear, from the persistence of *Fistulamina* and the virtual absence of batostomellids, to be more closely related to these earlier faunas than to those of the succeeding Permian. By the Upper Carboniferous eastern Australia was probably cut off from free migration of faunas from the north, for there is no evidence of any one of the numerous genera of Bryozoa which were at that time evolving in the North American and European seas.

In the Lower Permian an abundant Tethyan fauna resembling that of the Lower Carboniferous of eastern States re-appeared in Western Australia. These faunas were clearly derived from a common faunal source, the early Carboniferous derivatives which migrated along the east coast being primitive representatives of genera which much later, having reached a higher stage of their development, migrated into the Permian basins of Western Australia. This widespread late Palaeozoic fauna did not migrate as far as eastern Australia during the Permian.

The wide divergence between the eastern and Western Australian faunas is not due to any difference in age, since the bryozoan faunas of Western Australia are the Permian representatives of a general type of fauna which existed for a long part of the Upper Palaeozoic, and the generally similar time range of the different areas of Permian sedimentation in eastern and Western Australia has long been established; nor is difference in facies sufficient reason for the distinct faunas, since Bryozoa are abundant in many different types of facies in both areas.

The Western and eastern Australian faunas have frequently been referred to as "warm-" and "cold-water" faunas respectively, and difference in climate in part accounts for the distinct faunas, but seems insufficient to do so fully. The type of fauna and the groups of genera found in the Western Australian Permian are spread over so large a part of the world that they must have been able to exist under a considerable variety of climatic conditions; intermittently the climate of eastern Australia, especially of New South Wales and Tasmania, was extremely cold during the Permian, and in some cases glacial erratics are associated with abundant Bryozoa; but some of the interglacial epochs were of long duration and the climate must then have been milder, and earlier, during the Lower Carboniferous, a varied bryozoan fauna rapidly reappeared during such milder intervals. In Western Australia also intermittent glaciation occurred during the Permian, and one glacial horizon, the Nura Nura Limestone of the Kimberley district, is correlated with the Callytharra Series of the North West Basin, which contains an abundant and varied bryozoan fauna, especially fistuliporoids. The great distance through which Permian deposits are distributed in eastern Australia must, like the interglacial epochs, have afforded some appreciable difference in climate, but the generic assemblage of Bryozoa is unvaried.

Limited migration between these provinces was possible during at least a part of Permian time, as shown by the occurrence of a few identical species in Queensland, Western Australia, and Timor, and to a lesser extent in comparing the faunas of New South Wales and Tasmania with those of Western Australia (Tables 4, 7); the occurrence of generally similar types of stenoporids in the Bowen River coalfield and in Western Australia also suggests relationship between the faunas of these two areas. This slight intermingling of faunas occurs earlier in Queensland, in the Dilly Stage, than in New South Wales, where the first evidences of migration are seen in the early part of the Upper Marine Series; but the fauna of each province retained without appreciable modification its own characteristics until marine Permian sedimentation ceased.

The eastern Australian Permian faunas may have been developed during the early part of the Permian from the poor and restricted Neerkol faunas, or were more probably (because of the absence of *Fistulamina* or any form derived from it, and because of the abundance of batostomellids, which were virtually absent from the Neerkol) faunas which migrated from a southern source northwards along the east coast of Australia.

The strong resemblance between the Tasmanian faunas and those of the Hunter Valley–South Coast Basin in New South Wales, and the gradual lessening of these resemblances through the central north coast basin in New South Wales and the areas of Permian deposition in Queensland also suggest that the eastern Australian faunas as a whole migrated from the south northwards; such migration was possibly influenced by cold south to north currents developed around the coastline of that time, and such currents could have been an effective barrier to any large-scale migration of the Tethyan faunas into the eastern Australian province.

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SUCCINOXIDASE OF POTATO TUBER.

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(Two Text-figures.)

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Synopsis.

The participation of a tricarboxylic acid cycle, similar to that of animal tissues, in the aerobic metabolism of plants would imply the participation of succinic dehydrogenase, an enzyme which, in animal tissues, is coupled with the cytochrome system, the whole forming the complex known as succinoxidase. Investigations carried out with potato (*Solanum tuberosum* L.) tuber have shown that this tissue contains an active succinoxidase system, that the system is associated with particulate components of the cytoplasm and that succinic dehydrogenase is coupled to the cytochrome system in the plant as in the succinoxidase of animal tissues. Also associated with these particles, which resemble and may be identical with mitochondria, are the enzymes, fumarase and malic dehydrogenase.

Introduction.

The participation of a tricarboxylic acid cycle, similar to that of animals tissues, in the aerobic metabolism of plants would imply the participation of succinic dehydrogenase, an enzyme, which, in animal tissues, is coupled with the cytochrome system, the whole forming the complex known as succinoxidase. The *in vitro* demonstration of succinic dehydrogenase activity in plant material has, however, been accomplished in relatively few instances. Okunuki (1939) found succinoxidase activity in pollen of *Lilium auratum*. Slight succinic dehydrogenase activity has been detected in extracts of seedlings of some Leguminosae (Damodaran and Ramaswamy, 1940). Damodaran and Venkatesen (1941) demonstrated the succinoxidase system in preparations of young seedlings and pods of certain Leguminosae and examined in detail an active preparation of the enzyme from seedlings of *Phaseolus mungo*. Goddard (1944) has also reported a low succinic dehydrogenase activity associated with cytochrome oxidase preparations from wheat germ.

From an examination of the effect of malonate on the accumulation of succinate, Bonner (1948) concluded that succinic dehydrogenase must function in the metabolism of pyruvate by segments of *Avena* coleoptile. Laties (1949) has also demonstrated the accumulation of succinate in the presence of malonate in spinach leaves and in excised barley roots.

The purpose of the present investigation was the study of the succinoxidase system of the potato tuber both in relation to succinic dehydrogenase and in relation to the cytochrome system. During the course of the investigation work bearing on this problem has appeared from other laboratories. Cytochrome oxidase activity in preparations from potato tuber has been demonstrated by Levy and Schade (1948) and studied in detail by Goddard and Holden (1950).

In general the results of the present work show, as do those of Levy and Schade and of Goddard and Holden, that potato tubers contain an active succinoxidase system, that the system is associated with particulate components of the cytoplasm, and that succinic dehydrogenase is coupled to the cytochrome system in the plant as in the succinoxidase of animal tissues.

Plant Material.

Mature tubers from *Solanum tuberosum* L. (variety: Factor, grown at Blayney, N.S.W.) were used throughout. Fifty pounds of freshly harvested tubers were stored at approximately 15°C. and aliquots removed as needed. No systematic differences in

succinoxidase activity were noticed during the storage period of five months, nor were differences found between potatoes from the two successive harvests used during the investigation.

Reagents.

Cytochrome c was prepared from horse cardiac muscle according to the method of Keilin and Hartree (1937), but was dialysed against distilled water rather than against 1% sodium chloride (Potter, 1941). The concentration was determined by measuring the absorption at 550mμ after oxidation with ferricyanide and reduction with hydrosulphite.

Calcium cyanide was made according to Robbie and Leinfelder (1945) and estimated gravimetrically by precipitation as silver cyanide.

Phosphate buffers (a mixture of Na_2HPO_4 and KH_2PO_4) were used throughout. Hydrogen ion determinations were made by means of a Leeds and Northrop glass electrode pH meter.

All solutions were made from A.R. chemicals.

Substrates and inhibitors were neutralized to litmus with sodium hydroxide where necessary.

Methods.

Succinoxidase activity was followed by measurement of oxygen uptake according to the standard Warburg manometric technique. Potassium hydroxide was employed in the centre well for absorption of carbon dioxide. In an examination of the effect of cyanide on the aerobic system, calcium cyanide–calcium hydroxide mixtures (Robbie, 1946) were employed. Carbon dioxide output was measured by the direct method of Warburg. Determination of dehydrogenase activity was done by the Thunberg technique carried out in an atmosphere of nitrogen. Estimates of activity were based on the time needed for complete decoloration of the redox dye used. All experiments were conducted at 37°C. Succinic and fumaric acids were estimated quantitatively according to Krebs *et al.* (1940). Chromatographic identification of organic acids followed the procedure of Lugg and Overell (1948).

Preparation of Enzyme.

The tubers were first scrubbed in running tap-water, immersed for one minute in a saturated, filtered solution of bleaching powder (CaClOCl), and thoroughly rinsed in tap-water. The potato (300 gm.) was then diced into 100 ml. of 0·02M phosphate buffer (pH 10·2). The diced material was next ground for one minute in a mechanical macerator (overhead-drive Waring blendor). The pH of the mixture was maintained at approximately 7·2 during this operation by the addition of 1N sodium hydroxide, bromthymol blue being employed as an external indicator. The brei was now filtered through muslin and allowed to stand in the refrigerator for ten minutes, after which the supernatant was decanted from the sedimented starch and centrifuged at approximately 1700g for ten minutes. The supernatant from the centrifugation was removed by decantation and the residue, which contained the enzyme, suspended in 20ml. of 0·01M Na_2HPO_4 for experiments on succinoxidase and in 20ml. of 0·01M KH_2PO_4 for experiments on succinic dehydrogenase activity. Two millilitres of this preparation, containing 0·8–1·0mg. total nitrogen, was used in each experimental vessel.

All vessels and solutions employed were chilled before use and the entire preparation of the enzyme was carried out at a temperature of 5°C. or below.

Experimental.

Demonstration of Succinic Dehydrogenase Activity.

Potato tubers contain an active succinic dehydrogenase as judged by ability to catalyse the reduction of 2,6-dichlorphenolindophenol at the expense of succinate under anaerobic conditions in the Thunberg technique. The enzyme is an insoluble one, bound to particles which are sedimented in 10 min. in a field of 1700g, as noted above. Microscopic observations show that the preparation as described above consists of particles roughly 1μ in diameter.

The standard method adopted for preparation of the particle-bound enzyme involved sedimentation by centrifugation from the extract at pH 7·2. The pH of the extract before and during centrifugation is critical, since it exerts an effect on the amount of

TABLE 1.

Effect of pH during Preparation on the Endogenous Substrate Level of Succinic Dehydrogenase from Potato Tuber.

Main tube: 2·0 ml. enzyme, 0·5 ml. 0·2 M phosphate buffer (pH 7·3), 0·1 ml. 0·2 M succinate or 0·1 ml. water.
Sidearm: 0·3 ml. 0·05% 2,6-dichlorphenolindophenol.

	pH of Extract.	Decoloration Time (Min.).	
		No Added Substrate.	Added Succinate.
Expt. 1 ..	7·96	100	4·5
	7·53	100	4·5
	6·48	100	5
Expt. 2 ..	6·48	55	3·5
	6·00	20	4
Expt. 3 ..	6·02	33	4
	5·76	21	4
	5·42	9	3
Expt. 4 ..	5·35	3	1
	5·02	1	1
	4·46	1	1
	3·98	1	1
	3·44	1	1

endogenous substrate contained in the enzyme preparation. The data of Table 1 show that when the extract is maintained at acidities greater than pH 5, the enzyme preparation obtained contains material which causes the rapid reduction of the redox dye in the Thunberg technique even without the addition of further substrate. This effect is minimized when the extract is maintained at pH values above 7.

Even preparations made by grinding potato tubers in water contain some succinic dehydrogenase activity, as is shown in Table 2. The preparation for this experiment was made by treating diced potato with one-third of its weight of distilled water for

TABLE 2.

Succinic Dehydrogenase Activity of Enzyme Prepared by Maceration of Tissue in Distilled Water.

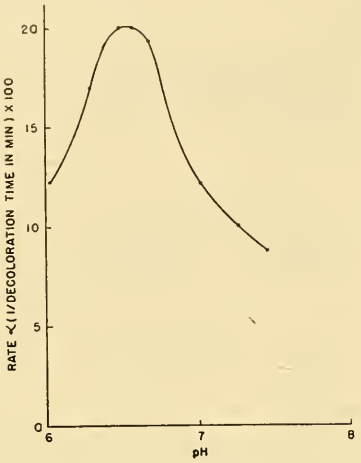
Main tube: 2·0 ml. enzyme, 0·5 ml. 0·2 M phosphate buffer (pH 7·3), 0·1 ml. 0·2 M succinate or 0·1 ml. water.
Sidearm: 0·3 ml. 0·05% 2,6-dichlorphenolindophenol.

	Decoloration Time (Min.).
Control	35
+Succinate	8

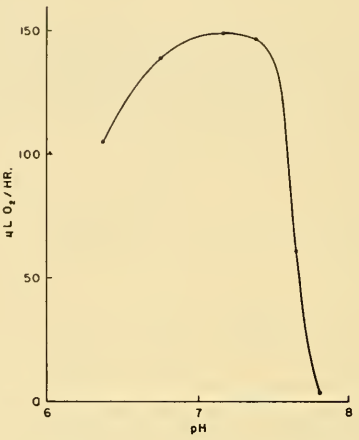
two minutes in a Waring blendor. The enzyme was then separated by centrifugation as described above.

pH.—The succinic dehydrogenase of potato was found to have a pH optimum of 6·5 in phosphate buffer, as shown in Text-figure 1. Succinic dehydrogenase from muscle (Ohlsson, 1921) and from bacteria (Cook and Alcock, 1931) has been shown to

demonstrate maximal activity, as measured by the rate of decoloration of methylene blue at pH 9.



1



2

Text-figure 1.—Effect of pH on succinic dehydrogenase activity. Main tube: 2·0ml. enzyme, 0·5ml. 0·2M phosphate buffer, 0·1ml. 0·2M succinate. Sidearm: 0·3ml. 0·05% 2,6-dichlorphenolindophenol.

Text-figure 2.—Effect of pH on succinoxidase activity. Each flask contained 2·0ml. enzyme and 0·5ml. 0·2M phosphate buffer. The sidearm contained 0·2ml. cytochrome c (final concentration 2×10^{-5}M), 0·1ml. 0·2M succinate or water to 0·3ml.

Redox Dyes.—The activity of potato succinic dehydrogenase as measured in the Thunberg technique is markedly affected by the nature of the redox dye employed (Table 3). Methylene blue and thionine were relatively ineffective as hydrogen acceptors, while 2,6-dichlorphenolindophenol proved quite effective.

TABLE 3.

Effect of Nature of Redox Dye on Succinic Dehydrogenase Activity.

Main tube: 2·0 ml. enzyme, 0·5 ml. 0·2 M phosphate buffer (pH 6·5), 0·1 ml. water, 0·1 ml. 0·2 M succinate or 0·1 ml. water.
Sidearm: 0·3 ml. dye.

Redox Dye.	Conc. (M.).	Decoloration Time (Min.). No Added Substrate.	Added Succinate.
2,6-dichlorphenolindophenol ..	5×10^{-3}	No apparent change in 15 hours.	
	10^{-3}	120	33
	10^{-4}	75	2·2
	10^{-5}	0·2	0·08
Thionine (Lauth's violet) ..	10^{-3}	No apparent change in 240 min.	
	10^{-4}	240	50
	10^{-5}	10	9
Methylene blue	10^{-3}	No apparent change in 240 min.	
	10^{-4}	,, ,,	,,
	10^{-5}	,, ,,	,,

On the basis of the data of Table 3, 2,6-dichlorphenolindophenol at a final concentration of 10^{-4}M was chosen for all further Thunberg experiments.

Succinate Concentration.

Data on the relation of potato succinic dehydrogenase activity to substrate concentration are presented in Table 4. The Michaelis-Menten constant, Km, derived from

these data, is $1{\cdot}9 \times 10^{-3}$M. The Km for muscle succinic dehydrogenase has been found to be 1×10^{-3}M (Lardy, 1949).

TABLE 4.

Effect of Concentration of Succinate on Succinic Dehydrogenase Activity.

Main tube: 2·0 ml. enzyme, 0·5 ml. 0·2 M phosphate (pH 6·5), 0·1 ml. water, 0·1 ml. succinate or 0·1 ml. water.
Sidearm: 0·3 ml. 10^{-3} M 2,6-dichlorphenolindophenol.

Succinate Concentration (M.)	Decoloration Time (Min.).
	75
$6{\cdot}67 \times 10^{-2}$	3·3
$3{\cdot}33 \times 10^{-2}$	2·5
$1{\cdot}67 \times 10^{-2}$	3
$6{\cdot}67 \times 10^{-3}$	3·5
$3{\cdot}33 \times 10^{-3}$	4·5
$1{\cdot}67 \times 10^{-3}$	6·2
$6{\cdot}67 \times 10^{-4}$	10·5
$3{\cdot}33 \times 10^{-4}$	36

Inhibitors.—Succinic dehydrogenase of animal tissues is known to be competitively inhibited by malonate (Krebs and Eggleston, 1940) and to be sensitive to SH-reagents (Potter and DuBois, 1943). Succinic dehydrogenase of potato tuber was likewise inhibited by malonate as well as by phenylmercuric acetate, a potent SH-reagent. It was not, however, inhibited by iodoacetate, a relatively weak SH-reagent (Table 5).

TABLE 5.

Effect of Varied Inhibitors on Potato Succinic Dehydrogenase.

Main tube: 2·0 ml. enzyme, 0·5 ml. 0·2 M phosphate buffer (pH 6·5), 0·1 ml. 0·2 M succinate, 0·3 ml. inhibitor or 0·3 ml. water.
Sidearm: 0·3 ml. 10^{-3} M 2,6-dichlorphenolindophenol.

Inhibitor.	Conc. (M.).	Decoloration Time (Min.).
Phenylmercuric acetate	—	1·2
	10^{-3}	75
	2×10^{-4}	75
	10^{-4}	24
	2×10^{-5}	2·3
	10^{-6}	1·8
	10^{-6}	1·8
Malonate	—	1·5
	10^{-2}	5·5
	10^{-3}	2·1
	10^{-4}	1·5
	10^{-5}	1·5
	10^{-6}	1·5
Indoacetate	—	1
	10^{-2}	1
	10^{-3}	1
	10^{-4}	1
	10^{-5}	1
	10^{-6}	1
Cyanide	—	2
	10^{-2}	0·8*
	10^{-3}	1*
	10^{-4}	2
	10^{-5}	2
	10^{-6}	2

* The slight increase in the rate of decoloration of the redox dye as noted here, was shown by control experiments to be due to an effect of the inhibitor in the absence of added substrate.

Demonstration of Succinoxidase Activity.—The potato enzyme preparation described above is not only able to oxidize succinate anaerobically, but is also able to oxidize succinate aerobically with the uptake of oxygen. This oxidation is markedly increased by the addition of cytochrome c to the reaction mixture, as is shown in Table 6. Succinic dehydrogenase of potato tuber appears therefore to be, like the corresponding enzyme from animal tissue, linked with the cytochrome oxidase system and may thus be referred to as a succinoxidase.

TABLE 6.

Presence of Succinoxidase in Particulate Potato Succinic Dehydrogenase.

Each flask contained 2·0 ml. enzyme and 0·5 ml. 0·2 M phosphate buffer (pH 7·0).

The sidearm contained 0·2 ml. cytochrome c (final concentration 2×10^{-5} M), 0·1 ml. 0·2 M succinate or water to 0·3 ml.

	μl. O_2 Uptake per Hour.
Control (no substrate, no cytochrome)	0
+cytochrome c	4
+succinate	11
+cytochrome c+succinate ..	80

pH.—The succinoxidase of potato tuber shows a pH optimum in phosphate buffer of 7·2 (Text-fig. 2). The system as a whole thus has a pH optimum different from that of succinic dehydrogenase, which has been shown above (Text-fig. 1) to be *ca.* 6·5. The pH optimum for muscle succinoxidase has been found to lie in the range pH 7·3–7·8 (Wieland and Frage, 1929).

Inhibitors.—The succinoxidase system is sensitive to phenylmercuric acetate, malonate, cyanide and iodoacetate (Table 7). Comparison of the results of Tables 5 and 7 shows that phenylmercuric acetate is an effective inhibitor of both succinic dehydrogenase and of the complete succinoxidase system. The complete system is even inhibited by concentrations of phenyl-mercuric acetate (10^{-5}M), which have little effect on dehydrogenase activity. Malonate at high concentrations (10^{-2}M and 10^{-3}M) is an effective inhibitor of both dehydrogenase and oxidase activity. Again, however, at a concentration of 10^{-4}M, which exerts no effect on the dehydrogenase, some inhibition of the succinoxidase system is still observed. Cyanide has no inhibitory effect on succinic dehydrogenase activity, but is an effective inhibitor of succinoxidase presumably exerting its effect on cytochrome oxidase. Iodoacetate slightly inhibits the succinoxidase system but has no effect on dehydrogenase activity.

Since phenylmercuric acetate is known to inhibit enzyme systems by its effect on sulphydryl groups, the possibility of reactivating these groups, by glutathione, as suggested by Barron and Singer (1945) was examined. The results of these attempts were, however, entirely negative (Table 8).

Fate of Metabolized Succinate.—The disappearance of succinate from a reaction mixture containing potato succinoxidase may be shown to correspond quantitatively to the reaction:

$$\text{Succinic acid} \xrightarrow{-2H+1/2O_2} \text{Fumaric acid} \underset{-H_2O}{\overset{+H_2O}{\rightleftharpoons}} \text{Malic acid}$$

(1) (2)

The increased oxygen uptake displayed by the system in the presence of succinate and cytochrome c takes place without concurrent increase in the small endogenous carbon dioxide evolution (Table 9). It must be concluded, therefore, that although the succinate is oxidized by the system it is not dismembered through further reactions of the Kreb's cycle.

TABLE 7.

Effect of Inhibitors on Succinoxidase Activity.

Each flask contained 2·0 ml. enzyme, 0·5 ml. 0·2 M phosphate buffer (pH 7·2), and 0·3 ml. inhibitor or 0·3 ml. water. The sidearm contained 0·1 ml. cytochrome c (final concentration 10^{-5} M) and 0·1 ml. 0·2 M succinate.

Inhibitor.	Concentration (M.).	μl. O_2 Uptake per Hour.	% Inhibition.
Phenylmercuric acetate ..	—	32	
	10^{-3}	0	100
	10^{-4}	0	100
	10^{-5}	17	47
	10^{-6}	28	13
Malonate	—	81	
	10^{-2}	16	80
	10^{-3}	44	46
	10^{-4}	49	40
	10^{-5}	62	24
	10^{-6}	66	19
Cyanide	—	100	
	10^{-3}	12	88
	10^{-4}	30	70
	10^{-5}	54	46
Iodoacetate	—	81	
	2×10^{-2}	60	26
	10^{-2}	69	15
	10^{-3}	75	7
	10^{-4}	76	6

TABLE 8.

Effect of Glutathione on Inhibition of Succinoxidase by Phenylmercuric Acetate.

Each flask contained 2·0 ml. enzyme and 0·5 ml. 0·2 M phosphate buffer (pH 7·2). The sidearm contained 0·1 ml. cytochrome c (final concentration 10^{-5} M), 0·1 ml. 0·2 M succinate, 0·1 ml. phenylmercuric acetate (final concentration 10^{-5} M), 0·1 ml. glutathione or water to 0·5 ml.

	μl. O_2 per Hour.
Control	0
+succinate+cytochrome c	40
+succinate+cytochrome c+phenylmercuric acetate	24
+succinate+cytochrome c+phenylmercuric acetate+glutathione (10^{-2} M)	28*
+succinate+cytochrome c+phenylmercuric acetate+glutathione (10^{-3} M)	15*
+succinate+cytochrome c+phenylmercuric acetate+glutathione (10^{-4} M)	16*

* These figures have been corrected for autoxidation of glutathione under the conditions of the experiment.

TABLE 9.

Oxidation of Succinate: Examination of Oxygen Absorption and Carbon Dioxide Evolution.

Each flask contained 2·0 ml. enzyme and 0·5 ml. 0·2 M phosphate buffer (pH 7·2). The sidearm contained 0·2 ml. cytochrome c (final concentration 2×10^{-5} M), 0·1 ml. 0·2 M succinate or water to 0·3 ml.

	−μl. O_2 per Hour.	+μl. CO_2 per Hour.
Control	0	5
+succinate	0	7
+succinate+cytochrome c	56	7

Identification of Reaction Products.—Identification of the actual oxidation products (Table 10) was carried out as follows. The aerobic oxidation of succinate was followed manometrically in the usual fashion. At the end of the experimental period (one hour) the manometer flasks were removed from the bath and to each cup was added 1ml. 5% metaphosphoric acid and the contents mixed. The contents of each flask were filtered through No. 1 Whatman filter paper, the flask washed repeatedly with small quantities (2–3ml.) water and the washings collected. The filtrate and washings were pooled and divided into two portions. On one portion succinic acid was estimated with the aid of heart muscle succinoxidase. The other portion was reduced in such a way as to convert any fumaric acid to succinic and the total succinic and fumaric acids then determined as succinic acid by the muscle preparation (Krebs *et al.*, 1940).

TABLE 10.

Quantitative Examination of the Fate of Added Succinate.

Eash flask contained 2·0 ml. enzyme (total nitrogen 0·8 mg.) and 0·5 ml. 0·2 M phosphate buffer (pH 7·2). The sidearm contained 0·1 ml. cytochrome c (final concentration 10^{-5} M), 0·2 ml. 0·2 M succinate or water to 0·3 ml.

	Succinate Added (Mg.).	μl. O_2 Absorbed in One Hour.	Succinate Disappearance Corresponding to Observed Oxygen Consumption (Mg.).	Succinate Disappearance (Analytical) (Mg.).
Control	0	5	0	0
+cytochrome c	0	7	0	0
+succinate	4·4	23*	0·19	0·2
+succinate+cytochrome c ..	4·4	132	1·39	1·4

* The enzyme preparation employed in the final section of this paper was prepared by centrifugation at −5° C.; the lower temperature maintained during the preparation resulted in an enzyme with some succinoxidase activity without added cytochrome c.

The validity of this procedure was established by recovery experiments carried out under the conditions of the experiment with succinic and fumaric acids added in amounts such as might be expected to be present. The method is accurate to ±0·1mg. succinic acid under the conditions of the experiment, and 80–90% recovery was obtained with added fumarate.

TABLE 11.

Identification of Organic Acids formed during the Aerobic Oxidation of Succinate.

	Rf Values of Plant Acids.		
	Acid Tested Separately.	Acid in Mixture.	Acid Detected in Reaction Mixture.
Succinic	0·701	0·694	0·687
Fumaric	0·818	0·811	0·817
Malic	0·448	0·444	0·449

Solvent: n-butanol/formic acid/water. Chromatographic separation carried out at 4° C.

If only reaction (1) were involved, fumaric acid should be present in amounts that would be readily estimated by the method used. Fumaric acid did not, however, appear as expected. On the contrary, only small increases in succinate concentration after

reduction were obtained. It was, therefore, suspected that fumarase might be present in the system and might then convert the fumarate formed to an equilibrium mixture of fumarate and malate (Krebs *et al.*, 1940). That this is indeed the case and that both fumarate and malate are products of the oxidation of succinic acid by the potato enzyme preparation was demonstrated with the aid of paper chromatography (Table 11).

The aerobic oxidation of succinate was followed by the Warburg technique. At the end of the experimental period (one hour) the flask contents were acidified (pH 2) with sulphuric acid and extracted with ether in a continuous extractor for thirty-six hours. The ethereal extract was concentrated, 2·0ml. water added, the ether removed by heating on a water bath, and the residue concentrated to approximately 1ml. Ten μl. of this extract was then applied to one end of a strip of filter paper and the chromatogram developed with butanol saturated with formic acid. The control (no added substrate) from the Warburg experiment was also extracted and examined in the same manner but no organic materials were detected. Comparable Rf values for succinic, fumaric and malic acids were determined by parallel experiments with the individual acids as well as with a mixture of the three acids. Twenty μg. of each acid was used in each case.

Discussion.

It has become increasingly evident that the particulate fraction of the cytoplasm is intimately concerned with the respiratory activity of animal tissues, since on these particles, the mitochondria, are located *inter alia*, all the enzymes necessary for the metabolism of pyruvate to carbon dioxide and water *via* the Krebs cycle (Green *et al.*, 1948). It is of interest, therefore, that in plants also it can be demonstrated that some at least of the enzymes participating in the tricarboxylic acid cycle are located on particles present in the cytoplasm—particles which would appear to correspond to the mitochondria of animal tissues. It has been possible to prepare particles similar to those described in this paper but which possess malic dehydrogenase activity in addition to the enzymes succinic dehydrogenase, fumerase and cytochrome oxidase. It will be of interest, therefore, to determine if further enzymes of the cycle are located on these particles and whether or not particles may be prepared from plant tissues which are capable of carrying out the complete oxidation of pyruvate by way of the Krebs cycle.

Summary.

An enzyme complex has been prepared from potato tuber which is capable of converting succinic acid to a mixture of fumaric and malic acids. In this complex the conversion of succinic acid to fumaric aid is coupled to the uptake of molecular oxygen *via* the cytochrome system. The enzyme complex is associated with particles which resemble and may be identical with the mitochondria.

Acknowledgement.

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THE NOMENCLATURE OF *HETERONYCHUS SANCTAE-HELENAE* BLANCHARD (COLEOPTERA: SCARABAEIDAE; DYNASTINAE).

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Synopsis.

Heteronychus sanctae-helenae Blanchard is an important pest of crops and grassland in coastal New South Wales. The reasons for the change of the name of the species by Arrow, in 1937, from *arator* F. to *sanctae-helenae* Blanchard, are examined. It is concluded that *H. sanctae-helenae* Blanchard is the valid name, while *arator* F., the type of which is in Kiel, must be transferred to the genus *Hybosorus*.

Heteronychus sanctae-helenae Blanch. is an important pest of crops and grassland along the New South Wales seaboard. Its distribution extends from Byron Bay in the north to Moruya in the south (Wallace, 1946). The species is a native of South Africa and was introduced into New South Wales about the year 1920, the first record of its occurrence being that of Gurney (1934). In Western Australia it was first observed in 1938 at Albany; it is now widespread in the Perth area. In 1949 it appeared in numbers in the neighbourhood of Adelaide.

The species (as an adult) is responsible for considerable damage to gramineous crops, especially maize, and to vegetable and florists' crops. It is troublesome in turfed areas such as golf greens and grass tennis courts. The importance of the pest in pastures is not known, but the larvae may well be an important factor in the decline of pasture grasses after drought.

Until 1937 this species was known in the literature and in collections as *Heteronychus arator* (F.), 1792. The later name, *Heteronychus sanctae-helenae* Blanchard, 1853, was adopted by Arrow in his Catalogue of Dynastinae of 1937, with *arator* Burmeister (*nec* Fabricius) as a synonym, implying that *arator* F. was a different species and that Burmeister had misidentified it.

The reason for this change was not immediately clear, as the specimen labelled *Geotrupes arator* in the Banks collection in the British Museum certainly belongs to the species which we now know as *sanctae-helenae*. Because of the importance of the species as a pest I have thought it advisable to investigate the matter and if possible to stabilize the change of name. Fabricius described many species from the Banks collection specimens, so that there was reason to believe that this specimen might be regarded as the type. Burmeister's redescription of *H. arator* F. is based on this specimen, as he states that he saw a specimen named by Fabricius, standing as *Geotrupes arator* in the Banks collection, and adds that this species was wrongly referred to *Hybosorus* by Illiger and Schönherr.

Prell (1936) states that the *Geotrupes arator* (F.) in the Fabrician collection in Kiel is a species of *Hybosorus*, and therefore is not even a Dynastid.

There are, therefore, two specimens of different species, one in the British Museum, one in Kiel, either of which might be considered to be the type of *arator* F. The choice must depend on the Fabrician description.

It is noteworthy that in the descriptions of the species immediately before and after that of *arator*, and elsewhere, Fabricius writes "Mus. Dom. Banks", indicating that the description is based on a specimen in the Banks collection. This is omitted in the case of *arator*, the implication being that the type is not in the Banks collection but elsewhere. In addition, the description states "Clypeus integer, subscaber". It is more likely that Fabricius would have described the clypeus of *H. sanctae-helenae* as "scaber".

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The evidence therefore favours the acceptance of the specimen in Kiel as the type of *Scarabaeus arator* F. The species represented in the Banks collection then becomes *Heteronychus arator* Burmeister (*nec* Fabricius), 1847, but the continued use of the name *arator* in *Heteronychus* is inadmissible, as it is a secondary homonym. The next available name for the species, *Heteronychus sanctae-helenae* Blanchard, 1853, is therefore valid.

I am indebted to Messrs. P. B. Carne, C. F. Jenkins and C. R. Wallace for the information on the status of the grass in New South Wales.

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CONTROLLED POLLINATION OF *EUCALYPTUS*.

By L. D. Pryor.

(Plate vi.)

[Read 29th August, 1951.]

Synopsis.

Successful cross-pollination in several pairs of *Eucalyptus* species and the methods employed, are recorded.

Self-fertility has been found in all species examined, but possibly some self-sterile individuals exist.

Attempts at wide crossing were unsuccessful.

Introduction.

At various times the possibility of hybridization between species in the genus *Eucalyptus* has been discussed and in the taxonomic treatment of the genus some described species have been considered as possible hybrids by both Maiden and Blakely. There has been little if any record, however, of controlled hand-pollination within the genus apart from some successful attempts which have been made by Brett (1949) and also Gilbert and Martin (1949) in Tasmania.

Recently abundant evidence has been produced by Brett (1949) and Pryor (1950) to show that under field conditions hybrids between several well-established species can be found quite easily. The evidence for this has been principally morphological and that secured from progeny tests. A rigorous demonstration of the contentions requires that, in addition, the supposed hybrids shall be synthesized by controlled pollination. A critical examination of the methods of pollination, both artificial and natural, is also necessary in many other ways. It is important to know the extent of self-sterility in the genus, the amount of out-crossing in self-fertile species, and similar things before we can hope to understand the complex genetic structure within the genus. This genetic knowledge seems essential before *Eucalyptus* taxonomy can be placed on a scientific basis. Barber (1950) has strongly emphasized this need for genetic knowledge and the experimental method in taxonomy in general in Australia, while some knowledge of the mechanism of reproduction is a prerequisite to breeding *Eucalyptus* for economic or aesthetic needs.

Pollination Methods.

The method of reproduction in the species examined is one which aids cross-fertilization of each individual flower. Usually the pollen is shed soon after the operculum falls, and from most anthers often within the first twenty-four hours. However, to a varying degree some inner anthers retain pollen, which is not shed until later, and then as they unfold more or less brush the stigma and no doubt encourage self-pollination if there has not already been successful pollination. The stigma in most cases is apparently not receptive until several days after the operculum falls, and then it seems to remain receptive, often for four or five days, and sometimes up to ten days. This means that the flowers are protandrous, which is common in many genera. In a few flowers examined a little pollen has been shed before the operculum falls, but the extent to which this occurs cannot be determined without more examination. Apparently Mueller had this in mind when he expressed the opinion that cross-pollination is unlikely in a genus where a calycine lid guards the stigma.

There seems to be little wind-pollination and undoubtedly the genus is principally insect-pollinated. The arrangement of the stamens, stigma and nectaries, as well as the time of maturation of pollen and stigma, favours cross-pollination in any one flower

with the help of insects. The flowers when open attract many kinds of insects, and in some localities birds may be important.

Emasculation is a simple matter and may be effectively carried out, just before the operculum falls, by cutting through the tissue just below the staminal ring but above the top of the ovary. With most species the stamens and operculum come away freely leaving the stigma uninjured, but in a few species examined the stigma is tightly enclosed by the filaments and the stamens and operculum cannot be removed, if the stigma is to remain undamaged, without a second cut longitudinally to free them. If this has to be done the speed of emasculation is greatly reduced.

The method of preparing flowers for controlled pollination is quite easy; the principal experimental difficulty is to prevent burning of the prepared flowers after bagging. Where there is no free air circulation, such as by the use of brown paper bags, or alternatively transparent cellulose bags, the flowers and young stems often die. This is particularly the case with those species which flower in mid-summer or autumn. Burning can generally be prevented by using muslin bags, but these possibly permit the entry occasionally of stray pollen which, while of little importance in a general breeding programme, may be troublesome if some critical examination is being made of reproductive methods. While not easy with large trees, shading in some way is necessary in these cases. Improved methods for this work should result with more investigation.

After pollination it is usually apparent in three months whether the fruit has set. Unfertilized fruit does not as a rule develop and often falls. With most species examined the fruit is ripe in ten to twelve months after pollination and may be harvested then. The seed may be developed and viable a little earlier, but the fruit is often difficult to open if not fully ripe and the seed may not be plump.

Very little fruit is set and almost no fertile seed obtained from flowers that have been emasculated and placed in muslin bags, showing that wind-pollination is practically absent and in fact the occasional pollination which occurs probably results from a very small insect, such as a thrip, a chance dropping of pollen or perhaps some pollen shed before the stamens were removed.

In most of the trials fresh pollen was used from flowers opening at the time the prepared flowers of the seed parents were receptive. Two pollinations, seven days apart, were made in most cases. There is little doubt that pollen can be stored, however, and successful germination was obtained with pollen that had been stored a month in a desiccator at 50% humidity and at about 35°F. Germination tests can be made successfully with many species, using a 10% honey solution and placing in an incubator at 70°F. The most striking feature from preliminary tests of this kind was the great variability in germination percentage between pollen from flowers on different branches of the same tree and even at times between different flowers on the same branch. Germination percentage declines after three months' storage in a refrigerator. Dry storage at room temperature results in quicker loss of power to germinate.

These preliminary tests indicate that separation of flowering times by as much as three months, and probably more, is not likely to be an obstacle to successful cross-pollination if the species are compatible and no barriers to successful fertilization exist. Much more study of the possibilities in this direction is necessary.

Interspecific Hybridization.

After the basic method had been successfully determined as above, a series of trials was made using principally *E. bicostata* and *E. Maidenii* as female parents. These trials aimed to assess the possibilities of interspecific hybridization and to learn where general barriers might exist within the genus. Because it was necessary, for the reasons described, to use muslin bags the chance of some occasional stray pollen fertilizing a flower could not be entirely removed. This means that some of the low numbers of fertile seed obtained must be regarded with suspicion. Where there have been substantial quantities of seed obtained—about fifty or more from ten to twenty flowers—there is no doubt that the pollination has been successful, and this is at once

obvious from the seedlings because of the marked differences obtained in the lots of seedlings from the same female parent but with different pollen parents.

Table 1 shows the results obtained with the species mentioned as female parents.

Keeping in mind the limitations of the data due to the failure to exclude all possibility of chance pollination or perhaps occasional self-pollination before the operculum falls, the trend is at once clear in compatibility in cross-pollination.

TABLE 1.

Seed Parent.	Pollen Parent.	Number of Flowers Treated (Approx.).	Number of Fruit.	Number of Plants Raised.
E. Maidenii F. Muell.	*E. bicostata* Maiden, Blakely & Simmonds.	40	35	90
	E. rubida Deane & Maiden ..	12	10	35
	E. Blakelyi Maiden	10	7	33
	E. Macarthuri Deane & Maiden ..	10	4	10
	E. Maideni F. Muell.	6	4	16
	E. cinerea F. Muell...	10	3	16
	E. ficifolia F. Muell.	10	2	1*
	†*E. Bridgesiana* R. T. Bak. ..	10	1	—
E. bicostata Maiden, Blakely & Simmonds (Horse yards).	*E. bicostata* Maiden, Blakely & Simmonds (another tree).	15	12	Harvested too early. Germination except for a few plants a failure.
	E. Maidenii F. Muell.	15	12	
	E. Maidenii F. Muell.	15	10	
	E. Maidenii F. Muell.	10	7	
	E. Blakelyi Maiden	10	2	
	E. ficifolia F. Muell.	10	1	
	E. cinerea F. Muell...	6	—	
	Self	8	—	
E. bicostata Maiden, Blakely & Simmonds (Acton Park).	Self	15	15	Not yet raised.
	E. Maidenii F. Muell.	10	7	
	†*E. Bridgesiana* R. T. Bak. ..	10	1	
	‡*E. delegatensis* R. T. Bak. ..	6	—	
	E. Macarthuri Deane & Maiden ..	8	—	
E. Blakelyi Maiden (Capital Hill).	*E. Blakelyi* Maiden	6	4	12
	E. rubida Deane & Maiden ..	5	2	3
	E. cinerea F. Muell...	5	1	—
	E. melliodora A. Cunn.	10	—	—
	Control (not poll.)	7	—	—
E. Blakelyi F. Muell. (Acton).	*E. cinerea* F. Muell...	12	8	9
E. cinerea F. Muell. (Arboretum).	*E. Blakelyi* F. Muell.	6	5	21

* Appears to be pure *E. Maidenii*.
† = *E. Stuartiana* F. Muell.
‡ = *E. gigantea* Hook. f., non Dehnh.

Highly successful cross-pollination is achieved by using pollen of the same species and of more or less closely related species, for example, *E. Maidenii* with *E. bicostata*, *E. Blakelyi*, *E. Macarthuri* and *E. cinerea*, which are all in the anther group of Blakely, Macrantherae; whereas *E. ficifolia* and *E. Maidenii*, *E. bicostata* and *E. delegatensis*, *E. Blakelyi* and *E. melliodora* are pairs in widely separated groups, and practically no setting of fruit has been obtained.

There is no doubt that successful crosses between *E. Maidenii* and *E. Blakelyi*; *E. Maidenii* and *E. cinerea*; *E. Maidenii* and *E. rubida*; *E. Maidenii* and *E. Macarthuri*; and *E. Blakelyi* and *E. cinerea* have been achieved, because of the distinct characters already developed in these progenies.

In the main, the F1 hybrids show juvenile characters intermediate between the parents.

Striking evidence of successful cross-pollination is furnished by the *E. Maideuii* × *E. Macarthuri* hybrids due to the incorporation of the highly distinctive geraniol oil of *E. Macarthuri* in the F1 hybrid after having been transmitted by the pollen of *E. Macarthuri*.

The trend is therefore clear that the more widely separated the species within the genus, the less likely that cross-fertilization can be achieved. To determine the absolute limits and whether any progeny obtained is fertile will require more experiment.

This supports the field evidence that hybrids between species within the different anther groups of Macrantherae, Renantherae and Terminales are rare or absent.

In one case, in addition to *E. Maidenii* × *E. bicostata* the reciprocal cross has also been made between *E. cinerea* and *E. Blakelyi*. The hybrid progeny with *E. cinerea* the seed parent, and the other with *E. Blakelyi* the seed parent, is intermediate, at the ten pairs of leaves stages, in morphology between the parents. Both progenies are closely similar to each other but at the same time quite distinct from open-pollinated seedlings of each parent.

Self Sterility.

Krug and Alves (1949) have stated that with the species of *Eucalyptus* examined in Brazil they believe them self-sterile. This is contrary to the condition revealed in the species examined here. The species critically examined are substantially different from those used by Krug and Alves, the latter dealing with species common on the north coast of New South Wales, in the coastal climate, while the species which have been subject to experiment here grow naturally on the cold Southern Tablelands. It is clear that those on which the experiments have been made can successfully self-pollinate because, if flowers are bagged before the operculum falls (and in one experiment with *E. Maidenii* double bags were used consisting of an outer one of muslin and an inner one of brown paper), good fruit is set, giving fertile seed. On the other hand, if the flowers were emasculated and then bagged, fruit did not set and no fertile seed was obtained. In a further experiment with the three species, *E. Maidenii*, *E. Blakelyi* and *E. bicostata*, bagging, emasculation and hand-pollination with pollen of the same plant were followed by good setting of fruit and production of ample fertile seed. This particular experiment on *E. bicostata* was duplicated on separate trees. It led to an interesting case of individual variation which must be examined in more detail. In the second tree, unlike the first, flowers bagged before opening did not set seed, therefore apparently not selfing. In addition, flowers emasculated and bagged did not set when self-pollinated with other flowers of the same tree, but similarly emasculated and bagged flowers pollinated with pollen from another tree of *E. bicostata* set ample fruit.

This suggests that either the particular tree is self-sterile or produced defective pollen in 1949, or perhaps does so always. Further examination, is necessary to find the complete explanation, but in any one of the three cases there could be a factor of considerable importance in the production of hybrid seed in quantity.

Summary.

Simple trials show that many species of *Eucalyptus* are protandrous, entomophilous, and with a mechanism to aid cross-fertilization of each flower but some capacity for self-pollination if crossing fails.

Emasculation is easy and controlled pollination simple, provided the parents are fairly closely related within the genus. Successful controlled pollinations have been achieved with several pairs of species, and in two cases reciprocal crosses have been made.

Absolute barriers and the limit of crossing, although indicated, have yet to be accurately determined. Self-fertility exists in a number of species.

Burning of flowers and stems following bagging must be carefully guarded against.

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EXPLANATION OF PLATE VI.

Fig. 1.—Progeny obtained from hand-pollinated capsules from the one tree of *E. Maidenii*. The four plants at the left are the result of cross-pollination with *E. rubida*. Central four plants, cross-pollination with *E. cinerea*. The four plants on the right, pollination with *E. Maidenii* from another tree of the same species. The variation in population in form clearly indicates the success of the controlled pollination.

Fig. 2.—Progeny obtained from controlled pollinations on a single seed parent individual of *E. Maidenii*. The four plants on the left are the result of pollination with *E. Blakelyi* pollen; the central four, *E. bicostata*, and the four plants on the right are from open-pollinated capsules on the same tree. The marked variation in the form of the progeny as well as other characteristics, such as colour, not apparent in the photograph, indicates the success of the pollination.

Fig. 3.—Progeny from a seed parent of *E. Maidenii*. The four plants on the left are from open-pollinated capsules on the parent tree. The four plants on the right are as the result of hand-pollination with *E. Macarthuri*. Characters intermediate with *E. Macarthuri* are apparent in the more tapering leaves, particularly noticeable in the first and third individuals of the group. The unmistakable presence of geraniol in these individuals is striking confirmation of the hybridization.

Fig. 4.—The four plants on the left were obtained from a *E. cinerea* seed parent after crossing with *E. Blakelyi* by hand. The four on the right were raised from seed from open-pollinated flowers. The intermediate characters of the hybrid population are at once apparent.

Fig. 5.—The four plants on the left were obtained as the result of hand-pollination of a tree of *E. Blakelyi* with *E. cinerea*. The progeny is intermediate. The four plants at the right were the result of open-pollination on the same tree. This is a reciprocal cross of species in Fig. 4, but not with the same individuals.

A GENETIC ANALYSIS OF SOME *EUCALYPTUS* SPECIES.

By L. D. Pryor.

(Plates vii–xi.)

[Read 29th August, 1951.]

Synopsis.

Genetic analysis by progeny testing based principally on morphological seedling characters, has revealed probable F1 hybrids, and segregating swarms between several species. There is at present no evidence of hybridization between certain major taxonomic groups of the genus.

Introduction and Methods.

The genus *Eucalyptus* is a complex one in which the separation of species by the ordinary taxonomic method is difficult. As it has become better known the number of described species has become more numerous. Even so, it is still easy to find individuals and even populations which do not fit any described species as well as is ordinarily the case within the majority of genera. One cause of trouble is that some of the described species cover a latitude of variation which is much smaller than that of others. In short, there has been "splitting" in some groups and not in others, and it has been somewhat cynically observed that the density of *Eucalyptus* species increases as one approaches centres of botanical study.

The past taxonomic approach in the genus has resulted in the naming, usually as species, of divergent forms of varying biological status. If this process were continued it would result in a multiplication of species which would contribute little to the understanding of the genus or to its practical classification. A more reasonable taxonomic approach involves the reclassification of many forms as geographical or ecological subspecies, but the difficulty does not end there because some of the variation is not of the geographic kind which would allow conveniently the erection of subspecies.

Some variation encountered suggests that there is active hybrid development with F2 and back-cross segregating swarms. Many of the F1 hybrids have been given specific names, e.g. *E. unialata* (Brett, 1937 and unpub.). There is another type of variation which again it is difficult to place in the category of subspecies. Eucalypt forests show always a complex mosaic pattern, one species giving way to another under very slight changes of such ecological conditions as aspect, edaphic qualities or other slight habitat changes. The one species as it occurs in successive pieces of the mosaic may show slight but fairly constant differences. Brett (1937) has termed these species *polymorphic* and suggests that the polymorphs have arisen by fixation under varying conditions of selection of segregates of previously existing swarms. The situation as he describes it shows many similarities to the introgressive hybridization of Anderson (1949). These categories of variation, if they exist, present problems for taxonomy which have so far not been satisfactorily resolved.

From accumulated knowledge of field variation of *Eucalyptus* on the Southern Tablelands and Highlands of New South Wales an attempt has been made at a genetic analysis of several of the species of this region and preliminary evidence which fully supports many of Brett's contentions has been obtained. The condition with *Eucalyptus*, Brett suggests, seems to arise from the large number of species often growing side by side, the general lack of sterility barriers between species, the stage of evolution of the genus, the effect of sub-recent climatic changes and the still more recent effect of settlement.

As luck would have it, one of the most consistent and distinctive sets of characters possessed by different species is the morphology of the juvenile leaves.

This factor permits in many cases a preliminary assessment of the genetic make-up of a plant within a few months by the simple means of growing seedlings from selected individual trees. Apart from this source, which has been the principal means of getting information, a series of preliminary experiments on controlled pollination has been carried out which has indicated clearly that hybridization in many cases is a simple matter (Pryor, 1951).

Segregation in Open Pollinated Progenies.

a. E. pauciflora *Hybrids.*

The situation in one of the hybrids included under "*E. vitrea*" has been discussed previously (Pryor, 1950) where the individual concerned was a hybrid between *E. pauciflora* and *E. dives*. Seed was collected from a somewhat similar tree with morphological characters intermediate between *E. pauciflora* and *E. Robertsonii*. Seedlings were raised and fifty unselected plants in a block were taken from the flat and grown on in tubes (Pl. vii, fig. 2). At eight inches' height they exhibit characters showing complete segregation to parental types and intermediates (see Table 1). For some specific characters an approximation to the Mendelian ratio for the independent assortment of characters in the F2 generation is achieved. The juvenile foliage of the putative parents is quite distinct. In the case of *E. Robertsonii* (Pl. vii, fig. 1) it is narrow-lanceolate, sessile, thin, opposite for a large number of pairs, glandular hairy on the stems. In *E. pauciflora*, on the other hand, the leaves soon become petiolate and become alternate after four or five pairs, they are thick and rather broadly oblong, and the stems are almost smooth. The population obtained has some individuals which are indistinguishable from seedlings of *E. Robertsonii*, and others which cannot be separated from *E. pauciflora*. There is little doubt that the parent tree is an F1 hybrid and that the generation raised, which is probably from seed that has been produced by selfing, is an F2 generation. Similar individuals can be found almost wherever there is a junction in the field between *E. pauciflora* and *E. Robertsonii*, although they are not numerous and never form a pure stand or even a consistent major component of a stand.

In the area in which this seed was collected there was a considerable number of trees which would be considered *E. Robertsonii*. Nevertheless, though this is the only possible determination amongst described species, many of the individuals are inclined to be smooth-barked on limbs three or four inches in diameter, somewhat heavy-leaved and with fruits that are coarser than are often found on *E. Robertsonii*. From one of these trees a small amount of seed was also collected and about twelve plants were raised. While the number was small, three of the twelve plants corresponded with individuals in the progeny from the F1 hybrid which were intermediate between the two parental types. The deviation from an ordinary population of *E. Robertsonii* was far too great to do other than lead to the conclusion that the parent tree in this case could not have been "pure" *E. Robertsonii* (Pl. vii, fig. 3). Had there been no morphological indications of this, one might have concluded that some of the seed in the capsules was of hybrid origin. Since most of the flowers are probably selfed on the one tree, if not individually self-fertilized, the variation in the progeny in the light of the morphological character of the parent is consistent with what one would expect in an F3 or later generation, or from a back-cross. It is quite probable in the regrowth area concerned that there is a population containing many segregates between *E. pauciflora* and *E. Robertsonii* (Pl. viii, fig. 4) with a bias in survival towards those individuals with a preponderance of *E. Robertsonii* characteristics.

Field examination of many stands suggests that mingling between various ecotypes of *E. pauciflora* and ecotypes of Peppermints (*E. radiata*, *E. Robertsonii* and *E. dives*) is common, and this is perhaps one of the most frequent hybrid combinations found on the Southern Tablelands.

E. pauciflora enters into other combinations in addition. A stand was examined at Barney's Range, near Cooma, where there is an unusual occurrence side by side of *E. pauciflora* and *E. Rossii*. After some search two trees were found which were

intermediate between these two species. Seed was collected from one and 50 plants again raised without selection in pricking off from the flat. Complete segregation to the putative parents was again attained although the juvenile characteristics of these two species are not so clearly distinctive as in the previous case (Pl. viii, fig. 5). Nevertheless the trend is unmistakable and the amplitude of variation in morphological characters and the correspondence of the extreme forms closely with juvenile foliage of the recognized putative parent species is such that there is no other readily acceptable explanation than that we have an F2 population.

E. pauciflora has characteristics which are almost unique in the genus in its practically parallel veins in the leaves, the very thick leaves and large pyriform fruit. It appears these characters persist prominently in hybrid combination and the presence of *E. pauciflora* genes is therefore readily detected. Progeny tests are not yet complete but it is highly probable that *E. pauciflora* × *E. delegatensis* hybrids may be readily found, and several trees are known which seem to be F1 hybrids of this combination. One tree was also found on the dividing range near Badja which looked like a hybrid between *E. pauciflora* and *E. fastigata*. On the other hand, so far no individuals have been found in the field which suggest that *E. pauciflora* enters into combination with Gums such as *E. Dalrympleana* or *E. Blakelyi*, or with Boxes such as *E. melliodora*, with all of which it can easily be found growing side by side.

b. E. Rossii *Hybrids*.

Eucalyptus Rossii, which, as has been mentioned, hybridizes with *E. pauciflora*, is commonly found in hybrid combination with other species. One of the commonest of these is with *E. macrorhyncha*. Using the same procedure as in the examination of *E. pauciflora* and Peppermints, a tree on Mount Jerrabomberra was examined. It has field characters intermediate between *E. macrorhyncha* and *E. Rossii*. The bark is smooth on limbs of six inches diameter or less, the fruit is rather small, with a flat-domed disc compared with *E. macrorhyncha*; the leaves are also small and shiny for "normal" *E. macrorhyncha*. The progeny obtained from seed of this tree provides a most striking example of segregation and independent assortment of many characters (Pl. viii, fig. 6). The juvenile characters of the two species are strikingly distinct. *E. macrorhyncha* (Pl. viii, fig. 7) has ovate-lanceolate or broadly elliptical leaves covered densely with "stellate" hairs. *E. Rossii* (Pl. ix, fig. 8), on the other hand, has narrow-lanceolate, glabrous, grey-glaucous leaves. This affords an outstanding example of the existence of an F1 hybrid and it is so distinctive that there is little need for further demonstration.

In the same locality seed was also collected from another tree with similar morphological characteristics. The variation in the progeny was much more restricted than in the first tree, although the trend is clearly in the same direction to the putative parents, *E. macrorhyncha* and *E. Rossii* (Pl. ix, fig. 9). The conclusion, therefore, is that though the morphological form of the parent is closely similar to that of the undoubted F1 hybrid, this second tree must be a member of a later filial generation or back-cross of the same hybrid combination in which the genetic variability has been considerably reduced (see also Pl. ix, fig. 10).

The existence of F1 hybrids has been established on the basis of evidence of this kind between several other pairs of species. *E. Rossii* × *E. dives* (Pl. ix, fig. 11) is found quite frequently and progeny tests show marked segregation in some individuals, whereas other individuals closely similar morphologically show less, as in the case of *E. macrorhyncha* × *E. Rossii* combinations.

E. Rossii also hybridizes freely with *E. Robertsonii* where these two species occur side by side. Blakely (ined.) proposed a variety of *E. Robertsonii* on material from the Australian Capital Territory which is close to, if not identical with, the F1 hybrid *E. Rossii* × *E. Robertsonii*. The juvenile foliage of these two species is so distinct that segregation is at once apparent in seedlings (Pl. x, fig. 12).

c. Miscellaneous Hybrids.

A common hybrid combination is between *E. Robertsonii* and *E. fastigata*, and F1 individuals have been located which segregate markedly when propagated (Pl. x, fig. 14). The segregation is easily discerned because the juvenile characters of each parent are so distinct from those of the other.

Other hybrids have been found and tested between *E. Blakelyi* and *E. elaeophora* (Pl. x, fig. 15) and between *E. maculosa* and *E. elaeophora* (Pl. xi, fig. 16). Individuals are occasionally found in which the morphological characters are intermediate between *E. Blakelyi* and *E. elaeophora*. Segregation of characters is again marked in the seedling stage and the sessile, opposite, orbicular, glaucous juveniles of *E. elaeophora* are so strikingly distinct from the stalked ovate-lanceolate, green, alternate, juvenile leaves of *E. Blakelyi* that observation of segregation is quite simple. An F1 hybrid has been progeny-tested and other similar individuals have been located on Black Mountain (Pl. x, fig. 15).

Likewise, extreme differences exist between the juvenile foliage of *E. maculosa* and *E. elaeophora*, and a progeny test of an anomalous individual has given a filial population showing marked segregation to the putative parental types in the juvenile foliage (Pl. xi, fig. 16).

Another interesting individual is an undoubted F1 hybrid between *E. viminalis* and *E. glaucescens*. This individual was found on the Tinderry Ranges while examining the vegetation in company with R. G. Brett. Segregation in the progeny is easily recognized for the same reasons (Pl. xi, fig. 18).

Further combinations are being investigated but, since adequate diagnostic characters are not displayed in the juvenile forms, results will not be available until the progeny is more mature. Continued collection will produce more evidence as a wider number of species can be examined.

Table 1 shows the way in which characters have been observed to segregate in the different progenies examined.

Taxonomic and Evolutionary Implications.

a. Nomenclature.

The analysis given above is still incomplete, as it is based on juvenile characters only, but problems of classification in *Eucalyptus* are profoundly affected by facts established by genetic analysis of this kind. There is little doubt that segregating swarms are common in the field and individuals from these have often been referred to species while the types of some so-called species are probably members of such swarms. The description of segregating forms as species is useless for taxonomy and the classification of such individuals should be made differently. One of the first steps in the revision of the genus *Eucalyptus* must be to determine which of the described "species" are F1 hybrids or segregates.

The position with regard to hybrids known as "*Eucalyptus vitrea*" has been discussed previously and some additional similar or related matters have been disclosed in the present study. For example, the F1 hybrid and the segregate between *E. Rossii* and *E. macrorhyncha* have both in the past been referred to *E. brevirostris*. Comparison of the material from the mature trees with the type of *E. brevirostris* shows that neither of these can be placed with that type, although they have some characters in common, notably the buds and the general fruit size. However, the rim of the fruit is quite different and the leaves are also different. There are some characters in *E. brevirostris* which suggest affinity with *E. regnans* on the one hand and a Stringybark on the other. The record of distribution of this species also suggests that it might well be a hybrid, as indeed Blakely himself supposed. It cannot, however, be a hybrid between *E. macrorhyncha* and *E. Rossii*. There is no type, therefore, with which the F1 hybrid *E. macrorhyncha* × *E. Rossii* corresponds. It is undescribed at present, and in any case should not be described as a species.

Another hybrid combination of particular interest is that of *E. fastigata* and *E. Robertsonii*. This illustrates one way in which the genetic approach has a marked

TABLE 1.

Table of Presumptive F1 Hybrids.

Presumptive Parents.	Characters Segregating in Progeny.									Remarks.
	Juvenile Leaves.							Other Characters.		
	Shape.	Petiole.	Colour.	Venation.	Arrangement.	Texture.	Hairs.	Stem Hairs.	Oil.	
Renantherae.										
E. pauciflora Sieb. ex Spreng. ×*dives* Schau.	Yes.	Yes.	Yes.	Yes.	Yes.	Yes.	—	—	Yes.	Part of " *E. vitrea* " of authors.
E. pauciflora Sieb. ex Spreng. ×*Robertsonii* Blakely.	Yes.	Yes.	—	Yes.	Yes.	Yes.	—	Yes.	Yes.	Segregation complete.
E. pauciflora Sieb. ex Spreng. ×*Rossii* R. T. Bak. & H. G. Sm.	Yes.	—	—	Yes.	—	Yes.	—	—	No.	Juveniles similar at first.
E. pauciflora Sieb. ex Spreng. ×*delegatensis* R. T. Bak.	Yes.	—	—	Yes.	—	Yes.	—	—	No.	Small progenies seen only.
E. Rossii R. T. Bak. & H. G. Sm. ×*macrorhyncha* F. Muell. ex Benth.	Yes.	—	Yes.	No.	—	No.	Yes.	—	—	Segregation complete.
E. Rossii R. T. Bak. & H. G. Sm. ×*dives* Schau.	Yes.	Yes.	—	No.	Yes.	—	—	Yes.	Yes.	Segregation incomplete.
E. Rossii R. T. Bak. & H. G. Sm. ×*Robertsonii* Blakely.	Yes.	Yes.	Yes.	No.	Yes.	Yes.	—	Yes.	Yes.	Segregation incomplete.
E. Robertsonii Blakely ×*fastigata* Deane & Maiden.	Yes.	Yes.	—	Yes.	—	Yes.	—	Yes.	Yes.	Segregation complete.
E. fastigata Deane & Maiden ×*macrorhyncha* F. Muell. ex Benth.	Yes.	—	—	Yes.	—	Yes.	Yes.	—	No.	Segregation incomplete.
Macrantherae.										
E. Blakelyi Maiden ×*elaeophora* F. Muell...	Yes.	Yes.	Yes.	—	Yes.	No.	—	—	No.	Segregation complete.
E. elaeophora F. Muell. ×*maculosa* R. T. Bak.	Yes.	Yes.	No.	No.	Yes.	No.	—	—	—	Segregation complete.
E. viminalis Labill. ×*glauceseens* Maiden & Blakely.	Yes.	—	Yes.	No.	—	—	—	—	No.	Segregation complete in some progenies, partial in others.

Explanation : Yes = segregation observed. No = segregation possible but not observed. — = characters similar in the two presumptive parents—segregation impossible to observe.

bearing on taxonomic conclusions. *E. radiata* and *E. Robertsonii* were regarded as distinct species by Blakely. One of the means of separation of these species is the appearance of sub-parallel venation in *E. radiata* as distinct from *E. Robertsonii*. The two species are obviously very closely related.

The presence of hybrids and segregates of *E. fastigata* and *E. Robertsonii* in the field accounts for the sub-parallel venation which is sometimes found in areas where the trees correspond generally with *E. Robertsonii*. One of the uncertainties which has led to the suggestion that *E. Robertsonii* and *E. radiata* should not be separated as distinct species is removed if it is recognized that this lack of consistency between the two species is, in the case of *E. Robertsonii*, a result of hybrid influence by *E. fastigata*, and the decision as to whether the two are "good" species rests on whether the two populations are sufficiently distinct.

There is no doubt that the type of *E. Robertsonii* which was collected by Blakely and de Beuzeville on Talbingo Mountain represents the population of the western part of the Southern Highlands, which has a number of characters different from *E. radiata*, the type of which comes from the Blue Mountains. These characters, though not marked, are nevertheless fairly distinctive. It seems, therefore, that *E. radiata* and *E. Robertsonii*, according to the definitions accepted in the concept, could be regarded either as species or alternatively as subspecies within the *E. radiata* group.

On the other hand, the position of *E. Westonii* is similar to that of *E. vitrea*. The hybrid between *E. maculosa* and *E. elaeophora* is identical with *E. Westonii*, the type locality of which is Mt. Majura, A.C.T.

In the vicinity of the type tree there are populations of segregates which vary more or less continuously between each of the supposed parents. There is little doubt that *E. Westonii* is an F1 hybrid between *E. maculosa* and *E. elaeophora* and that it is in consequence genetically unstable. It therefore should not be regarded as a species.

b. "Phantoms" and Clines.

The detection of the F1 hybrid between *E. Rossii* and *E. Robertsonii* has already been described where stands of these two species are side by side in the field; however, in other areas somewhat remote from stands of *E. Robertsonii* individuals are found which are intermediate between *E. Rossii* and a Peppermint of the *E. radiata* type. Usually there is no *E. radiata* or *E. Robertsonii* present, as at Black Mountain, A.C.T., and Mt. Jerrabomberra, N.S.W., but the progeny from the tree shows a limited degree of segregation which unmistakably reveals genetic diversity beyond that which is normal in one of the accepted species (Pl. x, fig. 13). The best explanation for such occurrences is that given by Brett (1949). He supposes that the genes of the *E. radiata* are preserved in hybrid form to some extent as a relict from former times when, probably due to somewhat different climate, the *E. radiata* was much more widely distributed. Brett has referred to such occurrences as a "phantom" of a species, and this appears to be quite apt. The same condition has been found with *E. fastigata* genes preserved in *E. macrorhyncha* on Mt. Macdonald, A.C.T. (Pl. ix, fig. 10). This aspect must be studied more closely as information which relates critically to the subject becomes available from the trials in progress.

E. Rossii also presents another phase of the same condition in that it appears to contain, in many instances, genetic influence in varying degrees from Peppermints and Stringybark species which could be expected as climatic changes and conditions for survival of some species become more difficult. *E. Rossii* shows minor variations in populations from place to place, apparently for this reason. Again this aspect must be treated separately when more experimental data are available.

Another distinct condition resulting from gene movement is illustrated in the clinal variation in *E. fastigata* and *E. radiata*.

The hybrid *E. radiata* × *E. fastigata* is common on the dividing range in the vicinity of Badja and in this locality exhibits an interesting feature. On the gentler grading sheltered slope on the western fall of the range *E. radiata* is confined to a narrow strip near the crest. At this point also hybrids of *E. fastigata* occur. As one then proceeds

down the slope, narrow-leaved, small-fruited forms of *E. fastigata* occur which gradually become coarser and pass without discontinuity to typical *E. fastigata* in the middle and lower parts of the slope. This variation in a cline according to exposure grades from a form intermediate between the two parent species to *E. fastigata*. A clinal sequence from the intermediate to *E. radiata* is not to be found in this locality, presumably because the site favours the combination on the *E. fastigata* side of the mode of the hybrid combination.

The same kind of clinal variation in individuals was observed from the area of the occurrence of the F1 hybrid *E. pauciflora* × *E. Rossii*, the gradation being from this form to *E. Rossii* as the conditions become warmer.

c. Gene Invasion.

The evidence produced in the examination of *E. glaucescens* suggests that gene invasion of this species by *E. viminalis* is a likely explanation of the facts.

E. glaucescens is an uncommon species which occurs in small communities on rocky areas in sub-alpine regions. It has close affinity with two Tasmanian species, *E. Gunnii* and *E. urnigera*. This relationship and its scattered distribution suggest that it is a relic of a group of species or a common precursor which flourished at some earlier period in the south-east highlands and in Tasmania. Wherever it is in contact with *E. viminalis* (and this is probably usual) it is being hybridized and invaded by the more successful genes of that species. The evidence for this is that in the small progeny test segregates intermediate in character between the apparent F1 hybrid and the typical *E. glaucescens* are of low viability, whereas those segregates leaning to *E. viminalis* are highly successful (Pl. xi, figs. 18 and 19). If this is so, it is an illustration of gene invasion referred to by Brett (1950) and is one way in which a species can be virtually extinguished. Specimens of *E. glaucescens* collected by A. B. Costin near the Victorian border have produced some plants tending towards *E. viminalis* (Pl. xi, fig. 19), thus clearly indicating the presence of the genes, though the parent could not be taken for *E. viminalis*, and it could not be an F1 hybrid because of the absence of segregation of the type expected in an F2 generation.

With *E. Perriniana*, by way of contrast, the position is quite the reverse. It is a species of similar sub-alpine distribution, but, where examined, no trace of hybrids can be found. While it is apparently a diminishing relic population, now occurring only on hard sites, simple competition from more vigorous species appears to be the cause of its near extinction.

d. Sterility Barriers.

The evolution of the genus and the possible extent of the conditions described above will be strictly limited by any barriers to breeding within the genus. These are not yet fully known, but field occurrences suggest that hybridization is, at least under natural conditions, confined within the major taxonomic divisions of the genus as given by Blakely. Experimental controlled pollinations confirm this in general terms but not absolutely (Pryor, 1951).

On the other hand, Brett (1937) says there is some evidence of intergroup hybrids, as, for example, *E. ovata* × *E. pauciflora*, and *E. risdonii* × *E. viminalis*.

While there is perhaps evidence of selection of similar characters, e.g., large leaves or glaucousness, in unrelated species growing side by side in a particular habitat, a careful search has so far failed to produce one of the wide crosses between the three taxonomic groups, Macrantherae, Renantherae and Terminales, which often occur side by side in the field on the Southern Highlands.

More critical work is necessary to establish the limits and such points as whether such progeny is viable or, if so, whether it is fertile.

Summary.

A genetic examination, principally by progeny testing, has been made of several species common on the Southern Highlands of New South Wales and in Victoria. Morphological seedling characters are of critical diagnostic value in the genus *Eucalyptus*

and the segregation of some of these characters in progenies strongly suggests that a number of the individuals examined are F1 hybrids. Other individuals similar in their general morphology are revealed as probably hybrid but of a later filial or back-crossed generation.

From the evidence obtained by progeny tests it is considered likely that segregating swarms between well-established species occur in a number of cases. Under field conditions hybridization between three of the major taxonomic groups of the genus *Eucalyptus*, namely, Macrantherae, Renantherae, and Terminales, as given by Blakely, has not been observed and it is considered that this, though perhaps possible, is unlikely. Further work is in progress to examine the position with regard to other species combinations and to examine various aspects of genetic behaviour within the genus.

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EXPLANATION OF PLATES VII-XI.

Plate vii.

Fig. 1.—*E. Robertsonii.* Progeny showing slight variation characteristic of a population falling within the defined limits of the species without hybrid influence.

Fig. 2.—*E. pauciflora* × *E. Robertsonii,* Cotter House, A.C.T. An F2 generation raised from a probable F1 hybrid. Segregation is complete and there is independent assortment of characters. The extreme left is identical with *E. Robertsonii* and the extreme right is *E. pauciflora.* The development of broad leaves, but practically sessile and opposite, in the fifth from the left, is a mixture of *E. pauciflora* and *E. Robertsonii* characteristics, whereas the petiolate leaves but relatively narrow, is a mixture of *E. pauciflora* and *E. Robertsonii* characteristics of a different degree. The development of alternate leaves is noticeable in the final pair, especially of the fourth from the left and the seedling on the extreme right.

Fig. 3.—*E. Robertsonii,* Cotter House, A.C.T. There is unmistakable *E. pauciflora* in this population, as is indicated by the seedling on the extreme left. The second from the left shows thick and broad leaves but retains the Peppermint character of sessile, opposite leaves. The seed parent of these seedlings appears to be Peppermint (*E. Robertsonii*) but was rather clean-stemmed and with larger fruits and somewhat heavier leaves than is "normal". It clearly contains *E. pauciflora* genes.

Plate viii.

Fig. 4.—*E. pauciflora,* Cotter House, A.C.T. This shows a tendency to *E. Robertsonii,* particularly in the individual at the extreme left. The leaves are narrower and inclined to be sessile and opposite to an extent greater than that characteristic of *E. pauciflora,* which is typical in the two individuals on the right. The parent of this population, however, must have been part of a hybrid swarm between *E. Robertsonii* and *E. pauciflora.*

Fig. 5.—*E. pauciflora* × *E. Rossii.* An F2 generation raised from an apparent F1 hybrid from Barney's Range. The thick broad-lanceolate leaves of the plants on the left stand sharply in contrast with the narrow-lanceolate, rather thin-stemmed and thin-petioled leaves on the right. Characters which are more critically distinct may be expected to appear as the trees become older, the juvenile characters being in this pair of species rather more similar than in many others.

Fig. 6.—*E. macrorhyncha* × *E. Rossii.* An F2 population showing complete segregation from *E. macrorhyncha* type on the left to *E. Rossii* on the right. Note the change in leaf shape and petiole length. The indumentum of "stellate" hairs characteristic of *E. macrorhyncha* shows a similar gradation. There is a marked tendency for the intermediate hybrid type (similar in form to the F1 hybrid), third from the left, to be the most vigorous.

Fig. 7.—*E. macrorhyncha.* A population characteristic of the species showing the typical leaf shape and at times slightly crenate leaf margins.

Plate ix.

Fig. 8.—*E. Rossii,* Jerrabomberra. A population without hybrid influence showing relatively uniform characteristics of the progeny.

Fig. 9.—*E. macrorhyncha* × *E. Rossii.* Progeny from a tree which was not an F1 hybrid, showing a type tending to *E. macrorhyncha* in the plants at the left, and a type approaching *E. Rossii* in the types at the right. Compare with Fig. 7, where the segregation runs from one putative parent to the other, indicating a broader range of variation.

Fig. 10.—Progeny from an apparent *E. macrorhyncha* hybrid, Mt. McDonald, A.C.T. The progeny suggests strong affinity with *E. fastigata* in the form on the right-hand side. The two individuals at the left are closely similar with normal *E. macrorhyncha*. The fourth from the left is roughly intermediate between *E. macrorhyncha* and *E. fastigata*. This suggests the preservation of *E. fastigata* genes in hybrid combination in a locality in which *E. fastigata* no longer exists.

Fig. 11.—*E. dives* × *E. Rossii*. Note the broad, opposite, sessile leaves on the plant on the left, grading to lanceolate, petiolate leaves approaching *E. Rossii* on the right. The fourth from the left is becoming distinctly alternate. Probably not an F2, but a later generation however.

Plate x.

Fig. 12.—Progeny from a parent belonging to the hybrid swarm *E. Rossii* × *E. Robertsonii*. The plant on the left is close to *E. Robertsonii*. Note the progressive development of stalked leaves becoming alternate as one proceeds to the right, a generation later than an F2 generation.

Fig. 13.—Progeny from a tree on Mt. Jerrabomberra of a narrow-leaved Peppermint type. Appears to be clearly a hybrid between a Peppermint of the *E. Robertsonii* or *E. radiata* type and *E. Rossii*, the characters of the putative parents being shown in the gradation from left to right, the Peppermint being at the extreme left. The fifth from the right, however, indicates a probable influence of *E. dives*, showing that this is not a simple hybrid. The occurrence of this tree is remarkable, as there are no *E. dives*, *E. radiata* or *E. Robertsonii* now on Mt. Jerrabomberra. The trees from which the seed was taken to raise these plants are about 30 years old and appeared following disturbance in road making about 30 years ago.

Fig. 14.—Progeny from an F1 hybrid between *E. fastigata* and *E. Robertsonii*. Arranged to show the sequence of characters from *E. fastigata* on the left to *E. Robertsonii* on the right. Note the change from alternate, petiolate broad-lanceolate leaves at the left, to opposite, sessile narrow-lanceolate leaves on the right.

Fig 15.—Progeny from a hybrid between *E. elaeophora* and *E. Blakelyi*. Showing complete segregation between the two putative parents, *E. elaeophora* on the left with opposite, orbicular, sessile leaves, to *E. Blakelyi* with petiolate, broad ovate-lanceolate, alternate leaves at the right. Note the gradations of characters between the two extremes and also the lack of vigour in the intermediate types.

Plate xi.

Fig. 16.—Progeny from *E. Westonii*, Black Mountain, A.C.T. Indicating three main gene types. At the extreme left, a Blue Gum resembling *E. goniocalyx*, and the centre, types tending to *E. elaeophora* or *E. Bridgesiana*, and at the right, *E. maculosa*. A complex gene mixture that needs further analysis. A variation in vigour of the various combinations is also interesting.

Fig. 17.—*E. glaucescens* × *E. viminalis*. Seedlings raised from a supposed F1 hybrid from the Tinderry Mountains. Photographed in November, 1949. Compare with Fig. 18, in which the order of arrangement is reversed, *E. glaucescens* being at the extreme right. The plant second from the left, which is showing signs of weakness, is the second from the right in Fig. 18 and is, in the six months' interval, dead.

Fig. 18.—*E. glaucescens* × *E. viminalis*—progeny raised from a supposed F1 hybrid collected on the Tinderry Mountains. Note the segregation in the seedlings in the F2 generation between *E. viminalis* type at the extreme left and *E. glaucescens* at the right. Photograph taken in May, 1950, indicating the difficulty in raising segregates which approach *E. glaucescens*, the fourth from the left being almost dead. Compare this plant with the same individual in Fig. 17, which is the same population of five plants taken in November, 1949.

Fig. 19.—Progeny from a tree of *E. glaucescens* showing the presence of *E. viminalis* genes. The seed was collected by Mr. A. B. Costin from a tree, apparently *E. glaucescens*, at Tingiringi. The unmistakable influence of *E. viminalis* is apparent in the two individuals at the right.

INVESTIGATIONS OF THE PREFERENCES SHOWN BY *AEDES (STEGOMYIA) AEGYPTI* LINN. AND *CULEX (CULEX) FATIGANS* WIED. FOR SPECIFIC TYPES OF BREEDING WATER.

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Synopsis.

Comparative experiments are outlined showing the reaction of *Aëdes aegypti* and *Culex fatigans* to two types of water, representative of field habitats, these being tap water and a "foul" medium for which a manure infusion was used. Results are given showing the oviposition responses of the adult females to both types of water and the survival percentages of the larvae of the two species when reared in these media.

Each species showed preference for the foul medium for oviposition, that shown by *C. fatigans* being complete. *C. fatigans* larvae were more able to survive than *A. aegypti* in the foul medium at all stages of introduction into infusions of varying maturities. It was also shown that development of a scum on the manure infusions was more lethal to the latter species.

Introduction.

The reason for the differences shown by mosquitoes in the selection of larval habitats is a problem which has received much attention from various workers. From early observations in the field it was obvious that the occurrence of mosquito larvae was not haphazard and that no one species is found in all types of water, marked preferences being noticeable. Classifications of habitat have been given by Hopkins (1936), who proposed a grouping according to the situation of the water (e.g. ground water, rock pools), and Lee (1944) whose classification is based on the state of the water itself (e.g. fresh, polluted). During earlier investigations masses of physico-chemical data were obtained by such workers as MacGregor (1929), Senior-White (1934), Beattie (1932). Few significant results were obtained, but Buxton (1934), examining Beattie's results, shows that her conclusion correlating larval prevalence with ammonia nitrogen was significant. More recently work by Thompson (1940–41), Woodhill (1941) and others concerning the selection by the adult female of the site of oviposition seems to be of a more positive nature.

In this investigation *A. aegypti* and *C. fatigans* were selected as representing typical cases of different breeding habits. *A. aegypti* is an entirely domesticated species, breeding in and around human dwellings, usually in fresh water contained in artificial receptacles. It is rarely recorded in foul water, whereas *C. fatigans*, on the other hand, shows a distinct preference for such water. This investigation is of a preliminary nature and was approached from two angles, namely, oviposition responses, comparing the reaction of the two species to water which was believed to be typical of the location in which the larvae have been recorded; and larval experimentation, to see if there was any effect shown by the rearing of the species found in one habitat type, in the alternate type. The two media used were a horse manure infusion and tap water (i.e. the normal reticulated water supply of Sydney, which contains 0·0062% dissolved salts).

Breeding Technique.

The *A. aegypti* eggs were obtained from a stock which has been continuously bred at the Zoology Department, University of Sydney, since 1938. Eggs of *C. fatigans*, which were collected from tubs outside the laboratory, were usually obtainable in sufficient numbers all the year round, but in winter it was at times necessary to maintain a laboratory culture. The technique used for breeding mosquitoes was similar to that used by Woodhill (1936). A laboratory culture of *A. aegypti* was continuously maintained, as fresh eggs were used during the larval experimentation.

This was also done with *C. fatigans* when sufficient eggs were not obtainable outside the laboratory.

The "foul" medium was prepared by mixing approximately equal volumes of dried horse manure and water. These infusions were allowed to mature for three different periods—7 days, 10–11 days, and 14–15 days. They were made up at varying times so that the three states of maturity required would be available at the same time.

Experimentation.

Oviposition Responses.

Males and females of the two species (about 100 of each) were released into separate uniform cages, 12″ × 10″ × 9″, and given blood feeds and raisins. In each cage

Table 1.

Number of Eggs Deposited by C. fatigans *and* A. aegypti.

Observation Number.	*Culex fatigans.*				*Aëdes aegypti.*	
	Tap Water.		Manure Infusion.		Tap Water.	Manure Infusion.
	Number of Rafts.	Number of Eggs.	Number of Rafts.	Number of Eggs.	Number of Eggs.	Number of Eggs.
1	Nil	Nil	4	299	299	489
2	,,	,,	7	455	440	727
3	,,	,,	9	571	560	960
4	,,	,,	9	612	138	436
5	,,	,,	1	75	130	613
6	,,	,,	9	635	89	741
7	,,	,,	7	483	548	2,765
8	,,	,,	10	780	75	180
9	,,	,,	5	381	1,009	1,841
10	,,	,,	5	351	545	1,521
11	,,	,,	21	1,552	77	883
12	,,	,,	9	678	105	747
13	,,	,,	3	156	195	4,990
14					11	153
15					166	805
16					495	3,472
Mean percentages ..		0		100	17·7	82·3

were placed two oviposition dishes, one containing tap water and the other "foul" water which had stood for at least ten days before use. They were placed at opposite ends of the cage, the position reversed daily, and the cages placed parallel to the window in order to eliminate any positional or phototactic response. The eggs were collected and counted at regular intervals, and a record kept of the data and numbers of females feeding. After collection of the eggs the contents of the oviposition dishes were always replaced. This procedure was followed even when no eggs had been laid. Results are given in Table 1.

Under statistical analysis the preference shown by both species for foul water proved significant, giving the probability $P = \frac{1}{2^{32}}$.

Experiments with Larvae.

Fifty larvae at known stages were placed in uniform dishes containing 200 c.c. of the manure infusions (at the required stages of maturity) plus food and incubated

at 80°F. In each experiment controls were kept by placing larvae in tap water with food in the normal manner. The amount of food used in each case was approximately 0·35 gm. The cultures were incubated and the pupae removed as they developed until all the surviving larvae had pupated. The numbers of mature pupae resulting were recorded.

The possibility of interference by scum formation was taken into account. For comparison an effort was made in some cases to find the effect of the water alone, without the interference of the scum. Removal of the scum daily with cotton wool was satisfactory.

TABLE 2.

Percentage Aëdes aegypti *Surviving to Mature Pupal Stage.*

Larvae Stage of Introduction.	Scum Condition on Surface.	Number of Replications.	Percentage Survival.			
			Control. In Tap Water.	In Manure Infusions.		
				7 Days Maturing.	10 Days Maturing.	14 Days Maturing.
50 3rd stage larvae in each replication	Present.	6	99	70	88	98
50 2nd stage larvae in each replication	Present.	6	99	38	74	98
50 2nd stage larvae in each replication	Removed.	9	96	44	80	
50 1st stage larvae in each replication	Present.	6	96	0	58	94
50 1st stage larvae in each replication	Removed.	9	96	3	82	
50 eggs introduced into each replication	Present.	12	99	4	44	94
50 eggs introduced into each replication	Removed.	6	99	9	90	

Table 2 gives the results obtained for *A. aegypti* at known stages of introduction into the "foul" medium cultures. These figures are compared with the controls taken through at the same time in tap water.

Obviously from the results the lethal stage is during the first larval stage, probably when newly emerged, so this stage was selected for a comparison of the effect on the two species. Table 3 gives the results obtained when 50 newly emerged first-stage larvae were introduced into each culture.

TABLE 3.

Percentage of A. aegypti *and* C. fatigans *Surviving to Mature Pupal Stage.*

Scum Condition on Surface.	Number of Replications.	*Aëdes aegypti.*			*Culex fatigans.*		
		In Tap Water. Control.	In Manure Infusion.		In Tap Water. Control.	In Manure Infusion.	
			7-Day Infusion.	11-Day Infusion.		7-Day Infusion.	11-Day Infusion.
Present ..	6	99%	3%	60%	99%	62%	92%
Removed ..	6	99%	5%	84%	99%	74%	96%

The figures in Table 2 and Table 3 show the *percentage survival* of the two species. For use in the summary these figures have been converted to *percentage mortality* by subtraction from the 100% level.

Discussion.

Oviposition Responses.

The potentialities of any water as a breeding ground depend primarily upon the response of the female to that water. With the possibilities of phototactic and positionary responses eliminated, results for *C. fatigans* apparently ratified field observations. This species showed a complete preference for foul water, laying 100% of the eggs on this medium. In the field, *C. fatigans* is generally recorded in water with a high organic content. The occurrence of this species in clean water would be due to the inability of the female to find a more suitable breeding place.

A. aegypti did not show a complete preference for the "foul" water, but nevertheless did have a very marked preference. In a total of 16 observations, when 29,905 eggs were laid, 82% were deposited on the "foul" water. In the field, even when foul water of the type used is available, *A. aegypti* larvae have rarely been recorded in it and almost invariably occur in the water contained in rain water tanks and similar containers. In all its usual breeding places the organic content is relatively low, yet in the laboratory, under optimum conditions, the species preferred to lay its eggs on water with a high organic content. These results seem to correspond with those obtained by Dunn (1927). He found that, by placing containers with various types of water in the open and allowing *A. aegypti* to breed at will, the species showed a distinct preference for water to which leaves had been added, rather than ordinary tap water. Apparently *A. aegypti* is attracted by some factors which are indicative of a higher food content.

From the evidence of these findings further oviposition experimentation is indicated, giving a comparison of varying degrees of foulness or putrefaction rather than a comparison with tap water, and also types of putrefaction, for example, using leaves. It must also be noted that during these experiments the infusions used were all over ten days' maturity. Considering the larval findings with infusions of seven days' maturity, it may be interesting to see the results of similar experiments using only the seven-day infusion. A rejection point may be obtainable, giving a lead to the actual limiting factor.

Larval Cultures.

The horse manure infusion proved a satisfactory medium and was easy to handle. Initial observations were made on these infusions by exposing them to field conditions so that the approximate time of entry of *C. fatigans* could be determined, giving the time at which the infusion became a potential breeding ground. As the seventh day after preparation was found to be the critical time for laying of eggs, it was decided to see if there was any effect on *A. aegypti* by placing larvae in this medium. As *C. fatigans* was then able to breed in these cultures it was considered unnecessary to carry out comparable experiments between these species at first. The method was altered variously to show the effect of infusions of different degrees of maturity on the larval stages. Table 2 shows the results in a condensed form.

No statistical analysis was necessary for the verification of these results. The major diminution of the population, such as in the introduction of first-stage larvae and eggs into the seven-day infusion, was obviously significant. The effect of the seven-day infusions on all stages was the most noticeable. The earlier the larval stages at introduction, the greater the mortality became; however, there was a slight rise in survival with the introduction of eggs. In all cases the removal of the scum led to a slight rise in survival rate. After ten days' maturity the infusions became much less toxic, but still showed this increase in mortality with the introduction of earlier larval stages. The scum exerted a similar effect in these infusions, and with its removal the percentage survival increased appreciably. This effect was greatest on first stage larvae eggs. The 14-days infusion exerted no major influence on survival,

for in all cases it was almost normal. Scum formation in these experiments was only slight when present, and it was never considered necessary to remove it.

Having shown that the manure infusions had a definite toxic effect on the larvae of *A. aegypti*, experiments were then carried out to compare the results with those obtained from *C. fatigans*. Due to the difficulty encountered in setting up exact numbers of *C. fatigans* eggs because of the raft form, it was decided to use newly hatched first-stage larvae. This stage also presented the most critical stage in the development of *A. aegypti* in the infusions. The results are shown in Table 3. For the seven-day infusions the percentage survival of *A. aegypti* was 3%, compared with 62% for *C. fatigans*. These increased to 5% and 74% when the scum was removed. For the eleven-day period the percentages were: *A. aegypti* 60%, and *C. fatigans* 92%, with the scum left, and increasing to 84% and 96% when the scum was removed. The results here for *A. aegypti* also closely correspond with those previously shown in Table 2.

A limiting factor is only evident for the seven-day infusions. As well as preferring the manure infusion for egg laying, *A. aegypti* showed that they were quite able to breed after the infusion was 14 days matured. At seven days the infusions were almost completely toxic and could prevent breeding. At 10–11 days the larvae were able to survive in sufficient numbers to set up a large community. With this increasing ability to survive in the maturing medium the lethal factor is lost. At this time some other factor must come into existence in the field which deters the setting up of a community. As well as showing a complete preference for oviposition, *C. fatigans* showed a greater ability to survive in the manure infusion. The scum forming on the cultures was shown to have more effect on *A. aegypti* than on *C. fatigans*. This is probably due to the form of the respiratory siphon. The scum, however, was not the sole deterrent factor on *A. aegypti*. It is regretted that a method for measuring the scum satisfactorily was not devised. In view of the work carried out by Beattie (1932), it is suggested that the lethal factor present is related to a change in the concentration of some nitrogen product.

Summary.

1. *Aëdes aegypti*, when allowed a choice between clean tap water and foul water (manure infusion) for oviposition, showed a distinct preference for foul water, the percentages of eggs deposited on the two types of water being 17·7% and 82·3% respectively.

2. *Culex fatigans*, when allowed a choice, showed complete preference for the foul water, no eggs whatever being deposited on tap water.

3. In the seven-day manure infusions *A. aegypti* larvae showed a higher mortality the younger the stage exposed. The percentage mortality in each stage was: larvae introduced at the third stage gave 30% mortality; second stage, 62%; first stage, 98½%; eggs, 96%.

4. A similar result was obtained with *A. aegypti* in 10–11 day manure infusions; but, even with early stages, there was sufficient survival to allow successful breeding. The mortality percentages were: third-stage larvae introduced, 12%; second-stage larvae, 26%; first-stage larvae, 41%; eggs, 56%.

5. *A. aegypti* larvae developed almost as well in 14–15 day infusions as in the controls.

6. Scum formation was shown to have some effect on survival of *A. aegypti* in the 7-day and 10–11 day infusions. The percentage mortality decreased in all cases with the removal of the scum. The effect of the scum was most noticeable with the introduction of eggs and first-stage larvae in 10–11 day infusions, the percentage mortality decreasing to 10% and 17% respectively when the scum was removed. (Cf. par. 4.)

7. *C. fatigans* was more able to survive in foul water in all experiments than *A. aegypti*. The actual mortality percentages with first-stage larval introduction were as follows:

(*a*) In seven-day infusions with the scum untouched, *A. aegypti* showed 97% mortality and *C. fatigans* 38%.

(*b*) With the scum removed these decreased to 95% and 26% respectively.

(*c*) In 11-day infusions with the scum untouched, *A. aegypti* showed 40% mortality and *C. fatigans* 8%.

(*d*) With the scum removed these decreased to 16% and 4% respectively.

ACKNOWLEDGEMENTS.

The author's thanks are due to Dr. A. R. Woodhill for his advice while carrying out this work, and to him, Professor P. D. F. Murray, and Dr. W. A. McDougall, Queensland Department of Agriculture and Stock, for many helpful criticisms during the preparation of this paper.

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A MITE FROM A BEEHIVE ON SINGAPORE ISLAND (ACARINA:LAELAPTIDAE).

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Papua–New Guinea.

(Five Text-figures.)

[Read 25th July, 1951.]

Synopsis.

Four mites found in separate brood capsules in a hive of *Apis indica* are described as *Myrmozercon reidi*, n. sp. It is thought likely that they belong to an undescribed genus; they are quite close to *Myrmozercon* but it is felt that the erection of a new genus on nymphal characters alone is not justified.

These mites were found in November, 1944, and given to me by Mr. John Reid, Entomologist from the Institute for Medical Research at Kuala Lumpur (at the time a member of the Federated Malay States Volunteer Forces, and a prisoner of war in Changi Camp). While investigating mortality among bees (*Apis indica*) in one of the hives kept for the camp hospital, he found four mites sealed in separate brood capsules. The mites were alive and apparently feeding on the bee pupae; one mite actually had its proboscis inserted into a pupa. There was no shed mite skin in any of the brood capsules (*i.e.*, there was no evidence that any stage of metamorphosis had taken place while the mites had been enclosed in the capsules).

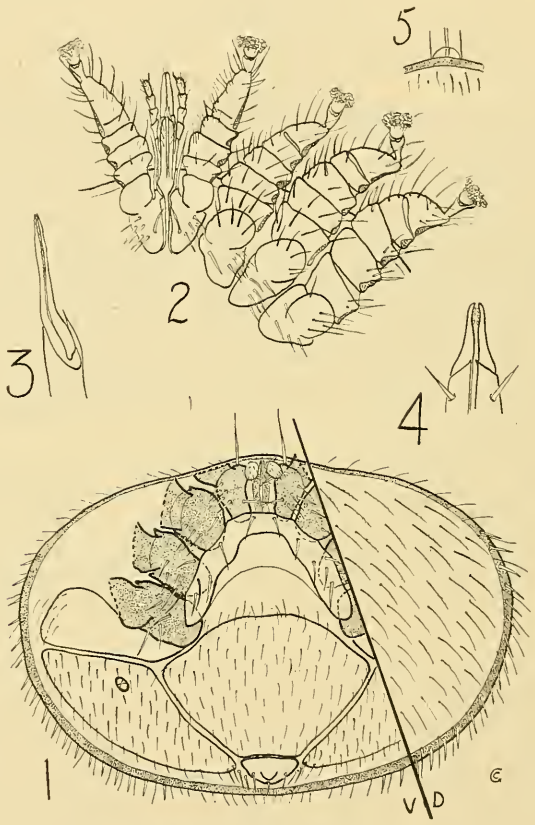
The cause of the trouble among the bees was wax moth (probably family Galleriidae). Careful search revealed no more mites, in any stage, and it was finally assumed that the ones found must have attached themselves to foraging bees and so been transported into the hive, where they had managed to enter the brood capsules, being sealed up with the pupae. That four were found among less than two hundred capsules opened seems to indicate that this is a common occurrence, possibly the normal habit of the mite.

Three of these mites are smaller than the fourth and have the anal plate separate from the ventral plate, whereas in the fourth the anal plate is closely attached to, probably fused with, the ventral plate. One of the smaller ones was dissected and was found to have a testis overlying each second coxa. I can find no genital opening on any of the specimens, and it seems, therefore, that these are all deutonymphs, the smaller ones male, the larger one female. They are quite close to the genus *Myrmozercon*, and while it is likely that they belong to some as yet undescribed genus, I do not feel justified in erecting a new one on nymphal characters alone, and so I include them in *Myrmozercon*.

Myrmozercon reidi, n. sp.

Deutonymph: Body a transverse ellipse with a slight, smoothly-rounded projection anteriorly; almost half as wide again as long; flattened, dorsum convex, venter concave. Male: L. 1050μ to 1090μ, W. 1500μ to 1540μ; female: L. 1125μ, W. 1600μ. Colour brown. A single dorsal shield covering the whole body, with a narrow thickened margin, smooth, bearing setae as follows: general surface with sparsely-set fine setae up to 150μ long, about 50μ apart, those on the anterior half bearing minute setules, those on the posterior half plain; from the inner edge of the thickened margin arise fine plain setae 75μ to 150μ long; at the sides, from two-fifths to four-fifths of the distance back around the circumference, arising from the middle of the thickened margin, are stout, sharply-tapering spines averaging 77μ in the male, 85μ in the female, from 20 to 25 at each side; all setae and spines pointing posteriorly or postero-laterally.

Venter: Coxae close together, set in a semicircle well forward under the body, coxae i at the anterior margin. The proboscis and palps completely retractable; when retracted they lie between coxae i (Text-fig. 1), but when they are projected coxae i move close together (Text-fig. 2), almost as if their squeezing action were forcing and holding the mouthparts forward. An arch-shaped sternal plate overlies the tips of the coxae; it bears five pairs of strong, stout, tapering spines as follows: one medial to the tip of coxa i, one opposite the tip of coxa ii, and three overlying the tip of coxa iii (there are neither metasternal plates nor epigynal shield, so, following Trägårdh, it would seem that this sternal plate represents the fusion of all these, since it bears



Myrmozercon reidi, n. sp.

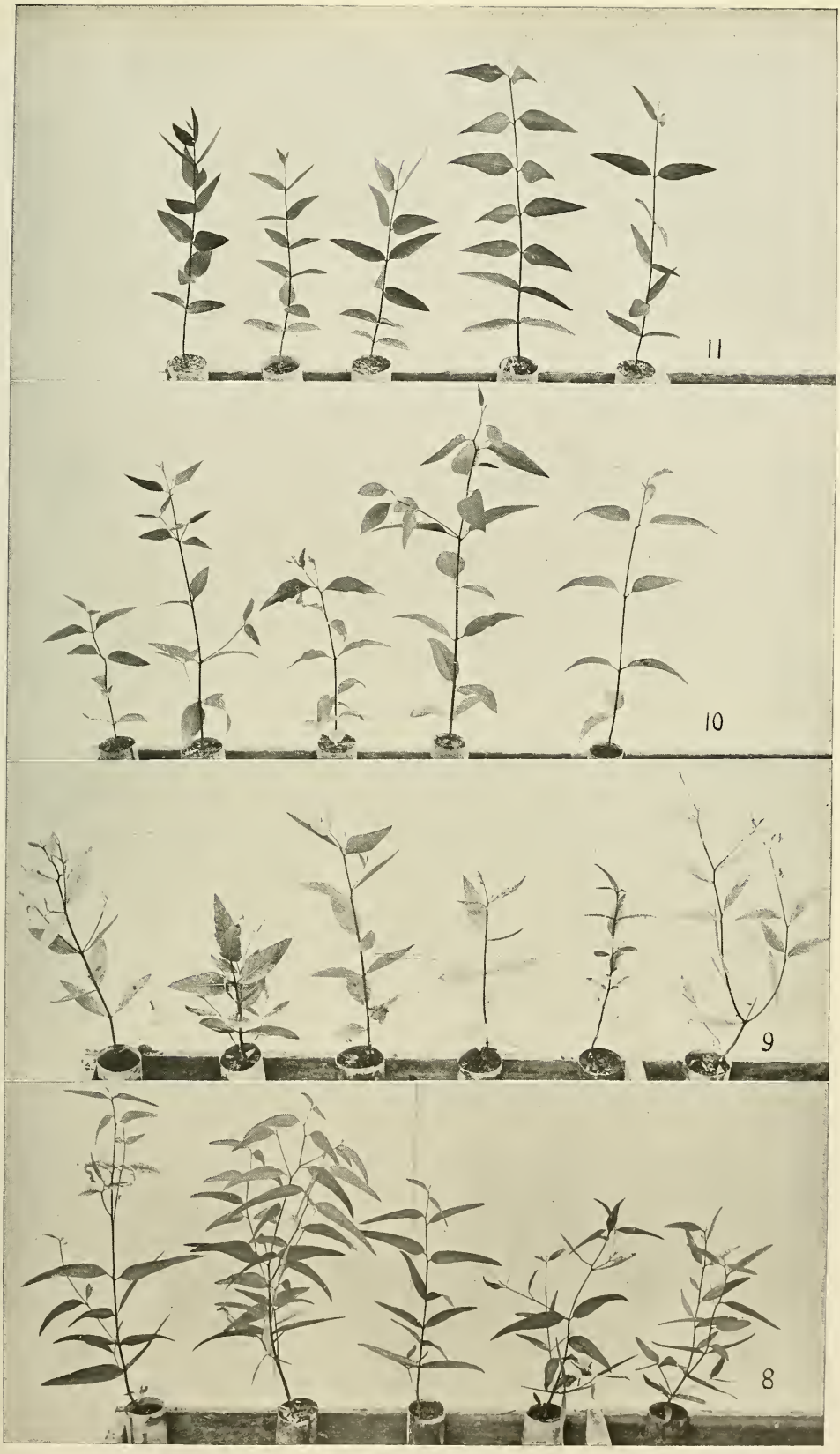
1, Composite dorsal and ventral view; proboscis retracted between coxae i. 2, Ventral view of appendages; proboscis projected and coxae i approximated. 3, Chelicerae and flagellum. 4, Hypostome and lingula. 5, Dorsal view of epistome.

five pairs of setae). Ventral plate pentagonal, occupying most of the posterior central region, its lateral tips behind coxae iv, its anterior point smoothly rounded, its posterior tip flattened; covered with sparsely-set short plain setae which extend forwards for three rows on to the integument. Anal plate small, triangular, placed at the posterior margin of the body; separated from the ventral plate by a narrow strip of integument in the male, but in the female closely applied to, apparently fused with, the ventral plate; anus with an anterior, backward-pointing triangular flap; a stout sharp seta at each side of the anus and a shorter, more slender median seta at the posterior tip of the anal plate; two stout setae on the strip of integument at each side of the anal plate. Stigmata well behind the lateral ends of coxae iv; peritreme large, almost two and a half times as long as wide, triangular, its apex curving back to alongside the anal

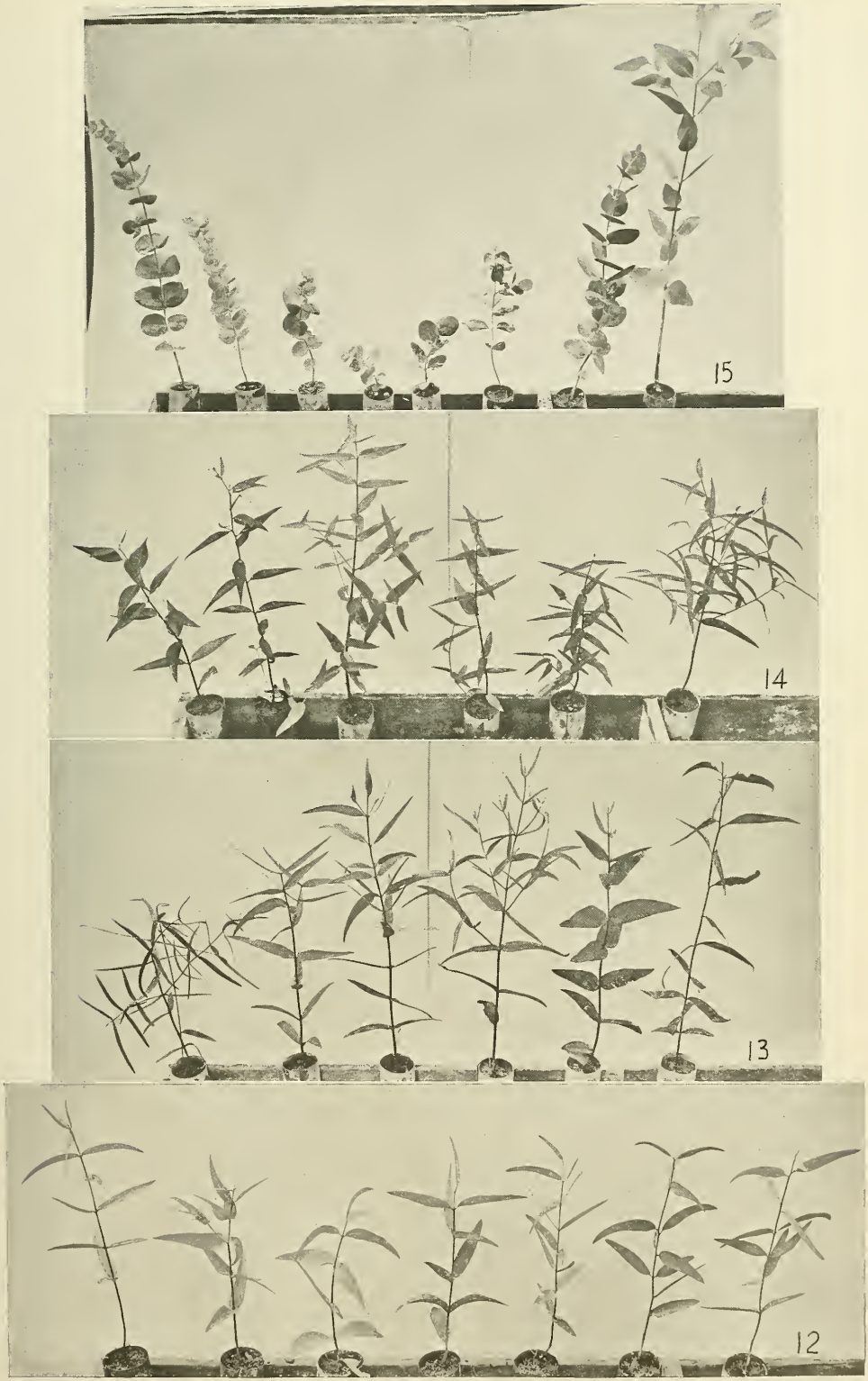
Controlled pollination of *Eucalyptus*.

1, 3. *Eucalyptus Robertsonii.* 2. *E. pauciflora* × *E. Robertsonii.*

4. *E. pauciflora.* 5. *E. pauciflora* × *E. Rossii.*
6. *E. macrorhyncha* × *E. Rossii.* 7. *E. macrorhyncha.*



8. *E. Rossii.* 9. *E. macrorhyncha* × *E. Rossii.*
10. *E. macrorhyncha* hybrid. 11. *E. dives* × *E. Rossii.*



12. *E. Rossii* × *E. Robertsonii*.
13. Hybrid Peppermint × *E. Rossii*.
14. F1 hybrid, *E. fastigata* × *E. Robertsonii*.
15. *E. elaeophora* × *E. Blakelyi*.

16. *E. Westonii.* 17, 18. *E. glaucescens* *E. viminalis.*
19. *E. glaucescens.*

plate; covered with sparse short plain setae. Metapodal plates roughly triangular, their apices behind coxae iv, their bases at the lateral margins of the body; with a few short plain setae over the bases and the adjacent integument.

Coxa i bearing a stout tapering plain seta, 160μ long, projecting straight forward from a shoulder on the anteromedial angle; a shorter, stout seta projecting medially, and a group of five stout setae on the lateral side. Coxa ii with one stout seta towards its anterior margin and a group of six posteriorly. Coxa iii with one anterior and five posterior setae. Coxa iv with four stout setae. Six segments in each leg, but the last two segments in leg i fused, and partly fused in the other three legs. Legs short, very stout, normally curved postero-ventrally; i, 500μ; ii, 525μ; iii and iv, 600μ long. Postero-ventral aspect of last five segments of each leg with a thickened plate. All segments with several stout sharp setae; no spurs on any leg. Tarsus i longer than the others, straighter and more slender; tarsi ii, iii and iv short, stout, curved. A large caruncle, but no claws, on each tarsus (Text-fig. 2).

Epistome only visible from above when proboscis projected; a small, translucent semicircle (Text-fig. 5). Mandibles with three segments, scissors-shaped, the medial fixed blade with a row of minute teeth; a small flagellum at the lateral side of the base of the blades (Text-fig. 3). Hypostome bifid, each half bearing three short stout forward-pointing setae; lingula bifid, each point bearing three small rounded projections on its medial surface (Text-fig. 4). Palpi of five segments, with a few fine setae on segments iii and iv; terminal segment rounded, with one short sharp stout seta on its disto-medial aspect, and covered with several fine straight setae.

Type at the British Museum; paratype at the School of Public Health and Tropical Medicine, University of Sydney.

A CRITICAL CONSIDERATION OF c-MITOSIS WITH REFERENCE TO THE EFFECTS OF NITROPHENOLS.

By Mary M. Hindmarsh,

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(Plate xiii.)

[Read 31st October, 1951.]

Synopsis.

Nitrophenols, as well as many other substances, suppress spindle formation and for this reason have been described as c-mitotic. Many authors either assume without justification that substances which suppress spindle formation have a common mode of action, or do not recognize that, by their use of this term, they imply a common mode of action for all such substances.

Although nitrophenol and colchicine cause spindle suppression, evidence is presented which indicates that their modes of action are probably different. It is essential that the term "c-mitotic" be confined to substances which have true colchicine action. If this distinction is not observed, further confusion must result, which will tend to hamper research on mitotic poisons.

In 1938 Levan described the cytological action of colchicine on plant cells. He showed that colchicine suppressed spindle formation and induced polyploidy without apparently affecting any other cell process. The name "c-mitosis" was given to this phenomenon. Since that time the cytological action of a large number of chemicals has been investigated and there are reports of numerous substitutes for colchicine. Among substances reported to have an action like that of colchicine are phenols and quinones (Levan and Tjio, 1948), veratrine sulphate (Witkus and Berger, 1944), cryptopleurine (Barnard, 1949), sulphonamides (Peters, 1946; Fuller, 1947) and various inorganic salts (Levan, 1945; Galinsky, 1949). Although these compounds are chemically unrelated, the fact that they are reported to cause a similar cytological effect suggests the possibility of a common mode of action. It seems reasonable to suppose that stages in cell division may be linked with metabolic processes and that cytological aberrations may well result from artificial disturbances in the metabolism of the cell. There are many substances which are known to interfere with physiological processes in the cell, and the cytological action of some of these may be of interest.

Recent workers on the phosphorylation mechanisms have made great use of 2,4-dinitrophenol, which seems to be a specific inhibitor of the phosphate transfer mechanism in both plant and animal cells. The mononitrophenols do not have this specific effect (Cross *et al.*, 1949). The mononitrophenols are reported to cause c-mitosis (Levan and Tjio, 1948*a*, 1948*b*). This would suggest that c-mitosis is not the result of interference with the phosphate transfer mechanism. In view of the importance of such a conclusion, it seemed desirable to reinvestigate the c-mitotic activity of nitrophenols.

During the course of this investigation it became apparent that there is a marked difference between the cytological abnormalities induced by colchicine and phenols. The cytological action of phenols does not seem to be "c-mitosis" and this may well apply to many of the substances which have been described as "c-mitotic". If this is so, it is essential to distinguish between true colchicine mitosis and other abnormal types of mitoses before attempting either to look for a common mode of action or even to evaluate the enormous literature on mitotic poisons.

Recovery experiments are an essential part of this type of investigation, as it is necessary to know whether the roots are alive at the end of the experiment and also whether induced cytological abnormalities are permanent or only temporary changes.

In the experiments to be described, onion bulbs with roots about 3 cm. long were transferred from tap-water to the test solutions for periods of 1, 2, 4, 8, 12, 24 and 48 hours. Solutions of dinitrophenol, o- and p-nitrophenol at concentrations 3, 30 and 300 mg/l were made up in tap-water. After treatment some roots were fixed in acetic-alcohol (3:1) and examined by standard aceto-orcein and Feulgen squash methods (Darlington and La Cour, 1947). The remaining roots were transferred back to tap-water for periods up to 48 hours, and recovery estimated by the ability of the roots to continue or resume growth. At intervals during recovery roots were fixed for examination.

TABLE 1.

Time of Treatment.	2, 4-dinitrophenol.			p-nitrophenol.		
	3 mg/l.	30 mg/l.	300 mg/l.	3 mg/l.	30 mg/l.	300 mg/l.
1 hour.	Metaphase chromosomes short and thick.	Spindle suppressed.	Spindle suppressed. Stickiness at anaphase. Resting nuclei granular.	Normal.	Metaphase chromosomes short and thick in few cells.	Spindle suppressed
2 hours.	Metaphase chromosomes short and thick. Spindle suppressed in a few cells.	Spindle suppressed. Stickiness at anaphase.	Spindle suppressed. Stickiness at anaphase and telophase. Resting nuclei granular.	Few metaphase with short, thick chromosomes.	Metaphase chromosomes short and thick.	Spindle suppressed. Stickiness at anaphase.
4 hours.	Metaphase chromosomes short and thick. Spindle suppressed in more cells.	As 2 hours.	As 2 hours.	As 2 hours.	Metaphase chromosomes short and thick. Spindle suppressed in some cells.	Spindle suppressed. Stickiness at anaphase and telophase. Resting nuclei slightly granular.
24 hours.	Spindle suppressed. Anaphase and telophase rarely found.	As 2 hours, but resting nuclei affected.	As 2 hours, but all cells becoming diffuse.	Metaphase chromosomes short and thick. Spindle suppressed in few cells.	Spindle suppressed. Resting nuclei slightly affected.	As 4 hours, but resting nuclei more granular.
In water after treatment.	All recovered.	Recovery after 2, 4, 8 hours. Not after 24 hours.	No recovery.	All recovered.	All recovered.	No recovery after 24 hours.

Cytological abnormalities induced by nitrophenols varied with the concentration, length of time of treatment, and division stages of the cells at the beginning of treatment. Cytological observations mentioned below are those obtained using dinitrophenol, but the effects with p- and o-nitrophenol were the same except that 2,4-dinitrophenol is effective at lower concentrations. This concentration difference is shown in Table 1.

At the lowest concentration abnormalities were observed after two hours. Metaphase and anaphase chromosomes were short and thick, but otherwise the mitotic figures were normal. After four hours most of the cells in metaphase developed a normal metaphase plate with short thick chromosomes, but a few cells had chromosomes scattered at random in the cytoplasm. Twenty-four hours' treatment allowed most cells

dividing during treatment to proceed to normal resting cells; some cells remained in "blocked" metaphase, but unlike colchicine-treated cells, there was no evidence of centromere division. These observations indicate that in the presence of nitrophenols at low concentration spindle formation is completely suppressed, at least in some cells.

At higher concentrations the effects of dinitrophenol were noticeable in one hour. In some cells a metaphase plate appeared in a normal manner; in others short thick chromosomes were scattered in the cytoplasm or clumped together in the centre of the cell. Anaphase stages were numerous; some were normal, some had lagging chromosomes, and some had short thick chromosomes. This variability in the behaviour of different nuclei could be due to irregular penetration across the root in a short period of time. More than two hours' treatment at 30 mg/l induced stickiness in anaphase chromosomes, with sticky bridges in anaphase and telophase stages.

Changes in the resting nuclei were observed after 48–60 hours at 3 mg/l, after 24 hours at 30 mg/l and after 2 hours at 300 mg/l. Some resting nuclei lost their fine-grained appearance, and the chromatin coagulated into coarsely grained masses, forming nuclei about the same size as healthy resting nuclei. Others appeared as small deeply stained "pycnotic" masses with nucleoli standing out as unstained spots. With longer treatment at the high concentrations resting nuclei and chromosomes became diffuse and unstainable, and even cell walls were indistinct.

Length of treatment at any one concentration influenced the ability of the roots to recover. When roots which had been in 3 mg/l for 1–24 hours were transferred to tap-water, all roots recovered, but after 24 hours in 30 mg/l or 1 hour in 300 mg/l no recovery was observed. These roots became soft and flaccid at the tip.

The cells of roots which recovered in tap-water following treatment all commenced normal division after varying periods of time. Again there is a relationship between length of treatment and concentration. Resumption of normal division is rapid after treatment at low concentrations, but much slower after high concentrations. When transferred to water, all dividing cells pass into the resting state and there is a delay depending on length of treatment at each concentration before division begins. As all the cells which resume division are normal and diploid, it is possible that only cells which did not divide during treatment are seen in mitotic stages after recovery.

If resting nuclei were affected, the roots did not recover when the nitrophenol was washed out. Roots which had been in 300 mg/l even for one hour did not have normal dividing cells after being in water for periods up to 48 hours. Abnormal division stages exactly like those of treated roots were observed in these flaccid roots. These results of recovery experiments, particularly those following treatment with 300 mg/l, showed that nitrophenols possess a strong toxic action. At concentrations of 30 and 300 mg/l, nitrophenols appeared to behave as poor fixatives gradually killing and fixing the cells in the stage in which they were when the substance penetrated the cells.

The cytological abnormalities induced by mono-nitrophenols on meristematic cells has been described by Levan and Tjio (1948) as "c-mitosis" over a limited concentration range. This term "c-mitosis" was originally used by Levan (1938) as follows. "The effect of colchicine is entirely specific and the modification in mitotic behaviour will be abbreviated 'c-mitosis'. The c-mitosis can be referred to one single moment, viz. an inactivation of the spindle apparatus connected with a delay of the division of the centromere. The effect thus produced may be expressed as a completion of the chromosome mitosis without nuclear or cellular mitosis."

Levan then discusses the "course of c-mitosis", referring the term not to "one single moment", but to the whole abnormal cell division process which results in telophase nuclei with twice the original number of chromosomes, and numerous polyploid cells in the meristem. This explanation of the term "c-mitosis" is unfortunately ambiguous. The first part of the explanation refers to the specific action of colchicine on the spindle mechanism, whereas the second part, and the subsequent discussion, refers to the whole cell division process. Since 1938 both the spindle

inhibition and the morphological picture of the colchicine mitosis have been described as "c-mitosis" by Levan and other workers. It seems necessary to make a distinction between these two aspects, since the work with nitrophenols indicates that spindle suppression is not necessarily the same as colchicine action.

It seems generally accepted that colchicine has the single effect of upsetting the spindle mechanism, thus altering metaphase and consequently anaphase separation and cell wall formation. Other cell division processes, including the stages from resting nucleus to metaphase and also centromere division, are allowed to proceed during colchicine treatment and the result is polyploidy.

As shown earlier (pages 159–160), nitrophenols are not "entirely specific" in their action. They cause inactivation of the spindle mechanism, but they also alter other vital and independent cell processes so that centromere division, that is "completion of the chromosome mitosis", rarely takes place in treated cells. A very small percentage of cells became tetraploid during treatment, probably only those beginning metaphase or anaphase at the time of treatment, but no tetraploid cells were seen in recovered roots. Therefore, polyploidy, the permanent consequence of "c-mitosis", was not observed as a result of nitrophenol treatment.

As nitrophenol-treated roots continue to grow by normal cell division when they recover, it is not possible to determine whether the cells which show abnormalities during treatment recommence mitosis on recovery. The normal diploid cells may come from the large number of cells which remain in resting stage during treatment and these may completely outgrow abnormal cells. Roots did not recover when the resting nuclei were visibly affected, and this may indicate either that these are the cells which continue growth or that granulation of the resting nuclei occurs only when all the cells are killed.

Attempts to explain the action of colchicine on cell division, or to correlate the physical and chemical properties of colchicine with those of other spindle suppressors so far have been unsuccessful. The explanation of this would seem to be that colchicine has a specific action on the spindle not possessed by other spindle suppressors. It has been suggested (Levan and Ostergren, 1943; Ostergren and Levan, 1943; Ostergren, 1944) that there is a negative correlation between water solubility and the ability of numerous substances to suppress the spindle. Colchicine, however, has a very high water solubility and a strong activity, and does not fit this general theory. This exception is too important to be disregarded and it must be assumed in contrast to the assumption of Ostergren (1944) that colchicine activity is not the same as the spindle suppression of other substances.

During division it is the spindle which is most sensitive to disturbance and there are many observations to show that it is easily upset by changes in the environment of the cell, e.g. temperature changes (Barber and Callan, 1943). Spindle formation in plant and animal cells almost certainly depends on a number of reactions in the cell and upset of one or more of these reactions may produce the same results at metaphase. If the term "c-mitotic" is to be used for any spindle inhibiting substance, it can be applied to a wide variety of substances which probably act on different parts of the spindle mechanism. On the other hand, if it is to be used for true colchicine-like action, it applies only to a particular action on one part of the cell division process. It would be better to retain the term "c-mitosis" for substances which are known to have the same specific action on the spindle mechanism as has colchicine and no other activity. This view agrees with that of Frahm-Leliveld (1949), who, after testing many substances, concluded that only colchicine and acenaphthene act as polyploidogenic agents on plant cells and are the only known "c-mitotic" substances.

Levan (1938) has shown that 2% colchicine for 72 hours produced cytological abnormalities but was not toxic to the cells. With high concentrations the toxic action of the nitrophenols is clearly demonstrated by recovery experiments. Treated cells which did not recover, retained their abnormal cytological figures until all cell contents became diffuse and unstainable, indicating that vital cell processes were stopped.

Concentrations of mononitrophenols reported by Levan and Tjio (1948) to induce "c-mitosis" were 5×10^{-2} to 2×10^{-3}M for o-nitrophenol, 1×10^{-2} to 1×10^{-3}M for m-nitrophenol and 2×10^{-2} to 2×10^{-4}M for p-nitrophenol. All solutions were diluted with distilled water. These concentrations are higher than those used in our experiments where $2{\cdot}16 \times 10^{-3}$M, the highest concentration, killed in less than 24 hours. The toxic action of phenols is very much greater in distilled water than tap-water, probably due to a different pH. As no recovery experiments were cited by Levan and Tjio, it is likely that roots in which c-mitosis has been described were dead at the time of sampling.

Results of experiments with low concentrations, where longer treatment was required before the cells were killed, showed that spindle formation was ultimately suppressed. The number of anaphase and telophase stages was reduced, indicating that the cells go to apparently normal daughter cells, if the spindle is already initiated at the time of treatment. After 24 hours' treatment there were no anaphase or telophase stages, but some suppressed metaphases in which centromeres had not divided. The onset of prophase was also affected as the number of cells dividing during treatment was reduced. This suggests that there is a general slowing down of the metabolism of the cell, which may be evidence for a toxic action even at the lowest concentration.

"Stickiness" of anaphase and telophase chromosomes occurred almost at once with the high concentration, but more slowly at the low concentrations. It is induced by many phenols (Levan and Tjio, 1948). Like spindle suppression, stickiness, particularly of anaphase chromosomes, results from treatment with a wide variety of organic substances and also by cold treatment (D'Amato, 1948). There is no evidence to suggest that these treatments all have the same specific action on the chromosomes.

It seems possible that the cytological abnormalities induced by nitrophenols reflect the general toxic action of these substances on the cells. Spindle suppression, stickiness of chromosomes, and granulation and pycnosis of the resting nuclei could be a direct result of the slow death of the cell. Phenols are known to precipitate proteins and the results for nitrophenols can be explained as a slow fixation process, which first affects spindle formation and then the onset of prophase, gradually slows the whole cell division process and kills the resting nuclei.

On the other hand, the nitrophenols at low concentrations may have a specific action on the spindle mechanism not at the same point as colchicine, as well as an unrelated toxic action which kills the cells before the abnormal mitosis is complete. As no abnormalities have been seen in recovered roots, it is not known whether inhibited metaphase cells found in roots after 24 hours at low concentrations undergo centromere division before reaching the resting condition. Further work is necessary at low concentrations before this possibility can be excluded.

It seems essential to make a distinction between the specific action of a chemical on one phase of the cell division mechanism and a general action which is apparent only on cells which are dividing. Colchicine has a specific action on one stage of the cell division process, whereas nitrophenols probably induce a general toxic effect by some metabolic derangement which is visible at first only in dividing cells. Some other substances described as c-mitotic may well have this general action and the literature should be re-examined from this point of view. The action later extends to resting nuclei which are killed. It is difficult to make the distinction with this type of experiment, as the course of an abnormal mitosis cannot be followed through a complete division. It is necessary to reconstruct the process from a knowledge of the normal mitosis and observations on a series of fixed roots.

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EXPLANATION OF PLATE XIII.

Effect of 2,4-dinitrophenol on Onion root tip cells. (All photographs × *ca* 1000.)

1-3. Metaphase after treatment with 3, 30 and 300 mg/l respectively.

4-5. Anaphase showing sticky bridges after 30 and 300 mg/l respectively.

6-9. Abnormal metaphase and anaphase stages after attempted recovery in water for 24 hours following treatment with 30 and 300 mg/l.

THE LIFE-HISTORY OF A PENAEID PRAWN (*METAPENAEUS*) BREEDING IN A COASTAL LAKE (TUGGERAH, NEW SOUTH WALES).

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(Plate xii and 96 Text-figures.)

[Read 26th September, 1951.]

Synopsis.

This paper deals with the life-history of a species of Penaeid prawn (*Metapenaeus*, n. sp., Crustacea, Decapoda) and is based on a study of both living and preserved specimens. The species is unique in that the whole life-cycle from egg to breeding adult is spent in a shallow coastal lake (Tuggerah, New South Wales); in all other species whose life-histories are known, the maturing adults migrate from estuarine waters to the sea, the larvae returning to the estuaries.

Stages from egg, through nauplius, protozoea, mysis, post-mysis and post-larval to adult were obtained and the larval stages are described and figured hereunder. The life-history follows the same general lines as that described by Heldt (1938) for a Mediterranean Penaeid species.

Introduction.

This study was part of the long-range programme of plankton and general marine investigations planned by the late Professor W. J. Dakin during his term of office as Professor of Zoology at Sydney University. This particular study was begun by him in 1945 and the field work was carried out by one of us under his direction during the years 1945–47. Two short notes indicating the general findings have already been published (Dakin, 1946, 1946*a*).

Professor Dakin had completed a large number of drawings and had made rough sketches and notes of all the stages in the early life-history before illness prevented his finishing the work. It was felt that this effort should not be lost, and, as one of us (I.B.) had been responsible for all the collecting, sorting and preserving of the stages, it was a relatively easy matter to complete the work.

Historical.

The general story of the Penaeids, which are the Australian prawns of commerce, together with full details of the species concerned in the fishery, has already been told (Dakin, 1938, 1940, 1946).†

When prawn investigations were first begun in this Department, all the Penaeid species which could be obtained along the New South Wales coast were collected and sent, in 1937, to Mr. Martin D. Burkenroad, of the Bingham Oceanographic Foundation at Yale, who at that time was engaged in a systematic revision of Indo-Pacific littoral Penaeids. Burkenroad verified our identifications of *Penaeus esculentus* ('Tiger' prawn),

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† In the year 1947 a chance discovery by fishermen led to commercial fishing for prawns on a fairly large scale in open waters off the New South Wales coast. For the first time 'School' prawns, *Metapenaeus macleayi* (Haswell), with mature gonads, were found. This seemed to prove Professor Dakin's theory that this species, like *Penaeus plebejus*, also migrated from the estuaries to the open ocean to breed.

A brief survey of the American Penaeid fishery (which is of very much greater economic importance than the Australian fishery), together with details of the breeding migrations, is of interest in that it indicates a very similar story (Idyll, 1950).

Just as this paper was going to press we were shown several specimens of females of *M. macleayi* with spermatophores attached. These were taken in oceanic waters off the northern New South Wales coast in the month of February, 1951, by Mr. J. H. Wharton, Biologist, State Fisheries Department.

P. plebejus ('King' prawn) and *Metapenaeus macleayi* ('School' prawn), but in a letter dated 30/7/38, stated:

> "Your two '*Metapenaeus monoceros*' from Lake Illawarra may be of the 'Dana' species, or possibly of *M. incisipes* Bate, or of my (MS.) *M. tweedii*, or of some other form. They are certainly not *M. monoceros*—since of the eight or ten species of the group (unpublished studies) this last is the one which does not range east of India. Determination of members of this group is difficult; it depends chiefly on details of the genitalia.
>
> "When you deal with hairy prawns with numerous but minute lateral telson armature, you are on difficult ground. I am unable to say how many Metapenaeus, which usually pass under the name of *M. monoceros*, may occur in the region of Sydney, but I now have records of two species. One of these, the 'Dana' sp. n., must at some season be frequent in your commercial catch, since the sample, from Sydney market, consists entirely of it. As the specimens are large and adult, they may well have been taken at sea by the trawlers."

And later, on 18th January, 1940, Burkenroad wrote: "Your 'Greasy Backs' are the same as the 'Dana' *Metapenaeus* sp. n."

This prawn species which, because of the very thick covering of minute hairs on the carapace, was known locally to fishermen as the "Greasy Back", had always been regarded by Museum authorities and other workers in Australia as *Metapenaeus monoceros* Fabr.

We have been unable to contact Burkenroad since the end of World War II, and there is no mention of the genus *Metapenaeus* in the only published work on the 'Dana' collections we have seen (Burkenroad, 1940). In order to avoid possible duplication, we have decided to refer to the species simply as quoted above from Burkenroad's letter, "Dana" *Metapenaeus* sp. n.

After Professor Dakin had first obtained our so-called *Metapenaeus monoceros* from Lake Illawarra (see Dakin, 1938, p. 166), efforts were made over the years to procure further specimens of this species. We were successful in obtaining only a few specimens in the summer months of 1938–39 from Cook's River, Sydney. These were all sent to Burkenroad, who stated they were also the "same as my 'Dana' *Metapenaeus* sp. n.". On the outbreak of war in 1939, this work was discontinued, but in February, 1945, we discovered that these same prawns were forming the bulk of the commercial catch sent to the markets, and inquiry indicated that they were being caught in Tuggerah Lakes (three closely-connected lakes, Tuggerah, Budgewoi and Munmorah), 70 miles north of Sydney. Cooked prawns in which the gonads were fully mature were obtained from the Sydney Fish Markets. The prawns themselves were comparatively small, only 3½ to 4 inches in length.

It is characteristic of the shallow coastal lakes along the New South Wales coast to become silted up at the entrance, and, especially in dry periods, to remain closed sometimes for as long as two years. It had been hoped to make a series of observations on the various Penaeid species under these conditions, particularly in view of the known habit of the group, in other parts of the world, of migrating to open ocean waters to breed.

At this same time (early in 1945) it was learned that Tuggerah Lakes *had* been closed for a period of approximately two years, and that the 'King' and 'School' prawns, by the end of the second year (the summer season 1944–45) were scarce but very large. None, however, was observed with any gonads. But the 'Greasy Backs' which, in that particular season, were very numerous, forming the bulk of the catch, all had mature gonads. This information seemed to fit in very well with our theories regarding the three species concerned. By the time all these details were known, it was too late in the season to carry out any field work to obtain larval stages, but plans were made for an intensive effort for the next summer season (the months of November, December, 1945, and January–March, 1946).

Unfortunately heavy rains caused flooding in the lake backwaters during the autumn, and in May, 1945, the entrance to Tuggerah Lakes was cut through and the

lakes have not been completely land-locked since that date. This entirely altered the physical conditions within the lakes, but the work was carried out as planned.

Fishermen who tested the prawning grounds in the lakes stated that small prawns first began to appear in October, but these were well under regulation size (3½ inches). By November, 1945, however, intensive fishing was being carried on with three species of prawns appearing in the catches—*P. plebejus*, *Metapenaeus macleayi*, and the so-called "Greasy Back". The two former were taken together, mainly in the largest lake, Tuggerah itself, and always at night. The "Greasy Backs" were generally caught alone in both Tuggerah and Budgewoi Lakes, and had a habit of shoaling during the day.

Many bulk catches were examined from different parts of the lakes and though a very careful search was made throughout the whole period of the investigation (1945–47) we were never successful in finding either *P. plebejus* or *M. macleayi* in the lakes with any signs of developing gonads.

From November to March, however, the "Greasy Back" females were very conspicuous in all catches because the gonads showed up as a dark green band along the dorsal surface of the abdomen (Plate xii, fig. 2). Random samples of many hundred specimens were taken, and the individuals sexed and measured. It was found that the females were larger than the males—the largest female actually measured by us being 5 inches, though the greatest number averaged between 3½ and 4 inches. We found only one male as long as 4 inches, the greater proportion being about 3 inches. The females in all samples counted formed more than 50% of the total catch, but it was felt that this was probably due to the size of the mesh of net used by the fishermen.

Close examination of specimens led us to suspect that, in common with many other marine animals, spawning took place at time of full moon. Our catches later substantiated this.

Collection of Material.

Since, to our knowledge, there had been no previous plankton collections in Tuggerah Lakes, a great number of exploratory hauls had to be made, and these were carried out on all three lakes. Nets of varying degrees of coarseness were used, from the finest mesh bolting silk to nets of coarse stramine. Since overseas work had indicated (Pearson, 1939) that the eggs were probably demersal, various methods, such as the attaching of heavy iron sledges to the nets, had to be devised for taking hauls just above the bottom layer of mud. This was extremely difficult since the floor of the lakes, which was only about 8 feet deep in the deeper parts, was very uneven. On more than one occasion in heavy southerly weather, the hauls had to be abandoned and a fresh start made after the net had become clogged with mud from the bottom.

Another difficulty, accentuated by the opening of the lakes to the sea, was the seasonal influx of Coelenterates. Finally two types of cones which had the same diameter as the net and which fitted over the mouth of the net, were used. One was made of flat galvanized sheeting with small holes punched all over it, and the other of small gauge wire netting. The guy ropes of the net were threaded through a hole in the peak of the cone, the base of which was firmly laced to the ring of the net. The current set up by these cones as the nets were pulled through the water served, to a certain extent, to force the jelly fish out of the course of the net, and the holes and wire mesh permitted the net to catch smaller organisms. The method was quite successful when dealing with the large medusa, *Catostylus mosaicus*, but when the Ctenophores came into the lakes, all our efforts were practically useless. The surface waters were almost solid Ctenophora, which were so soft that the cones merely broke them and the nets became coated with a thick gelatinous slime.

A large number of hauls using the different nets were taken at close intervals throughout the summer seasons of 1945–46 and 1946–47. Throughout the winter months of 1946 regular monthly hauls were made so that some idea would be gained of the general plankton constituents throughout the whole year.

Since we are able to state with certainty that no other Penaeid prawn taken in the lakes during this time had even immature gonads, and since the bulk of our catches were taken in Budgewoi Lake, at least eight miles from the entrance, where

there is no tidal flow, we have no hesitation in regarding the eggs and nauplii as those of the breeding *Metapenaeus*.

We were successful in obtaining eggs during February and March only, but Protozoea and Mysis stages were found in all months from November to March inclusive. We cannot be certain of the full number of nauplii but the most important stages in development were verified with living material. No aquarium facilities of any kind were available to us, but by means of a temporary laboratory set up in a tent on the lake shore we were able to watch the egg developing through 2, 4, 8, and 16 cell stages, and finally photographed several in which the nauplius could be seen actively moving round within the egg membrane. The newly hatched nauplius was also photographed (Plate xii, fig. 3). What we considered to be the last nauplius (Metanauplius) stage moulted into Protozoea I. We also observed the moulting of Protozoea I into Protozoea II, Protozoea II into Protozoea III, and Protozoea III into Mysis I.* It was only after very considerable difficulty and a week's concentrated effort that Mysis III stages were obtained. It is interesting to note here that we had chosen a particular week in February to make these catches, ten to eleven days after the full moon. In that week practically no stages other than late Mysis were found in any of the catches. This substantiated the assumption that spawning takes place at the time of full moon, as the time taken for an egg to develop to a late Mysis stage is about ten days. No Mysis were found in the surface hauls and it was only when the nets were weighted and hauled just above the bottom that we were successful in finding them. Heldt (1938) found that this was also the case with her Mediterranean Penaeid species: "Dans les pêches de plancton la quatrième mysis et la première post-mysis sont très rares."

We were able to keep most of the late Mysis alive until the first post-Mysis stage, but without aquarium facilities were unable to go further. From the above, however, we were able to place with certainty all our planktonic material as belonging to the one species. A very long series of post-larval stages from $\frac{1}{4}$ inch in length and leading to the young adult, finally left us in no doubt about the identity of the species of which they were the larval stages.

Larval and Post-Larval Stages.

A series of 16 larval stages was taken in the plankton hauls. They consisted of four Nauplius stages, three Protozoea stages, three Mysis stages and six post-Mysis stages. In addition several post-larval stages were taken, four of which have been described.

The Nauplius stages taken did not constitute a complete series, and it would seem that the full series, as obtained by Heldt, numbers eight—the possible missing stages being two, three, four and six. The three Protozoea, of course, constitute the full number of Protozoea stages, while three distinct Mysis stages have been obtained. Heldt (1938) records four Mysis stages for *Penaeus trisulcatus*, while the American workers record only two for their species.

There is quite a big gap between the first post-Mysis, which was obtained by direct moulting, and the next stage taken in the plankton hauls (5·073 mm.). From the 5·073 mm. stage onwards a series of ten stages (to 23·572 mm. stage) were taken. The first five of these are probably post-Mysis stages, while the other five are post-larval. The distinction between post-Mysis and post-larval stages has been made on the purely morphological basis that the first stage bearing biramous pleopods would be the first post-larval stage. The important difference between post-Mysis and post-larval stages is that propulsion is thoracic in post-Mysis and abdominal in post-larval. The loss of feathered exopodites from the peraeopods (first post-Mysis stage) would mean a loss of effective thoracic propulsion. However, the fact that the pleopods are still ill-developed at this stage means that abdominal propulsion would be equally ineffective. In fact, abdominal propulsion would not be effective until the appearance of biramous pleopods (7·835 mm. stage), and for this reason it is felt that this stage should be

* We have followed Heldt (1938) rather than Gurney (1927 and 1942) in the terminology used for these stages.

considered as the first post-larval stage. It is realized, of course, that ever since the appearance of a well-developed tail-fan at the moult to first Mysis, flexing of the abdomen has no doubt constituted quite an effective means of propulsion. Madame Heldt (1938) referred to the role of abdominal flexion in propulsion, but without the observation of live specimens, which was not possible in this study, it would not be possible to say just how effective a means of propulsion this would be in *Metapenaeus*. Heldt (1938) made this division into post-Mysis and post-larval at an earlier stage—she named the first post-larval as the stage preceding the one where biramous pleopods appeared.

Nauplius Stages.

First Nauplius (Text-fig. 1).—Several very early stages in the development of the nauplius, all still enclosed in the egg membrane (Plate xii, fig. 3), were taken. They later emerged as the first Nauplius larva.

The first Nauplius measures 0·23 mm. from the front end to the end of the body (not including the spines). The body is somewhat pyriform in shape when viewed from the dorsal or ventral aspect, but when viewed from a lateral aspect it has a ventral flexure. At this stage the body shows no signs of segmentation.

A pair (1 + 1) of spines extend out from the posterior margin of the body.

A Nauplius eye lies on the median ventral surface of the body close to the anterior border. This eye persists through to the Protozoea stages and probably into the Mysis stages.

The three pairs of appendages present at this stage, first and second antennae and mandibles, are large unsegmented club-shaped structures with a purely natatory function.

The first antenna (Text-fig. 1) is a uniramous appendage bearing three terminal setae and also three on the inner side and one on the outer side.

The second antenna (Text-fig. 1) is a biramous appendage bearing three terminal setae on the endopodite and one short spine and two terminal setae and three lateral setae on the exopodite.

The mandible (Text-fig. 1) bears no cutting surface at this stage, but consists of a biramous appendage. The exopodite bears three terminal setae, whilst the slightly longer endopodite bears two terminal setae and one on the inner side.

Fifth Nauplius (Text-fig. 2).—The next Nauplius stage which was taken in the catches corresponds to Heldt's fifth Nauplius for *Penaeus trisulcatus*. The only differences between Heldt's fourth and fifth nauplius stages are an increase in size; the presence of seven segments in the exopodite of the second antenna of the Nauplius four and eight in Nauplius five; and the growth of the terminal spine on the endopodite of the second antenna of the fourth Nauplius into a long hair in the fifth Nauplius.

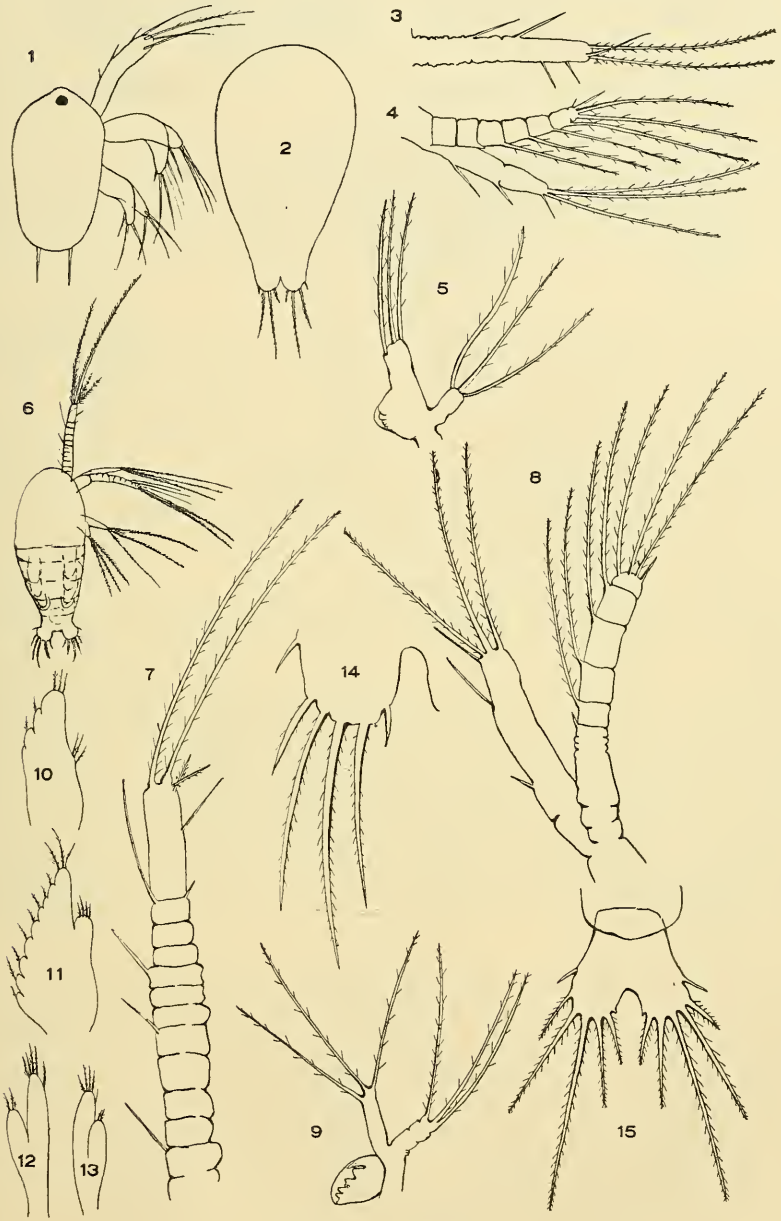
As the exopodite of the second antenna of this stage of *Metapenaeus* consists of seven and not eight segments, it would seem that it is a fourth Nauplius stage. However, the presence of three well-developed hairs and a spine on the endopodite of the second antenna identify it as a fifth Nauplius. Actually, Heldt gives the presence of three plumose hairs and a spine on the endopodite of the second antenna as one of the characteristics of the sixth Nauplius in *Penaeus trisulcatus*. However, the fact that the telson bears four pairs (4 + 4) and not six pairs (6 + 6) of spines at this stage of *Metapenaeus*, definitely classifies it as a fifth Nauplius.

The length of the body is now 0·27 mm.–0·29 mm., and the following significant changes have taken place since the first Nauplius stage.

The posterior border of the body is now quite deeply indented to form a definite furca bearing four pairs of spines. The first antenna (Text-fig. 3) is now segmented and the beginnings of a large number of segments are obvious at the base. It bears two long plumose hairs and a short spine at the end; two small hairs well towards the distal end on the outer side; two longer hairs on the inner margin—one in the middle of the distal segment, and one further down.

The exopodite of the second antenna (Text-fig. 4) now consists of seven segments—the division between the last two segments still being ill-defined. The most distal, or seventh, segment bears two long plumose hairs and a small spine at its extremity, while

the 3rd, 4th, 5th and 6th segments each bear a large plumose hair on their inner distal margins. A small spine is present on the inner distal margin of the second segment. The endopodite, which is still unsegmented, bears three long hairs and a spine at its



Text-figures 1-15.

1, First Nauplius, × 92.

2-5, Fifth Nauplius. 2, × 120; 3, First antenna, × 131; 4, Second antenna, × 66; 5, Mandible, × 164.

6-14, Seventh Nauplius. 6 × 34; 7, First antenna, × 170; 8, Second antenna, × 171; 9, Mandible, × 284; 10, First maxilla; 11, Second maxilla; 12, First maxillipede; 13, Second maxillipede; 14, Furca, × 462.

15, Eighth Nauplius, Furca.

distal end; a shorter hair two-thirds of the way down and one one-third of the way down on the inner margin.

There is now a very definite swelling at the base of the endopodite of the mandible (Text-fig. 5) which will eventually give rise to the cutting surface of the future mandible. The outlines of teeth can already be seen through the chitin on the inner side of this swelling. The exopodite and endopodite still bear the same number of hairs as at the first naupliar stage.

The maxillae and first and second maxillipedes are now visible under the cuticle on the ventral side.

Seventh Nauplius (Text-fig. 6).—The next stage in the series which was taken corresponds to Heldt's stage seven for *Penaeus trisulcatus*. The presence of six pairs (6 + 6) of spines on the furca marks it as either a sixth or seventh Nauplius stage, but the facts that the posterior border of the carapace is beginning to appear, and that the maxillae and first and second maxillipedes are now free, identify it as a typical stage seven.

The body now measures 0·671 mm.

The number of segments in the first antenna (Text-fig. 7) has increased, an additional small spine has developed on the distal outer corner of the most distal segment, and an additional two have appeared on the inner side of the appendage.

Signs of further segmentation of the exopodite of the second antenna (Text-fig. 8) are evident; a third hair has appeared, while the small spine, which was present at the fifth Nauplius stage, has now developed into a small hair. The most distal segment of the exopodite thus bears the full complement of four hairs—or what will be four hairs—found in the Protozoea stages. The endopodite remains unchanged.

The swelling on the base of the mandible (Text-fig. 9) has increased in size, and the cutting surface is now clearly visible under the cuticle.

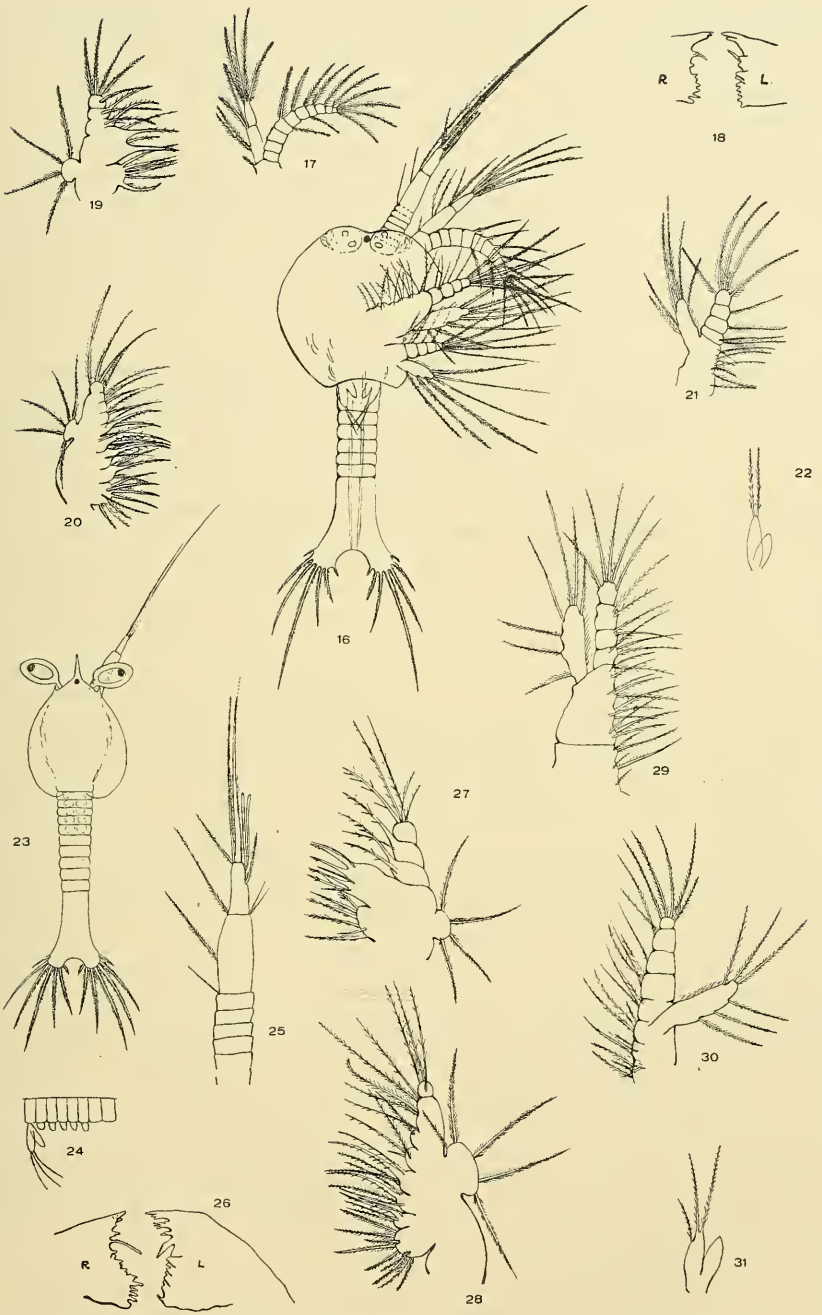
Eighth Nauplius.—One later Nauplius stage, with seven pairs (7 + 7) of the spines on the furca, was taken. Only one specimen was available for study and only the telson was drawn.

As the telson (Text-fig. 15) bears seven pairs of spines, it undoubtedly is a very late Nauplius stage. The degree of development of the maxillae and first and second maxillipedes at our seventh Nauplius makes it highly unlikely that there would be more than one Nauplius stage between Nauplius seven and the first Protozoea stage. It seems evident, then, that the telson figured belongs to the eighth Nauplius stage. Only two specimens of very late nauplii were found by us in the plankton catches. One, of which the telson is figured, was preserved, and the other which, so far as we could judge from low-power magnification of a living specimen in the field, was identical with it, moulted to the first Protozoea.

Protozoea Stages.

The last Nauplius stage is followed by the Protozoea stages. As Heldt (1938) has dealt very fully with the change in habits that accompany the change from the last Nauplius to the first Protozoea, it is not intended to cover this ground again. However, two factors which influence the future development of certain appendages of the Protozoea stages should be mentioned. These are, firstly that the larva now feeds and there is a great development of the maxillae and the cutting surface of the mandible; secondly, that certain of the thoracic appendages, the maxillipedes, now aid the first and second antennae in propulsion. Up till the end of the sixth Nauplius stage the maxillae and first and second maxillipedes are not free. By the end of the seventh Nauplius stage they are free but still poorly developed. However, during the Protozoea stages they increase greatly in size, acquire quite extensive feathered surfaces and are thus able to aid the first and second antennae in propulsion.

First Protozoea (Text-fig. 16).—The larva now measures from 0·781 to 0·872 mm. in length. All the larval stages show quite a considerable variation in length. (All lengths are from the base of the rostrum to the end of the telson—not including the rostrum or telson spines.)



Text-figures 16-31.

16-22, First Protozoea. 16, × 54; 17, Second antenna, × 68; 18, Mandible, × 67; 19, First maxilla, × 130; 20, Second maxilla, × 123; 21, Second maxillipede, × 91; 22, Third maxillipede, × 148.

23-31, Second Protozoea. 23, × 31; 24, Lateral aspect of abdomen; 25, First antenna, × 115; 26, Mandible, × 167; 27, First maxilla, × 160; 28, Second maxilla, × 164; 29, First maxillipede, × 126; 30, Second maxillipede, × 130; 31, Third maxillipede, × 135.

The shape of the body has changed considerably. It now consists of an enlarged oval anterior section, making up a little less than one-half the total body-length, and a long cylindrical hind portion, the abdomen. The abdomen, which is still unsegmented, ends in the now widely-forked telson, which still bears seven pairs (7 + 7) of spines. The fourth, or middle pair of spines is the largest, and remains so right up to the post-larval stages.

The Nauplius eye is still present. The paired adult eyes are visible as two opaque masses situated just beneath the carapace at the anterior margin of the body.

The first antenna (Text-fig. 16) consists of a basal five-segmented portion and two long distal segments. There are two large and one small terminal setae; two near the end on the outer side; and one on the inner side at the junction of the two large segments; one half-way down the second segment; and one on the most distal of the five basal segments.

The exopodite of the second antenna (Text-fig. 17) now consists of ten segments, while the endopodite has two segments. The last or most distal exopodite segment now bears four long terminal hairs—the small hair of the Nauplius seven stage having developed into a long plumose hair. The 4th, 5th, 6th, 7th, 8th and 9th segments each bear a hair on their internal borders, while the 4th and 6th segments each bear an external hair. The endopodite now bears five terminal hairs; and on the inner margin two at the junction of the two segments and two half-way down the first segment.

The mandible (Text-fig. 18) has now lost its biramous appearance, while the cutting surface, consisting of two distinct regions, is well developed. The right and left mandibles are quite similar at this stage, each having a long, pointed tooth and a short thick-set tooth separating the lower molar region of the mandible from the upper cutting region.

The first maxilla (Text-fig. 19) is a biramous appendage with a three-segmented endopodite and an unsegmented button-like exopodite. The two protopodite segments form two quite well-defined endites on their inner surface. The most proximal, or first, endopodite segment bears two hairs, the second two, while the terminal segment carries five. The exopodite carries four long plumose hairs, while the proximal endite carries six and the distal endite four rather short hairs.

The second maxilla (Text-fig. 20) is also a biramous appendage, the endopodite being five-segmented, while the exopodite again forms a button-like unsegmented structure. The first or most proximal endopodite segment carries three setae, the second two, the third two, the fourth two and the fifth three setae. The exopodite carries five long plumose hairs. The protopodite forms four endites on its inner surface carrying eight, four, four and three setae numbering from the most proximal endite.

The first maxillipede (Text-fig. 16) consists of a four-segmented endopodite and an unsegmented blade-like exopodite. The endopodite carries three setae on the first segment, one on the second, one on the third, and five terminal setae. The exopodite carries two terminal setae and also one internal and four external. The protopodite carries a large number of hairs on its inner surface.

The second maxillipede (Text-fig. 21) closely resembles the first maxillipede at this stage, except that it is smaller. The endopodite is four-segmented, while the exopodite is once again an unsegmented blade-like structure bearing two terminal setae and also one internal and three external setae. The endopodite carries two setae on the first segment, one on the second, one on the third, and five terminal setae. Once again, the protopodite is thickly beset with hairs on its inner surface.

Both Heldt and Pearson found for their respective species of *Penaeus* that the third maxillipede was not present in Protozoea I, but in our species it has definitely made its appearance and is an unsegmented biramous appendage at this stage (Text-fig. 22). It carries two terminal setae on the exopodite.

Behind the third maxillipede, there are five distinct thoracic segments already formed, which, in the second Protozoea stage, will carry the buds of the peraeopods.

Second Protozoea (Text-fig. 23).—The larva now measures from 1·0 mm. to 1.36 mm. in length.

The body still consists of the large anterior portion covered by the carapace, and a long cylindrical posterior portion. The carapace, which is lengthening rapidly and is now pear-shaped, still reaches only to the end of the ninth (third maxillipede) body segment. It is becoming more deeply indented posteriorly.

Anteriorly, the carapace now bears a rostrum and two supra-orbital spines, one on each side of the rostrum. The eyes at this stage are large and stalked and project well beyond the anterior corners of the carapace. The Nauplius eye still persists.

The six abdominal segments are now clearly visible, although the sixth is still not separated from the telson. The seven pairs of spines on the telson have increased considerably in size.

Apart from the acquisition of one seta half-way down on the outer side and a pair of hairs on the outer distal corner of the large second segment, the first antenna has undergone no change (Text-fig. 25). The second antenna has undergone no change at all.

The cutting surfaces of the mandibles (Text-fig. 26) display a definite dissimilarity between the right and left—the greater change having taken place in the left mandible.

The first maxilla (Text-fig. 27) carries an additional two to three setae on the distal endite, while the first or proximal endite and the fourth endite of the protopodite of the second maxilla (Text-fig. 28) each bear an additional seta.

The first maxillipede (Text-fig. 29) bears an additional seta on the inner surface of the second and third endopodite segments and a few extra setae on the proximal protopodite segment.

The second maxillipede (Text-fig. 30) which shows indications of a fifth endopodite segment, the first being very indistinctly divided from the protopodites, bears an extra seta on all the endopodite segments except the third.

The exopodites of the third maxillipede (Text-fig. 31) now bear three setae, two terminal and one on the outer edge.

Behind the third maxillipede the five thoracic segments, formed in the first Protozoea stage, now carry the buds of five pairs of peraeopods (Text-fig. 24).

Third Protozoea (Text-fig. 32).—The larva now measures from 1.53 mm. to 1.73 mm. in length, the greatest increase having taken place in the hind thoracic and abdominal regions.

The carapace, which still reaches only to the end of the ninth body segment, is now quite deeply indented at the posterior end. The supra-orbital spines, which are already decreasing in size, are now situated quite close together at the base of the rostrum.

The Nauplius eye persists.

The sixth abdominal segment, which is now completely separate from the telson, is by far the longest of the abdominal segments. The third, fourth and fifth abdominal segments each bear a median dorsal spine on their posterior borders; the fifth carries an additional dorso-lateral spine on each side. The sixth abdominal segment carries a minute pair of dorso-lateral and also a pair of ventro-lateral spines (Text-fig. 33). There are still no signs of abdominal pleopods.

The uropods are now completely free—the exopodite bearing six and the endopodite three setae. The telson still bears seven pairs of spines.

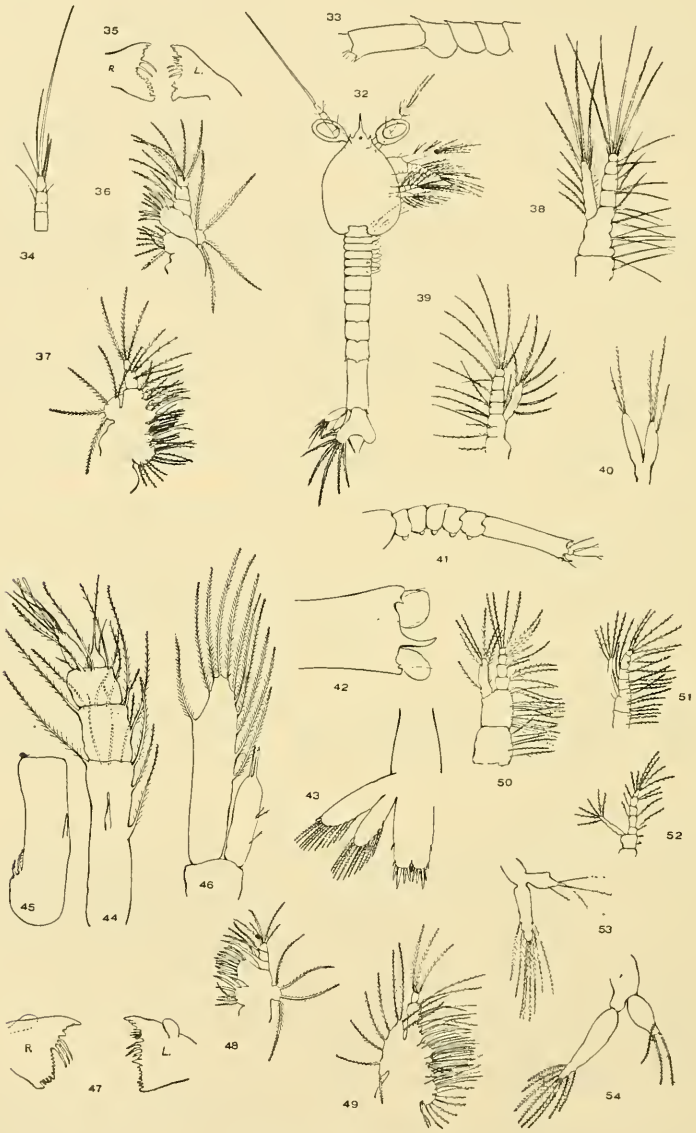
The first antenna (Text-fig. 34) now consists of four segments instead of the seven of the previous stage. This tendency towards a loss of flexibility of the first antenna is very important as it serves as a pointer to the fact that in the Mysis stages the first antennae will no longer be responsible for propulsion. The arrangement of setae has undergone no change since the previous stage.

The second antenna remains unchanged.

The dissimilarity between the right and left mandibles (Text-fig. 35) is now more evident. The right mandible bears two dentated spines between the molar and cutting regions, while on the left mandible, this intermediate region which was showing signs of forming spines in the previous stage, now bears seven spines, three of which are

dentated. The molar regions in both right and left mandibles have increased considerably in size.

Apart from the fact that the distal endite of the first maxilla (Text-fig. 36) now bears nine setae, the proximal endite eight, and the protopodite of the second maxilla (Text-fig. 37) now bears more hairs, the first and second maxillae have undergone no change since the previous stage.



Text-figures 32-54.

32-40, Third Protozoea. 32, × 24; 33, Lateral aspect of abdomen; 34, First antenna; 35, Mandible, × 82; 36, First maxilla, × 86; 37, Second maxilla, × 86; 38, First maxillipede, × 65; 39, Second maxillipede, × 54; 40, Third maxillipede, × 59.

41-54, First Mysis. 41, Lateral aspect of abdomen; 42, Ventro-lateral aspect of 6th abdominal segment; 43, Telson and uropods; 44, First antenna, × 88; 45, Lateral aspect of basal segment of first antenna; 46, Second antenna, × 54; 47, Mandible, × 103; 48, First maxilla, × 83; 49, Second maxilla, × 103; 50, First maxillipede, × 62; 51, Second maxillipede, × 49; 52, Third maxillipede, × 65; 53, First peraeopod, × 51; 54, Fourth peraeopod, × 76.

The first maxillipede (Text-fig. 38) bears two extra setae on the exopodite—one on the outer border and one on the inner border, and there are one or two additional hairs at the base of the proximal protopodite segment.

The exopodite of the second maxillipede (Text-fig. 39) bears an additional seta on the outer border and there is also one on the outer edge of the endopodite.

The endopodite of the third maxillipede (Text-fig. 40) now bears two terminal setae, while the exopodite still bears three setae.

The five thoracic segments behind the third maxillipede now bear quite well-developed biramous appendages which still show no signs of segmentation or setation (Text-fig. 32).

Mysis Stages.

A. First Mysis (Text-figs. 41–54).

B. Second Mysis (Text-figs. 55–57).

C. Third Mysis (early stages, Text-figs. 58–62; late stages, Text-figs. 63–67).

With the moult from the third Protozoea to first Mysis stage, the larva undergoes several quite radical changes.

Undoubtedly the most important development, and one which changes the whole appearance of the larva, is the growth of the peraeopods.

At the end of the third Protozoea stage they are biramous, unsegmented buds, but by the first Mysis stage they are quite distinct biramous appendages showing signs of segmentation, and bearing several setae. Up till the end of the third Protozoea stage, the antennae and maxillipedes are responsible for the propulsion of the larva through the water. However, at the moult to the first Mysis stage, the first antennae lose their feathery and flexible appearance, and propulsion is taken over by the peraeopods, aided to a small degree by the rapid jerking of the abdomen and tail fan.

A. *First Mysis* (Text-figs. 41–54).

The larva now measures 2·07 mm. in length.

The carapace reaches to the end of the fourteenth body segment (i.e., to the end of the fifth peraeopod segment). The supra-orbital spines have practically disappeared.

The third, fourth and fifth abdominal segments (Text-fig. 41) no longer bear dorsal spines and the fifth segment has also lost its dorso-lateral spines. The sixth abdominal segment now bears a median dorsal spine; one pair of ventro-lateral spines and a well-developed ventral hook (Text-fig. 42).

The telson and uropods (Text-fig. 43) now form a well-developed swimming tail-fan, and the prominent indentation of the posterior border of the telson, which was so characteristic of the Protozoea stages, has completely gone. It is replaced by a very small indentation, the two lobes diverging only slightly. Each lobe still bears seven pairs (7 + 7) of spines, the outer two pairs now being placed further up the sides of the telson.

The exopodites of the uropods now bear a spine on the external border near the extremity in addition to eleven feathered setae along the internal border and tip. The endopodites bear ten setae.

The first antenna (Text-fig. 44–45) still consists of four segments, but now bears an internal unsegmented branch attached to the extremity of the third segment. This internal branch, which is about one-third of the length of the outer or fourth segment, bears two terminal setae. At the base of the basal segment, on the outer side, is a swelling with a squared distal corner. This swelling will eventually lodge the statocyst, while the squaring of the corner will give rise to the stylocerite. There are two feathered setae on top of the swelling. The basal segment also bears a well-developed spine on the ventral face towards the inner border.

The second antenna (Text-fig. 46) has undergone quite a radical change. The exopodite has lost all signs of segmentation, and now consists of a plate-like structure with eleven hairs along its borders—six internal, three terminal, and two external. The endopodite remains unsegmented and only bears five setae—two terminal and three on the internal border.

The mandibles (Text-fig. 47) which have undergone very little change since the previous stage and still show a very marked dissimilarity, now bear a small bud which will eventually give rise to the mandibular palp.

Apart from the possible loss of one seta from the proximal endite, the first maxilla (Text-fig. 48) has undergone no change.

The exopodite of the second maxilla (Text-fig. 49) has increased greatly in size and is now beginning to take on the shape of the scaphognathite which it will eventually form. It bears nine setae along its border, whilst the number of setae on the internal borders of the protopodite has also increased.

The first maxillipede (Text-fig. 50) has undergone little change except that the number of setae on the exopodite has decreased to seven again, while the number on the protopodite segments has increased.

Much the same type of development has taken place in the second maxillipede (Text-fig. 51). The number of setae on the exopodite has decreased to five, while the number on the protopodite segments has increased. Three of the endopodite segments now bear a seta on the outer edge.

The third maxillipede (Text-fig. 52) which was rudimentary at the last Protozoea stage, has undergone a marked development. The endopodite is five-segmented and carries a number of hairs on its internal and external borders and at the extremity, while the exopodite, which is not segmented, bears six hairs at its extremity.

It is in the peraeopods (Text-figs. 53 and 54) that the most important change has taken place. In the third Protozoea they were rudimentary, biramous buds, but they now consist of a large unsegmented exopodite with eight terminal hairs, and a small unsegmented endopodite. The endopodite, which bears three to four hairs at the end, shows signs in the first three pairs, of bifurcation. This will eventually lead to the formation of the typical chelate appendages seen in the adult.

Slight swellings on the ventral surface of the abdominal segments (Text-fig. 41) indicate the future position of the five pairs of pleopods.

B. *Second Mysis* (Text-figs. 55–57).

The second Mysis measures from 2·14 mm. to 2·26 mm. in length.

The supra-orbital spines have disappeared from the carapace but the abdominal spines remain unchanged.

The slit between the two lobes of the telson is becoming smaller, while the space between the first and second and second and third spines is increasing (Text-fig. 56).

The exopodite of the uropods now bears twelve setae along the internal border and at the tip in addition to the spine on the external border. The endopodite still bears ten setae (Text-fig. 56).

The stylocerite on the basal segment of the first antenna (Text-fig. 57) is becoming more evident, while the ventral spine is still very obvious. The number of setae on the various segments has increased, while the internal branch has increased quite considerably in size and now makes up more than one-third of the length of the fourth or external antennular segment.

A spine has appeared on the external border of the exopodite of the second antenna a quarter of its length from the extremity. The endopodite is still one-half of the length of the exopodite.

The only change which has taken place in the mandible is an increase in relative size of the palp.

The first maxilla has undergone no change, except that, throughout all the Mysis stages, the endopodite is gradually decreasing in size.

The scaphognathite of the second maxilla has increased in size and now carries twelve hairs along its borders.

The first, second and third maxillipedes have undergone no change.

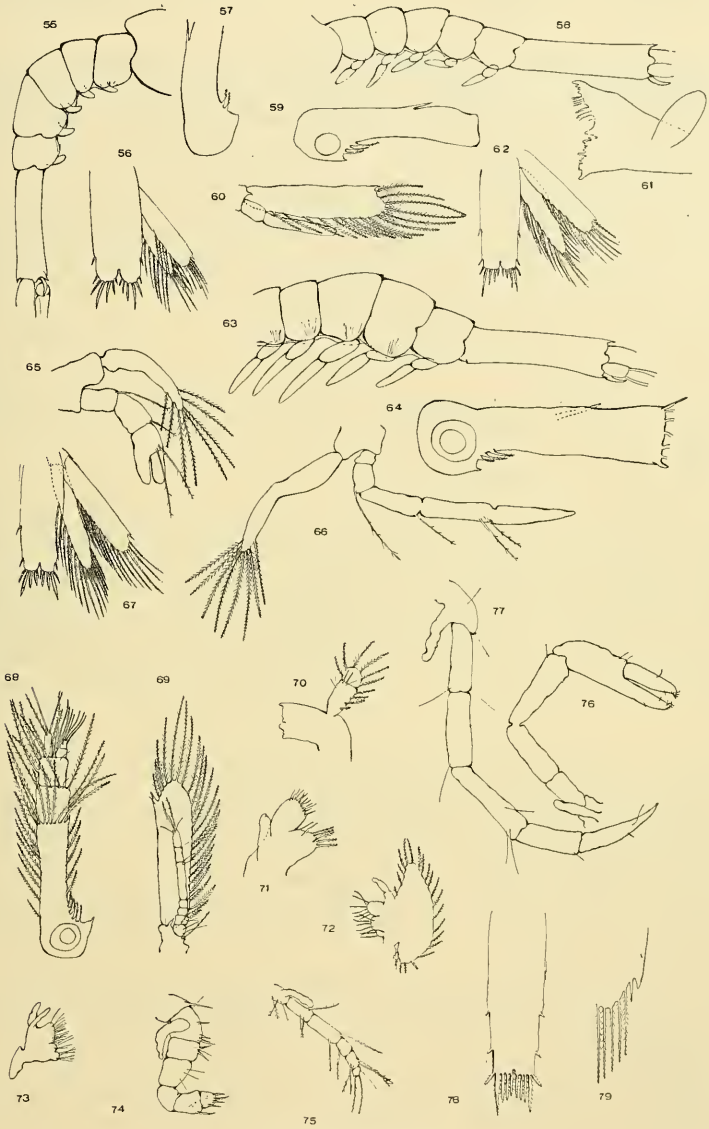
The endopodites of the peraeopods have increased considerably in length and show signs of segmentation into five segments.

The pleopod buds have increased in size and now are clearly visible on the ventral side of the abdomen (Text-fig. 55).

C. *Third Mysis* (*Early Stages*: Text-figs. 58–62).

The third Mysis measures from 2·41 mm. to 2·75 mm. in length.

The carapace remains practically unchanged, and there are indications of two minute rostral teeth.



Text-figures 55-79.

55-57, Second Mysis. 55, Lateral aspect of abdomen; 56, Telson and uropods, × 44; 57, Basal segment of first antenna.

58-67, Third Mysis. 58, Lateral aspect of abdomen (early stage); 59, Basal segment of first antenna (early stage); 60, Second antenna, × 40; 61, Mandible; 62, Telson and uropods, × 45 (early stage); 63, Lateral aspect of abdomen (late stage); 64, Basal segment of first antenna (late stage); 65, First peraeopod, × 98; 66, Fourth peraeopod, × 98; 67, Telson and uropods (late stage).

68-79, First post-Mysis. 68, First antenna, × 80; 69, Second antenna, × 44; 70, Mandible, × 15; 71, First maxilla, × 23; 72, Second maxilla, × 28; 73, First maxillipede, × 24; 74, Second maxillipede, × 60; 75, Third maxillipede, × 41; 76, First peraeopod; 77, Fourth peraeopod; 78, Telson, × 68; 79, Distal outer corner of exopodite of uropod.

The abdominal spines remain unchanged.

The indentation between the lobes of the telson is no longer conspicuous while the same increase in the distance between the lateral telson spines continues (Text-fig. 62).

The spine on the distal outer corner of the exopodite of the uropods is becoming larger, and while the exopodite still bears twelve setae, the endopodite now bears fourteen.

The stylocerite of the first antenna (Text-fig. 59) is now very clearly formed, while the basal swelling itself now lodges the statocyst. There are three hairs on the top of the statocyst swelling and the ventral spine is still well developed. The internal branch has increased quite considerably in size, is still smaller than the fourth antennular segment, and is still unsegmented.

The number of setae on the exopodite of the second antenna (Text-fig. 60) has increased to fifteen, while the endopodite is now completely devoid of setae. The latter now consists of two segments, a long distal segment which will ultimately give rise to the typical "feeler" of the adult, and a small basal segment. A spine has appeared on the ventral aspect of the distal protopodite segment.

The mandibular palp is larger but still unsegmented and does not bear any setae (Text-fig. 61).

While the exopodite has disappeared from the first maxilla, the exopodite of the second maxilla has continued to increase in importance and now bears twelve to thirteen hairs.

The first, second and third maxillipedes have undergone no change. The endopodites of the peraeopods are now definitely longer than the exopodites and clearly four-segmented. The bifidity of the endopodites of peraeopods one, two and three, which was evident in Mysis I and II, has now given rise to definitely chelate appendages, while the endopodites of peraeopods four and five are long, flexible, non-chelate structures. The exopodites on all five pairs of peraeopods still carry eight terminal setae.

The pleopods (Text-fig. 58) now show a definite division into a basal portion (the protopodite) and an unsegmented distal portion (the exopodite). They are still uniramous.

Late Stages of Third Mysis (Text-figs. 63–67).

In these later stages the two rostral teeth are now quite distinct.

The indentation between the lobes of the telson (Text-fig. 67) is now very small, while the first spine is placed almost half-way up the side of the telson. The protopodite of the uropods now bears a spine.

Another spine has appeared beside the spine described previously as being present on the exopodite of the uropods. The exopodite now bears thirteen hairs, while the endopodite still bears fourteen.

There are still three hairs on the top of the statocyst swelling of the first antenna (Text-fig. 64) and the internal branch, which is slightly smaller than the fourth segment, is not segmented. The fourth segment, however, is showing signs of division into two segments.

The number of setae on the exopodite of the second antenna has increased, while the endopodite has continued to increase rapidly in size, although it is still not as long as the exopodite.

The mandibular palp is now quite large but bears no setae nor shows signs of segmentation. The cutting surface of the mandible remains unchanged.

The only change in the first maxilla is an increase in the number of setae on the proximal endite, while the exopodite of the second maxilla still bears twelve–thirteen hairs.

The first, second and third maxillipedes remain unchanged except for the acquisition of an additional seta on the distal protopodite segment of the second maxillipede at the point between articulation of the exopodite and the endopodite.

The peraeopods have undergone no important changes. The endopodites have continued to increase in importance, but the exopodites are still quite well developed and still bear the eight terminal setae (Text-figs. 65 and 66).

The pleopods (Text-fig. 63) have increased considerably in size, but are still uniramous and bear no setae.

Post-Mysis Stages.

Heldt (1938) has dealt very fully with the development of the post-Mysis stages of several Penaeid species, and has classified the post-Mysis appendage development into four different types.

As there is a gap between the first and the five much later post-Mysis stages which were taken by us in the course of this survey, it was not possible to follow in detail all changes in the post-Mysis series of stages. However, reference will be made to these trends throughout the description of the first post-Mysis stages. Since we obtained the first post-Mysis larva by moult from the last Mysis, we had no doubts about this stage.

The larva reared from Mysis III measured 2·83 mm.

The rostrum still bears only two rostral teeth.

The posterior border of the telson is now completely straight, and the indentation between the two lobes almost gone. The first and second spines are gradually moving up the lateral border of the telson (Text-fig. 78).

The small spine which appeared on the external border of the exopodite of the uropods at the previous stage, has increased in size, whilst the other exopodite spine has also increased in size and is now almost as long as a very small seta (Text-fig. 79).

There are now five hairs on the top of the statocyst swelling of the first antenna (Text-fig. 68). The internal branch is longer than the fourth antennular segment, but it is still unsegmented. The outer branch (or fourth segment) is now clearly two-segmented and there has been quite a noticeable increase in the number of hairs on all the antennular segments. The ventral spine is still present.

The exopodite of the second antenna (Text-fig. 69) bears twenty-three setae, while the endopodite is now five- to six-segmented.

The mandibular palp (Text-fig. 70) is quite a large structure, bearing six hairs on the distal segment, and four hairs on the proximal segment. The number of hairs goes on increasing, and the distal segment continues to increase in relative importance in succeeding stages. The cutting surface has now lost practically all its teeth.

In the first maxilla (Text-fig. 71) the endopodite is very much reduced, while the endites have increased considerably in size and now bear a larger number of hairs, all of which seem to be shorter and thicker than in the previous stages. The endopodite never completely disappears and at a later stage grows into a long, thin, segmented structure such as Heldt describes for her species.

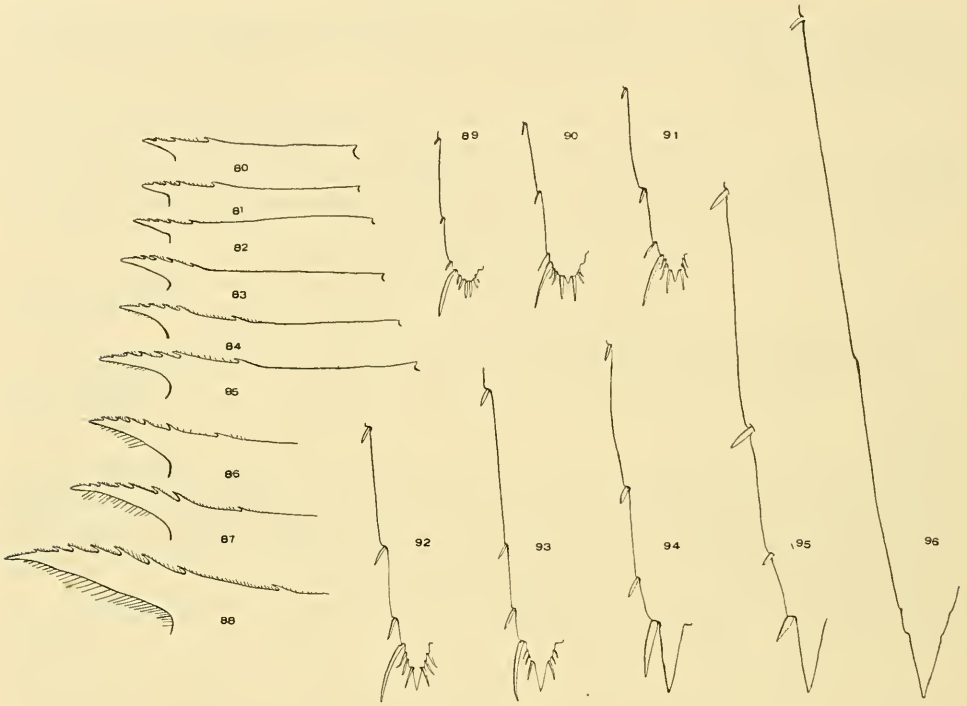
The endopodite of the second maxilla (Text-fig. 72) is reduced, but grows again, and in a 9 mm. post-larval stage is just as Heldt has indicated for *Penaeus trisulcatus*. The most proximal protopodite endite has disappeared completely, while the second one remains as a very small endite bearing a very few hairs. The two most distal endites are quite well developed. The exopodite has expanded quite considerably, and is gradually forming the scaphognathite. It now bears twenty-two setae along its border.

The endopodite of the first maxillipede (Text-fig. 73) has lost all signs of segmentation, while the hairs on this and the exopodite have gone also. The two protopodite segments have increased considerably in size and have acquired several more hairs on their inner borders. The endopodite, like that of the first maxilla, should regain its hairs and segments at a later stage.

The exopodites of the second (Text-fig. 74) and third (Text-fig. 75) maxillipedes remain as small withered chitinous structures, while the endopodites are quite powerful five-segmented appendages. The endopodite of maxillipede two is flexed backwards between its third and fourth segments. In the later stages the exopodites gradually develop again like the endopodites of the maxilla.

The exopodites of the five pairs of peraeopods have now almost disappeared and consist of small withered chitinous structures. They reappear at a later stage, but never develop to the extent that the exopodites of the second and third maxillipedes do.

The endopodites of the first, second and third peraeopods have developed into quite large and powerful chelate appendages, while the fourth and fifth still form rather longer, thinner, five-segmented non-chelate appendages.



Text-figures 80-96.

80-88. Rostrum. 80, 5·07 mm. stage, × 52; 81, 4·95 mm. stage, × 52; 82, 5·95 mm. stage, × 52; 83, 6·29 mm. stage, × 52; 84, 7·42 mm. stage × 52; 85, 7·84 mm. stage, × 52; 86, 9·28 mm. stage, × 52; 87, 11·34 mm. stage, × 52; 88, 16·67 mm. stage, × 52.

89-96. Telson. 89, 5·07 mm. stage, × 73; 90, 4·95 mm. stage, × 73; 91, 6·29 mm. stage, × 73; 92, 7·84 mm. stage, × 73; 93, 9·28 mm. stage, × 73; 94, 11·34 mm. stage, × 73; 95, 16·67 mm. stage, × 73; 96, 23·57 mm. stage, × 73.

The pleopods have increased in size though they are still uniramous appendages, but they now bear setae.

As Heldt (1938) has dealt very fully with the subsequent post-Mysis and post-larval development of several penaeid species, it was considered pointless to describe the further development of the individual appendages in detail, and so it was decided merely to follow the further development of the telson and see how this fitted in with the acquisition of the adult number of rostral teeth.

As mentioned above, there is quite a big gap in the post-Mysis series between the first post-Mysis and the next stage (5·07 mm.) obtained in the catches, but even so the number of rostral teeth in the latter has only increased to three (Text-fig. 80) and the posterior border of the telson is only slightly rounded. The fourth pair of telson spines have reached their greatest length at this stage (Text-fig. 89).

The faint beginnings of a fourth rostral tooth can be seen in a specimen 4·95 mm. in length (Text-fig. 81). The posterior border of the telson (Text-fig. 90) is showing signs of becoming pointed, while the fourth pair of telson spines is definitely becoming shorter. There are clearly four rostral teeth present at the 5·98 mm. stage (Text-fig. 82)

while by the time the 6·29 mm. length is reached, a trace of a fifth rostral tooth is evident (Text-fig. 83); also, the telson can be seen to have become distinctly more pointed, while the fourth pair of spines have shortened considerably (Text-fig. 91). At the 7·42 mm. stage, the fifth rostral tooth is clearly formed (Text-fig. 84).

Post-Larval Stages.

As previously mentioned, the next stage obtained (7·84 mm.) really constitutes the first post-larval stage taken, as it is in this stage that the pleopods become biramous. A sixth rostral tooth (Text-fig. 85) is just beginning at this stage, while the posterior border of the telson has continued to lengthen and the fourth pair of spines is shorter (Text-fig. 92).

By the time the 9·28 mm. length is reached, the sixth rostral tooth is well-formed (Text-fig. 86) while the telson is showing definite signs of approaching the adult form of a long, pointed structure with no spines. The posterior border is distinctly pointed, while the fourth pair of spines only just projects beyond the pointed posterior border. The last three pairs of spines have also shortened considerably (Text-fig. 93).

At the seven rostral teeth stage (11·34 mm.) the fourth pair of spines is shorter than the pointed posterior border of the telson, and the three small spines on the telson tip have gone altogether (Text-fig. 94).

The full adult number of eight rostral teeth are present at the 16·67 mm. length (Text-fig. 88), while the remaining pairs of telson spines have shortened considerably (Text-fig. 95). By the time the 23·57 mm. length is reached, only the most proximal pair of spines (i.e., the first) remain on the telson (Text-fig. 96). This last pair of spines disappears after the next one or two moults, thus giving rise to the adult telson which bears no large lateral spines at all.

For purposes of clarity, no reference has been made to the increase in the number of setae on the dorsal surface of the telson throughout the post-Mysis and post-larval stages. There are one or two long setae present on the dorsal surface of the telson near the posterior border in the first post-Mysis stage, and these increase in number, until finally, at the 23·57 mm. stage, the telson is thickly beset with setae along its edges, on the dorsal surface—from the tip to the base. In addition, several minute spines appear on the dorsal surface, but their development is entirely separate from, and must not be confused with the gradual loss of the seven pairs of spines which were present on the telson borders right from the last Nauplius stage.

Acknowledgements.

The field work in connection with this study was carried out with the aid of a Commonwealth Research Grant to the late Professor W. J. Dakin.

We are very deeply indebted to Mr. and Mrs. K. H. Hargraves of Toukley, Tuggerah Lakes. Without their generosity with their boats and gear and their personal help at all hours, day and night, in all weathers, we should never have achieved any success in the field. They allowed us to turn their home into a temporary laboratory and made us always welcome.

We should also like to thank Mr. Hilton Chalmers, who took plankton catches for us periodically at the Entrance; Miss E. C. Pope, M.Sc., of the Australian Museum, for help in the field; Miss H. Newton Turner, B.Arch., Biometrician of the C.S.I.R.O. McMaster Laboratory, for checking our sampling results; Professor E. A. Briggs, D.Sc., and Mr. A. N. Colefax, B.Sc., of the Zoology Department of the University of Sydney, for reading the manuscript, and finally Professor P. D. F. Murray, D.Sc., Challis Professor of Zoology in the University of Sydney, for his advice and forbearance during the writing-up of this paper.

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EXPLANATION OF PLATE XII.

Fig. 1.—Head of a mature female "Greasy Back" showing rostrum.

Fig. 2.—Adult female dissected to show gonads.

Fig. 3.—Eggs with Nauplii showing through egg membrane and one hatched nauplius.

(Photos. Gwen Burns.)

THE USE OF EXCISED SHOOTS IN LINSEED INVESTIGATIONS.

By H. B. Kerr,
Thomas Lawrance Pawlett Scholar, Faculty of Agriculture, University of Sydney.

(Plate xiv.)

[Read 28th November, 1951.]

Synopsis.

Investigations dealing with physiologic specialization in *Melampsora lini* (Pers.) Lév. and the genetics of resistance in crosses between varieties of *Linum usitatissimum* L. have been in progress at Sydney University since 1940. Techniques used by other workers were found to have certain disadvantages. The excised shoot technique has recently been developed to overcome these problems. It involves the excision of shoots above the cotyledons, and subsequent growth in tap water or nutrient solution. The advantages of the method are discussed and further developments indicated.

Introduction.

During 1948 investigations were commenced at Sydney University with particular reference to the inheritance of resistance to *Melampsora lini* (Pers.) Lév. The techniques adopted were those used by previous investigators (Waterhouse and Watson, 1941, 1943; Baker, 1945; Charles, 1947) at Sydney University, and patterned on U.S.A. work (Flor, 1947). Flor, of U.S.A., in his genetical investigations grew and tested his material in four and a half inch pots. He used the tip inoculation method, removing infected leaves as soon as the reactions became distinct and inoculating the same plants with new races of rust at 7–8-day intervals. Here this method was soon found to have distinct limitations.

It was frequently necessary to allow infected leaves to remain on the plant for some time after sporulation in order to distinguish between susceptible and certain mesothetic reactions. Spores liberated at this time were a serious source of contamination because these plants usually had to be inoculated with other races of rust. The most susceptible segregates usually had to be removed. Others, greatly weakened by the rust attack, often succumbed to root rot or a later rust infection. Even when infected leaves were removed, it was impossible to control the rust spread to the cotyledons and stem. In order to reduce contamination the infected shoot was cut back and fresh growth from the base inoculated with the second race. This control measure was only moderately successful, since prolonged growth of the plants in the glass house and successive rust inoculations made the plants particularly liable to root rot.

Development of the Excised Shoot Technique.

During 1948 it was noticed that linseed seedling tips, cut or broken off and left lying on a free water surface, continued to grow and soon developed a strong root system. Shoots of several varieties placed in tap water gave normal reactions when inoculated with different races of rust. Arnon's nutrient solution (Arnon, 1938) was subsequently used and a more vigorous growth obtained. The value of these observations was apparent, and after preliminary trials a new technique for linseed investigations has been developed.

Equipment and Method.

The equipment consists of a Pyrex dish approximately 12″ × 8″ × 2″ of about two litres capacity. Fitting into this is an aluminium grid made of two sheets clamped about half an inch apart. The bottom sheet, of slightly smaller dimensions than the dish, fits into it and is suspended in position by the top sheet, which slightly overlaps the edge of the dish. One hundred and forty ¼″ holes arranged in 14 rows of 10 holes

each are bored through both sheets (Plate xiv, fig. A). Although suspension of the grid in tap water or nutrient solution did not visibly affect the plant growth or rust reaction, it was lacquered as a precautionary measure. Thanks are due to the Food Preservation and Transport Division of the C.S.I.R.O. for this lacquering.

Seedlings to be tested with different races of rust are sown in four-inch pots. The seedlings are identified by the pot number and by loops of bell wire of different shapes and colour. When the seedling is about three inches high the growing shoot is excised about half an inch above the cotyledons and placed in a hole in the grid corresponding to its number in the series. The shoot may be inoculated with rust immediately, but if it shows signs of wilting may be stood over for a short period to recover. As the rust infection develops, the shoot forms a callus, often very large (Plate xiv, fig. D), and if rust infection is not severe it roots within three weeks (Plate xiv, fig. E). The rooted shoots may be transplanted and grown to maturity: quite sturdy plants have been obtained from the weakest specimens. Alternatively the shoots may be left to set seed *in situ* if it is desired to determine the flower colour or obtain only a small quantity of seed.

While the first shoot is being tested, the parent plant, kept out of range of infection, will throw out at least two basal shoots, which are available for further use. When ten plants have been grown in a four-inch pot, five shoots per plant have been obtained without difficulty, and this number may easily be increased by reducing the number of plants per pot or by cutting back rooted shoots and using them as a source of further shoots. A very large number may be obtained from plants growing in the field. The tendency of the main stem of vigorously growing spaced plants in the field to develop a heavy crop of buds from the leaf axils may be used to advantage. One hundred such shoots have often been counted on the one stem.

Modified Techniques.

The first has been developed for the race differentiation studies.

Several excised shoots of each of the 20 differential varieties are bound in bundles with a single twist of bell wire to weight them, and then placed in 2″ × 1″ glass tubes arranged in two rows of 10 in a wooden stand 3½″ × 1¼″ × 16″. The shoots in position are inoculated and incubated in the usual way. Clearly a great saving of space is effected (Plate xiv, fig. C).

Quarter-pint cream bottles and other larger glass containers have also been used (Plate xiv, fig. B). It is not necessary to water the shoots so frequently, since they fall with the level of the water in the container. These containers may be capped and used as incubation chambers by temporarily lowering the water surface till the shoots fall below the level of the mouth. After incubation the water level may be raised and the shoots floated back above the mouth.

Sydney tap water has been quite adequate to maintain growth and obtain normal rust reactions. Growth is not so rapid and succulent as in nutrient solution, but this is an advantage if the shoots have to be held back for any period prior to transplanting.

Root and Callus Formation.

Preliminary studies indicate that the rate and vigour of rooting of the excised shoot are not markedly determined by the size of the shoot nor by the meristematic activity of the growing point. Shoots from which the growing points have been removed appear to root as readily as normally excised shoots, so that a single stem may be cut into several lengths and each length rooted. By the time such cuttings have rooted, axillary buds have developed at the top and normal vegetative growth is resumed. Excised shoots from which the growing points have been removed and left lying horizontally on the surface of the water frequently take up water and develop a distinct callus at the lower cut surface. A vigorous callus forms even when such a shoot is inverted with the upper end under water and the cut surface exposed to the air. A large branch of the inflorescence of one plant, half broken away from the main

stem, was held in place with bell wire. It continued to grow normally and within a fortnight the injured surface had developed a strong callus.

Associated with this vigorous callus-forming capacity is the tendency, observed in a recent summer sowing of young seedlings, to develop small suppressed green hypocotyledonary buds. The bulk of these buds was observed at soil level, but many were noticed slightly higher up. Their development was probably stimulated by the light friction of the hypocotyledonary epidermis against the sandy soil particles in windy weather.

Advantages of the Excised Shoot Technique.

Since excised shoots are used problems of rust contamination are eliminated. Bench space requirements are reduced by more than 50%. The equipment is more easily handled and is cleaner than where pots are used, and the nutrient level can be kept constant from one test to the next. The use of young shoots eliminates any risk of rust reactions varying with increasing age. Root rotting organisms like *Pythium* and *Fusarium* have not yet affected growth of the shoots in solution.

The prolific shooting capacity of linseed makes it possible to test the one plant with a great number of races simultaneously or consecutively. Uninfected shoots may be kept in reserve against the loss of the parent plant or transplanted into the field for seed increase.

It is useful in plant breeding work, where it may sometimes be necessary to test a plant with a particular pathogen without exposing the parent plant to the disease or introducing the disease to the field. A rapid increase of valuable plants is possible. Thus a single plant has been increased a hundredfold in the last four months. Since each new plant can now be used for further increase, this number could be quadrupled in a fortnight. This should help to offset the relatively low seed yield obtained from fibre types. It may also be possible to maintain a particular plant or variety vegetatively from one season to the next and then increase it clonally. This will overcome problems of cross pollination.

Problems Encountered.

A few set-backs have been experienced in the course of this work.

The shoots succumbed rapidly to a bacterial invasion in hot weather, when overcrowded and grown under conditions of low light intensity. Chlorotic shoots suffered more severely than normal shoots, and unrooted more than rooted shoots. No trouble has been experienced recently, since every third row in the aluminium grid has been left empty to allow for better light conditions and circulation of air. It is not yet certain whether excised shoots will live through the summer without controlled-temperature facilities.

Two or three weeks after they have been placed in Sydney tap water containing Arnon's nutrient solution minus the trace elements, excised shoots pass through a stage when chlorosis of the new growth occurs. This does not affect the rust reactions shown by the leaves that were inoculated earlier. Later, with the addition of tap water to make up for loss caused by transpiration and evaporation, the chlorotic condition disappears. The chlorosis is probably due to a temporary trace element deficiency accentuated during rapid growth, but remedied by subsequent addition of tap water. Initial experiments suggest an iron deficiency. The addition of rusty nails to the solution has given adequate control.

Conclusion.

The technique has now been developed beyond the experimental stage and has become the basis of all glass-house studies at Sydney University. One hundred of the aluminium grids and dishes are in use, together with the equipment for the modified techniques.

Several interesting lines of work which are worthy of investigation are opening up, as for example, nutritional studies, their effects on rust reaction prior to and after rooting, studies on rooting physiology, and the relation of root development to general

plant growth. Heterosis studies based on terminal growth rates of the shoot are made easy since lateral bud development is normally suppressed.

Other avenues are opening up as the work proceeds.

Acknowledgements.

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I also wish to express my special indebtedness to Professor W. L. Waterhouse for his constant encouragement and advice.

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EXPLANATION OF PLATE XIV.

A : Grid with excised shoots in position and lifted out of pyrex dish to show heavy root development after about four weeks. × 1/3.

B : Cream jar with shoots floated above mouth of jar after incubation. × 5/9.

C : A set of the rust differential varieties in which the excised shoots are used in short specimen tubes placed in position in a frame. × 3/16.

D : Basal stems of excised shoots, after about five weeks, with roots removed to show extreme cases of callus formation. × 1.

E : Extensive root development shown by an excised shoot after about four weeks. Top growth removed for photographic purposes. × 1.

REMARKS ON SOME AUSTRALIAN *LAIUS* GUÉR. (COL.: MALACHIIDAE).

By W. Wittmer, Buenos Aires.

(*Communicated by J. W. T. Armstrong.*)

(One Text-figure.)

[Read 31st October, 1951.]

Synopsis.

The Australian species hitherto placed in *Laius* are distributed amongst five genera of which two, *Troglolaius* and *Flabellolaius*, are described as new. Only one, possibly two, species are retained in *Laius*; the majority are transferred to *Dicranolaius* Champ.; two to *Simoderus* Ab.; the *armicollis* group is placed in the new genus *Troglolaius* and one new species added, while *microcerus* is made the genotype of *Flabellolaius*. One synonym is noted *L. rugulipennis* Fairm. = *nodicornis* Blackb.

This note has been made possible through the kindness of Mr. J. W. T. Armstrong, from whom I received a rich collection of Australian Malacoderms, and the comparison of Fairmaire's holotypes in the Paris Museum and paratypes of several Australian species in the British Museum, London, which I had the opportunity to study in 1950. This study showed that the genus *Laius* Guér. contains elements which are foreign to *Laius*, and this to the extent that only one, or eventually two, species will remain in this genus as far as can be seen from the material so far received. The different genera can be easily recognized in the male through the key which follows. I take this opportunity to express my sincere gratitude to Mr. Armstrong, of Nyngan, Dr. Balfour-Browne (British Museum), and Prof. Jeannel and M. G. Colas (Paris Museum), who helped me generously by lending me the material of the respective museums. As I am continuing my studies on *Laius* and allied forms, I should welcome the opportunity of examining additional material from Australia.

Key to Genera (males only).

1. Anterior tarsi simple in both sexes, second (third) joint of the antennae strongly dilated in male ..... *Laius* Guér.
   Anterior tarsal joints 2 thickened, prolonged over 3 and nigropectinate at the tip in male, second (third) joint of the antennae simple or strongly dilated 2
2. Second (third) antennal joint strongly dilated 3
   Second (third) antennal joint simple 4
3. Remaining joints of antennae simple ..... *Dicranolaius* Champ.
   Remaining joints of antennae flabellate ..... *Flabellolaius*, nov.
4. Prothorax simple, without apical process, head simple, vertex not excavated .. *Simoderus* Ab.
   Prothorax with an apical process, hornlike, more or less extended over the head, head excavated at vertex ..... *Troglolaius*, nov.

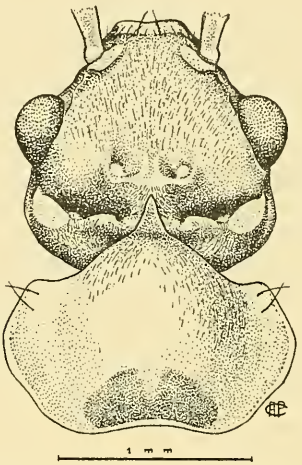
Laius Guér.

Among the material examined only *L. filamentarius* Lea was found to belong to this genus, but according to Lea's description *L. minutus* Lea might also belong to this section.

Dicranolaius Champ.

To this genus all those forms belong which have the general appearance of *Laius* but the second anterior tarsal joint thickened, prolonged over the third and nigropectinate at the tip in the male. The great majority of the Australian forms of *Laius* belong in this group. Lea ("Revision of the Australian and Tasmanian Malacodermidae", *Trans. Ent. Soc. London*, 1909, p. 151) says ". . . and the second joint of the front tarsi in the males is always of peculiar shape and tipped with black". It can therefore be assumed that all the species mentioned in his revision, except the few referred to in the next two genera, will have to be placed in *Dicranolaius* Champ. The following

were added by me on account of the character of this tarsal character, as described: *pallidus* Lea, *janthinipennis* Lea, *sordidus* Lea, *bellulus* Guér., *flavifrons* Lea, *cinctus* Redt., *plagiaticollis* Fairm., *conicicornis* Blackb., *major* Blackb., *sinus* Lea, *villosus* Lea, *carus* Lea, *nidicola* Lea, *alleni* Lea, *orthodoxus* Lea, *tarsalis* Lea, *cavicornis* Lea, *cyanocephalus* Lea, *rugiceps* Lea, *intermedius* Lea, *planiceps* Lea, *orcicornis* Lea, *intricatus* Lea, *trifoveicornis* Lea, *albomaculatus* Lea, *inconstans* Lea, *semimaculatus* Lea, *v-flavus* Lea, *maculiventris* Lea, *longus* Lea, *fimbriceps* Lea, *curvicornis* Lea, *tetrasticus* Lea, *c-purpureus* Lea, *acervatus* Lea, *flavonotatus* Lea, *stenotarsus* Lea, *concavifrons* Lea, *aulacophoroides* Lea *and rugulipennis* Fairm. The type of *L. rugulipennis* Fairm. (*Pet. Nouv.*, 2, 1877, p. 174) is identical with specimens of *L. nodicornis* Blackb. contained in the collection of the British Museum. *L. nodicornis* Blackb. (*Trans. R. Soc. S. Austr.*, 10, 1886, p. 263) must therefore be considered as synonymous with *rugulipennis* Fairm. (n. syn.).



Text-fig. 1.—*Troglolaius armstrongi*, n. sp.

SIMODERUS Ab.

This genus was erected by Abeille de Perrin in 1891 for one species from Siberia. The Australian *Laius flavopictus* Lea (*Trans. Ent. Soc. London*, 1909, pp. 152 and 166, figs. 148 and 149) and *L. effeminatus* Lea (*Trans. R. Soc. S. Austr.*, xlv, 1921, p. 86) have all the characters of *Simoderus* and must therefore be referred to it.

TROGLOLAIUS, n. gen.

Several Australian species are characterized, in the male, by the prothorax provided with a hornlike process extended more or less over the head and the head excavated at the vertex with two or more foveae or impressions. Antennae simple, 10-jointed, sometimes joints 8 to 10 curved and atrophied (*armicollis*). Second tarsal joint of anterior tarsi thickened, prolonged over third and nigropectinate at the tip. Last abdominal tergite deeply excavated in some species. The following species can be included in this genus: *Laius armicollis* (Lea), *Trans. Ent. Soc. London*, 1909, pp. 152 and 161, figs. 4 and 50; *Laius apicicollis* (Lea), *Trans. R. Soc. S. Austr.*, xli, 1917, p. 128; *Laius miraculus* (Lea), *l.c.*; *Laius sculptus* (Lea), *Trans. Ent. Soc. London*, 1909, pp. 152 and 162, figs. 61 and 144.

Genotype, *Troglolaius armicollis* (Lea).

TROGLOLAIUS ARMSTRONGI, n. sp.

♂. Head black, sometimes with a faint bluish metallic shine, except genae, one very small spot on the outer border of the two small interocular foveae and hind border of the deep, transversal frontal excavation, reddish. Antennae black with the first and second joints rufous underneath. Prothorax orange-red with a square black basal spot.

Elytra bright metallic blue or purple with a transverse, complete antemedian orange-red fascia, which is a little broader on the sides and suture than in the middle of each elytron and a small orange-red spot on the suture at the apex. Legs and abdomen black with a faint metallic shine.

Head with the eyes almost as broad as the prothorax, two small interocular foveae and a quite deep transversal excavation on the front, less deep in the middle (Text-fig. 1). Antennae short, serrate. Prothorax moderately transverse, hind angles rounded, base feebly marginate, apex rounded and in the middle with a pointed process extended over base of head, punctures small and sparse, surface clothed with a few erect black hairs near the middle towards the pointed process, and several very long setae on the side border. Elytra almost parallel, strongly wrinkled, clothed with long blackish hair intermixed with shorter whitish pubescence.

♀. Head simple, slightly transversely depressed on the front.

Length, 4·5 mm.

Hab.—Bogan River, N.S.W., Australia, on *Acacia pendula* leg. J. W. T. Armstrong. Holotype and allotype in Australian Museum collection (Nos. K.67692-3), paratypes in my collection. I have much pleasure in dedicating this very interesting species to its discoverer.

T. armstrongi is very closely allied to *T. sculptus* (Lea) and can be easily separated by the orange spotted apex of the elytra, which is metallic in *sculptus*.

FLABELLOLAIUS, n. gen.

Genotype of this division is *Laius microcerus* (Lea) (*Trans. R. Soc. S. Austr.*, xli, 1917, p. 130), characterized by having the antennae strongly flabellate from the fourth joint onwards in male. Anterior tarsal joint 2 thickened, prolonged over 3 and nigropectinate at the tip.

A REVISION OF AUSTRALIAN SPECIES PREVIOUSLY REFERRED TO THE GENUS *EMPOASCA* (CICADELLIDAE, HOMOPTERA).

By Harold F. Lower, Entomologist, Waite Agricultural Research Institute, University of Adelaide.

(Plate xv, and seventy-five Text-figures.)

[Read 28th November, 1951.]

Synopsis.

This paper deals with the taxonomy of Australian species of the genus *Empoasca* (Cicadellidae, Homoptera). As a means to this end, the external morphology of the genus as a whole is discussed with special emphasis on the male genitalia. A brief account of the distribution of the species together with their known economic importance is given and the paper concludes with keys to the species, re-descriptions in detail of the already described species, and the description of two new species.

Introduction.

Few, if any, complete studies of any Australian genus of leaf-hoppers have yet appeared. From time to time, new species have been described, often without recourse either to the types or the literature, in the transactions of various Australian and overseas learned societies. For the genus *Empoasca*, this has resulted in the accumulation of unsorted species, misidentifications, synonymy, and even the inclusion of species of other genera. Important economic species parade under synonyms, while others which do not occur in Australia are recorded as doing damage to crops. The confusion so established has been unwittingly perpetuated and added to by economic entomologists.

This study has therefore been undertaken, not with a view to making extensive additions of new species, but to establish the validity or otherwise of those already described, to give adequate re-descriptions of the accepted species, and to outline their external morphology. The re-descriptions are given in more than usual detail since I concur with Mayr (1942) that the fewer species of a genus there are known, the more exact should the descriptions be. Unfortunately, all the original descriptions leave something to be desired in this respect. Six only of the previously described species are shown to be valid, and to these, two new species are added.

The facts on which my conclusions are based are as follows: I have had, for study purposes, the loan of every collection of leaf-hoppers in Australia; the only area not represented is the Northern Territory. This material included the types of the six species deposited in Australian collections as well as all specimens identified by Dr. J. W. Evans. The authorities of the British Museum and the Hawaiian Sugar Planters' Association have displayed endless patience in checking specimens with the three types in their possession, and in providing drawings of, and information about, these. To reinforce this study, I have had material collected in the field for me by the officers of the various State Departments of Agriculture. The morphological discussion has been greatly assisted by the presence, in South Australia, of enormous numbers of *Empoasca viridigrisea* Paoli in potato crops. I have read every original description and, so far as I am aware, have missed no reference to the genus in Australia.

The limited number of known species gives no real picture of the actual position of the genus in Australia, since six of the eight have been collected from cultivated crops and are therefore of more or less economic importance. The two new species show that others await collection, especially from native vegetation in the semi-arid parts of the continent.

Economic Status of the Genus.

The economic losses caused by leaf-hoppers have long been recognized in older countries, but in Australia they have not yet received the detailed consideration which they merit. If some relatively isolated examples be excepted, the damage done is not

realized; it either passes unnoticed, or is ascribed to other agencies. Such damage may be done in three possible ways.

Leach (1940) estimated that ninety per cent. of the known vectors of virus diseases of plants occur in the Homoptera of which leaf-hoppers form a large part. As yet, no species of *Empoasca* is so implicated, but this is possibly due to our lack of knowledge of the biology of many species. Many closely allied forms are well-known vectors of such diseases.

Others are toxicogenic feeders, that is, their saliva, which they inject while feeding, has poisonous effects on plants. Such is *E. fabae*, the leaf-hopper responsible for the "hopperburn" disease of potatoes in North America, a disease which, for many years, was believed to be the result of adverse climatic conditions.

Many, when their rapid multiplication is favoured by their environment, can do enormous direct harm by the withdrawal, during their feeding, of large quantities of sap from growing plants. Such outbreaks may occur when a dry season, by restricting the growth of their natural food plants, forces them to migrate to neighbouring cultivated crops where they find ideal conditions.

Normally, most species are restricted in their breeding and feeding to particular families of plants, and the introduction of new crops belonging to these families may provide new sources of food for them. This has happened with both *E. terrae-reginae*, the cotton jassid, and *E. viridigrisea*, the vegetable jassid. The former originally bred and fed on native Malvaceae, but it has now become a major factor in limiting cotton production in Queensland (May, 1950). *E. viridigrisea*, which formerly lived on native Solanaceae, has now become an established pest of potatoes and tomatoes in all parts of Australia where these crops are grown. It has, however, adapted itself to a wide range of plants of various families, having been recorded as attacking tobacco, cotton, beans, lucerne, melons, celery, beet and many different weeds. (See Plate xv and Table 2.)

Apart from such obviously destructive species, others are annually responsible for minor losses in various crops. Experimental work in the U.S.A. has shown that losses of up to twenty per cent. may occur yearly in lucerne crops as a result of the feeding of species of *Empoasca* (Poos and Wheeler, 1943). To an unknown extent in South Australia and elsewhere, *E. viridigrisea*, and in Queensland and New South Wales, *E. alfalfae*, may be so involved.

Furthermore, as cultivation in Australia is extended, with its consequent destruction of native vegetation, leaf-hoppers may be expected to become ever-increasingly important crop pests, particularly in the warmer parts of the continent and in the artificial tropical environments provided in the Murray and other irrigated areas.

Historical Résumé.

The first recorded species of the genus was described by Fabricius in 1794 as *Cicada flavescens*. This was a European insect. Others were described under various genera until Walsh (1865), in the U.S.A., erected the genus *Empoasca* for what we now know to be three colour variations of *E. fabae*. These, he called *viridescens*, *obtusa*, and *consobrina*. *E. fabae* Harris thus became the genotype.

Because colour was largely used as a distinguishing character, and this may vary considerably in the one species, while two or more species may be almost identical in colour, the taxonomy became obscure. Damage done by a single species was attributed to several supposedly different species, while a number of species was grouped as one doing different kinds of damage in widely scattered areas.

The chaotic situation which had developed was made clear, and the mistakes rectified only after the researches of De Long (1931) had revealed the highly characteristic features of the male genitalia, and proven that distinct and constant differences in these existed between the species. Using these differences as his criteria, he revised the species in America, north of Mexico, and, in a lengthy series of subsequent papers, first by himself, and later, with the aid of collaborators, added greatly to the numbers and knowledge of the North American species.

The taxonomic history of *Empoasca* in Australia follows that common to the taxonomy of Australian Insecta generally. The earliest descriptions were made by over-

seas taxonomists working on material collected in Australia. As a consequence, the older types came to be deposited in overseas collections.

The first Australian species recorded was described as *Cicadula histrionicula* by Kirkaldy (1906), from material collected in Queensland by the Koebele and Perkins' expedition in 1904. This species came from the Bundaberg district.

Two more Queensland species, *Empoasca terrae-reginae* and *E. viridigrisea*, were added by Paoli (1936) from material in the British Museum. These came from Biloela and Bowen respectively.

The following six species were all described from Queensland by J. W. Evans: *E. bancrofti* (Evans, 1939), *E. athertoni* and *E. alfalfae* (Evans, 1941), *E. maculata* (Evans, 1942*a*), and *E. malvae* and *E. pulcherrima* (Evans, 1942*b*).

As will be shown later, *E. athertoni* is not an *Empoasca*, while *E. maculata* and *E. pulcherrima* are synonyms for *E. terrae-reginae* and *E. histrionicula* respectively.

The genus therefore contains six valid, described species, and to these, I now add *merredinensis* and *bractigera* bringing the number of species known to eight.

Distribution of the Genus (See map, Text-fig. A).

As stated above, six of the eight known species have been described from Queensland, to which State, so far as collections and records show, three of them, *histrionicula*, *terrae-reginae*, and *malvae*, are confined. Two species occur in New South Wales as well as in Queensland. These are *alfalfae*, apparently common in both States, and *bancrofti*. The latter insect is rare in collections. The single specimen of *bractigera* came from Mt. Keira in New South Wales, while all the specimens of *merredinensis* were collected near the town of Merredin in Western Australia.

In very great contrast to the apparently limited habitats of these species, is the exceptional distribution of *E. viridigrisea*, which ranges all over coastal Australia. It is found all along such areas of Queensland as a common pest of tomatoes and lucerne. It occurs in similar areas of New South Wales on potatoes, tomatoes, beans and lucerne. In Victoria, it has been collected far inland on tobacco plants.

I first identified specimens of it in South Australia in 1950. These came from the irrigation districts of Renmark and Berri, where they were infesting crops of tomatoes and potatoes. Shortly afterwards I collected it on cultivated Cucurbitaceae at Marion. A very heavy infestation destroyed a large area of potatoes at Athelstone, and at the same time it was common in lucerne at Mitcham.

In Western Australia the insects were first collected in 1942. These, and later specimens, came from districts as far apart as Manjimup in the south and Wyndham in the north. In these areas they were infesting solanaceous crops, other vegetables, and home gardens.

The fact that the one species is common wherever its introduced hosts are cultivated is very suggestive. Specimens from places as far apart as Wyndham in Western Australia, Adelaide in South Australia, Nathalia in Victoria, and Charters Towers in Queensland are identical. I have been unable to find either colour or morphological differences in specimens from these or any other areas in Australia, and this statement is based on the study of more than 2,400 specimens from all parts of the continent. Were the species endemic in these areas, one would expect that evolution would have resulted in at least a tendency towards sub-speciation. That such has not occurred when the environmental conditions are so varied, and when it is remembered that almost insuperable barriers to prevent natural dispersal exist, one is forced to the conclusion that this insect has been distributed through the agency of cultivated solanaceous crops since the coming of white settlement. This subject is of such interest that I intend to deal with it in a future paper.

A careful search of literature and collections, as well as of the records of the Tasmanian Department of Agriculture, has failed to reveal any species of *Empoasca* in Tasmania, though I anticipate that *E. viridigrisea* will yet be found in those parts of the island where potatoes are grown.

The Genus and its Systematic Position.

Until 1931 the genus was regarded as one of world-wide distribution, having native species in all the continents. In that year De Long (1931) demonstrated that the "genus" was much more complex than had previously been thought, and since then it has undergone subdivision.

De Long grouped the then known North American species into four subgenera. These, in a recent letter to me, he states he has now raised to full generic status and is erecting one or more genera for Mexican species.

His four North American genera are *Empoasca* s.str. Walsh (1865), *Kybos* Fieber, 1866, *Hebata* De Long (1931) and *Idona* De Long (1931).

Text-figure A.—Map showing known distribution of *Austroasca* in Australia.

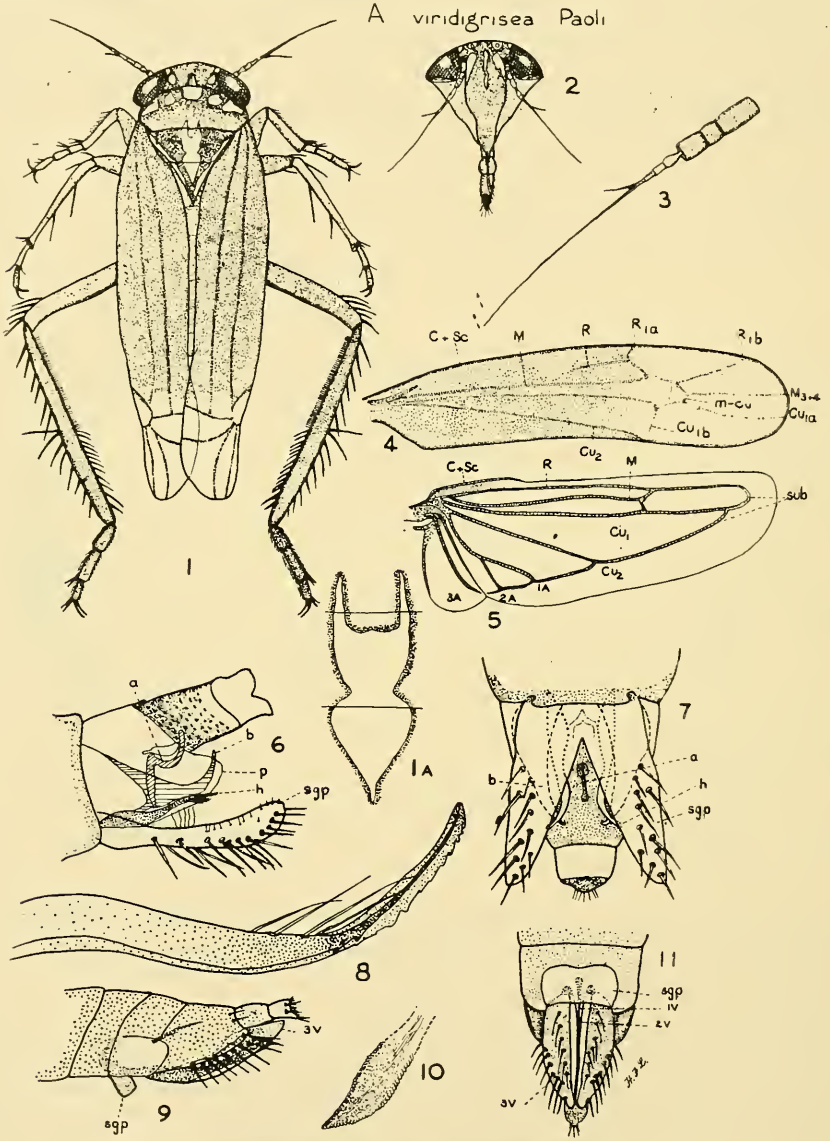
The map has been made from actual records only. The shaded areas are those in which *A. viridigrisea* is known to occur. The circles show where the other species have been collected. 1. *A. terrae-reginae.* 2. *A. alfalfae.* 3. *A. histrionicula.* 4. *A. malvae.* 5. *A. merredinensis.* 6. *A bancrofti* 7. *A. bractigera.*

Zakhvatkin (1946) has restored Fieber's old generic name *Chlorita* for certain Asiatic species, dividing it into the subgenera *Chlorita* s.str. and *Eremochlorita.*

To these I now add *Austroasca*, gen. nov., to include the Australian species formerly included in *Empoasca*, and subdivide it into *Austroasca* s.str. and *Paolia.* The distinguishing characters of the new genus are given below.

As knowledge of the whole "group" increases, the number of genera must be likewise increased. At present there is so little knowledge of the genera and species, more especially in Asia, Africa, and Australia, that I am unable to make use of the recognized taxonomic terms "tribe" or "group" for the assemblage of genera, since possibly no one at present is in a position to circumscribe it; at the same time the need is urgent for a term which will indicate the existence of such an unsorted and unknown "group" of genera. For such a "group" of genera I propose the use of the termination *iti* and refer to all the genera of "*Empoasca*" as the *Empoasciti.* No

taxonomic significance is to be attached to the term. It is purely one of convenience and signifies that such a "group" of genera exists and awaits the attention of a future specialist, having at his command a representative collection from all parts of the world so that the relationships between the genera can be defined and all these then placed in their correct taxonomic category.



Text-figures 1-11.—*A. viridigrisea* Paoli.

1, complete insect, × 9; 1A, details of median white mark on scutellum; 2, face, × 9; 3, antenna, × 109; 4, tegmen, × 9; 5, hind wing, × 9; 6, male genitalia (lateral view), × 27; 7, male genitalia (ventral view), × 27; 8, apical part of harpagone, × 109; 9, female genitalia (lateral view), × 9; 10, blade of first valvula of ovipositor, × 109; 11, female genitalia (ventral view), × 9.

The Empoasciti belong to the family Cicadellidae of the order Homoptera. They constitute a well-defined natural group of leaf-hoppers, slender, and usually of small size, few exceeding 5 mm. in length (Text-fig. 1).

Austroasca resembles the other genera of the Empoasciti in all major morphological structures except the dorsal hooks (see below). These have undergone such a reduction as to be vestigial or no longer in existence.

External Morphology of Austroasca.

In this section I deal with the external morphology of the Empoasciti, pointing out, in the appropriate places, those features which are characteristic of *Austroasca*.

The Head. (See Text-figs. 12, 30, 38, 45, 53, 59, 68.)

When any species of leaf-hopper is viewed dorsally, the insect being so orientated that the dorsal surfaces of the head and pronotum are in a horizontal plane, the visible part of the head is the crown (Evans, 1946). This is seen to project medially to a greater or lesser extent beyond the eyes, the extent of the projection (the crown production) varying according as the horizontal is departed from. In order to be able to make comparisons, a standard position must be adopted, and all the heads figured in this paper have been so orientated before drawing. The term has no morphological significance since it may comprise different morphological structures in different genera; it is merely a convenient term for descriptive purposes. The crown may be roundedly or angularly produced. In the Empoasciti it never includes any part of the fronto-clypeus.

In *Austroasca* it is always broadly, more or less roundedly produced, and the sharp, pointed crown characteristic of the genus *Idona* De Long never occurs. On either side, anteriorly, the dorsal half of each eye can be seen. The ocelli may or may not be partly visible in the standard position. They are never completely visible. As in leaf-hoppers generally, the crown is a very plastic feature and among the known species of *Austroasca* little correlation exists between crown shape and other morphological characters.

For purposes of comparing the extent to which the crown projects in different species I use what I term the Coronal Index (C.I.). This may be found as follows: An exact drawing of the crown is first made and the distance between the eyes measured at their anterior, visible, inner margins is the Eye Width (E.W.) (Text-figs. 20 and 21). The distance from the line joining these points to the anterior margin of the crown, measured medially, is the Crown Production (C.P.) (Text-figs. 20 and 21). From these measurements the Coronal Index is obtained by $\text{C.I.} = \frac{\text{C.P.}}{\text{E.W.}} \times 100$ (Text-figs. 20 and 21) and is a number, varying within very small limits, characteristic of each species irrespective of the considerable variations in size which occur among individuals of any given species. In some species, for example, *A. terrae-reginae*, slight sexual differences in the index occur, but these are never so large as to confuse the issue. The index for each species is an average. In the case of *A. viridigrisea*, more than two thousand specimens were measured. In all other species the index is an average of all the specimens available, as shown in Table 1. In no instance was the variation between minimum and maximum more than 1·5 per cent, an amount which, for this purpose, is insignificant.

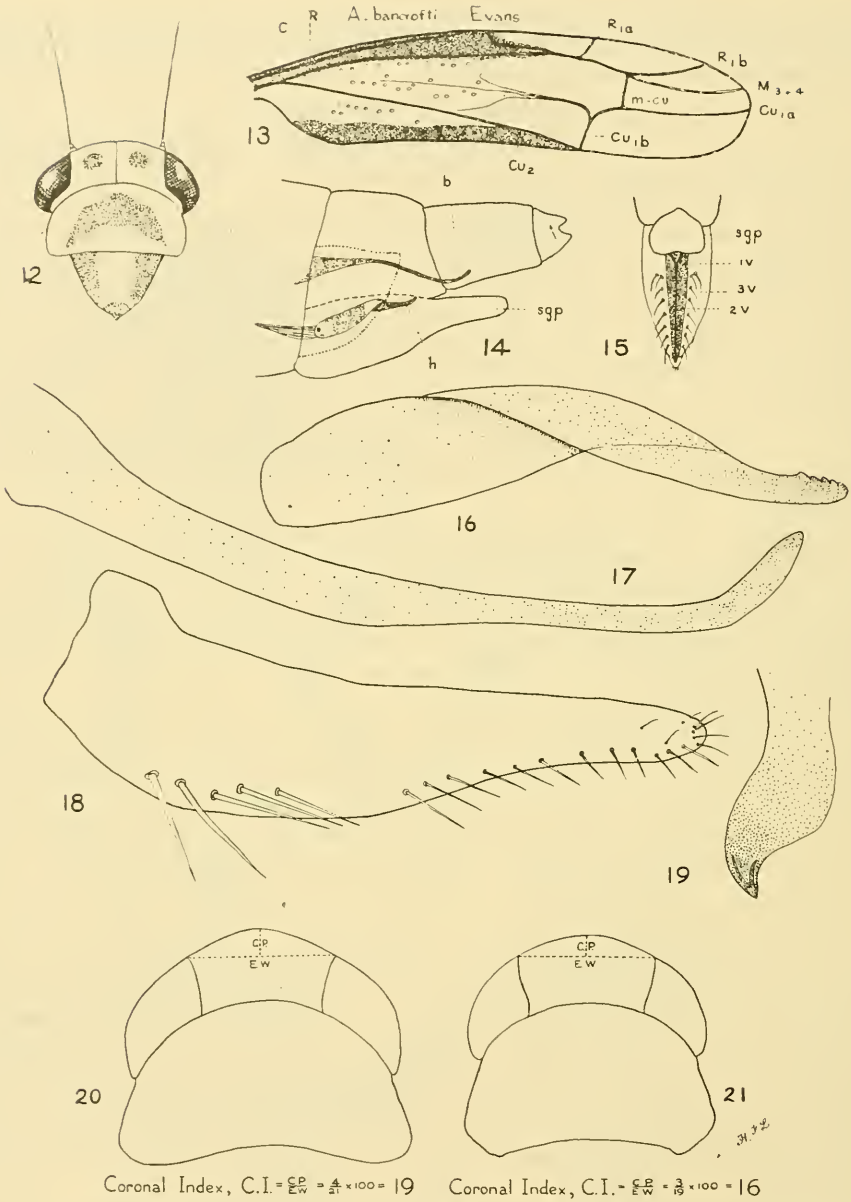
Crowns having a C.I. of 20 or more are obviously produced. Such are those of *A. terrae-reginae* (C.I. = 27, Text-fig. 53), *A. merredinensis* (C.I. = 27, Text-fig. 59), and *A. alfalfae* (C.I. = 23, Text-fig. 45).

Crowns having a C.I. of 15 or less tend to have their anterior and posterior margins broadly rounded and parallel. This group includes *A. bractigera* (C.I. = 10, Text-fig. 68), *A. bancrofti* (C.I. = 13, Text-fig. 12) and *A. viridigrisea* (C.I. = 13, Text-fig. 1).

In crowns of the intermediate group the production is not very obvious, though the anterior and posterior margins are no longer parallel. Such are *A. malvae* (C.I. = 19, Text-fig. 30) and *A. histrionicula* (C.I. = 17, Text-fig. 38).

The Face. (Text-fig. 2.)

When the head is viewed ventrally, three median sclerites are visible. These collectively form what is referred to as the face, and comprise a small, triangular



Text-figures 12-19.—*A. bancrofti* Evans.

12, crown, pronotum and scutellum, × 9; 13, tegmen showing peculiarities of venation, × 9; 14, reconstruction of male genitalia (lateral view), × 27; 15, female genitalia (ventral view), × 9; 16, harpagone, × 109; 17, brachone, × 109; 18, subgenital plate, × 22; 19, dorsal hook, × 109.

Text-figures 20 and 21.—Methods used in determining Coronal Index.

labrum, above which is the sub-rectangular ante-clypeus, while uppermost is a large, long sclerite, the "clypeus" of Snodgrass (1935), or preferably the fronto-clypeus of Evans (1946). In the Empoasciti the fronto-clypeus never transgresses on to the crown. Underneath the labrum lies the long and rather stout labium. The three median sclerites are long relative to their width, and this makes the face narrow and elongate. The facial sutures are usually difficult to observe.

On either side of the fronto-clypeus, and near its upper limit, is an ocellus. Each lies between the post-frontal sutures (Evans, 1946) and the eye. Sometimes they are situated on the corono-facial angle. The two ocelli vary somewhat in size in different species, but are never large and obvious.

On either side, near the termination of the frontal sutures (Evans, 1946) and close to the eyes, are the antennae (Text-fig. 3), which are about equal in length to the face. Each consists of a large scape, pedicel and third segment. Then follows a number of much smaller segments, the antenna terminating in a long flagellum. The antennal ledges over the bases of the antennae are vestigial.

The Thorax. (Text-figs. 12, 30, 38, 45, 53, 59, 68.)

The thorax is well developed. It consists of a wide, rather long pronotum, concave on its posterior margin, and a triangular scutellum.

The Tegmina. (Text-figs. 4, 13, 37, 44, 52, 58, 67, 74.)

The forewing or tegmen is long, narrow, slightly curved, and thickened on its basal three-quarters. Its venation is highly characteristic. In dealing with this I follow, with slight modifications, the notation of Evans (1946), who has given the most satisfactory interpretation so far suggested.

In the Empoasciti the general plan is as follows (Text-fig. 4). The anterior margin of the tegmen consists of C + Sc combined. Four long veins, R, M, Cu_1 and Cu_2, occur. R divides into two branches, R_{1a} and R_{1b}, both of which tend towards the costal margin of the tegmen. R_{1b} always reaches the margin; R_{1a} may or may not do so. R_s is always absent. The second long vein is M, which terminates at the tegmen apex as M_{3+4}, the anterior branch M_{1+2} always being suppressed. M may or may not unite with R in the apical part of the tegmen as R + M. The third long vein is Cu_1. This branches, at about two-thirds of its length from the base of the tegmen, into Cu_{1a}, which reaches the margin at the tegmen apex and runs sub-parallel to M_{3+4}. The second branch, Cu_{1b}, turns almost at a right angle and meets the posterior margin of the tegmen. The fourth long vein, Cu_2, terminates in the posterior margin of the tegmen very close to the termination of Cu_{1b}. A maximum of two cross-veins, r-m and m-cu, may be present. The cross-vein m-cu is always present; r-m is present only when the veins R and M retain their separate identities (Text-figs. 52, 58, 74). When R and M unite to form the combined vein R + M (Text-figs. 4, 13, 37, 44, 67) it is part of M which connects R_{1b} to M_{3+4}. The venation is distinct in the apical third only of the tegmen. The thickening of its basal two-thirds and the thinning of the veins in this region make these very difficult to see. Anal veins are never present.

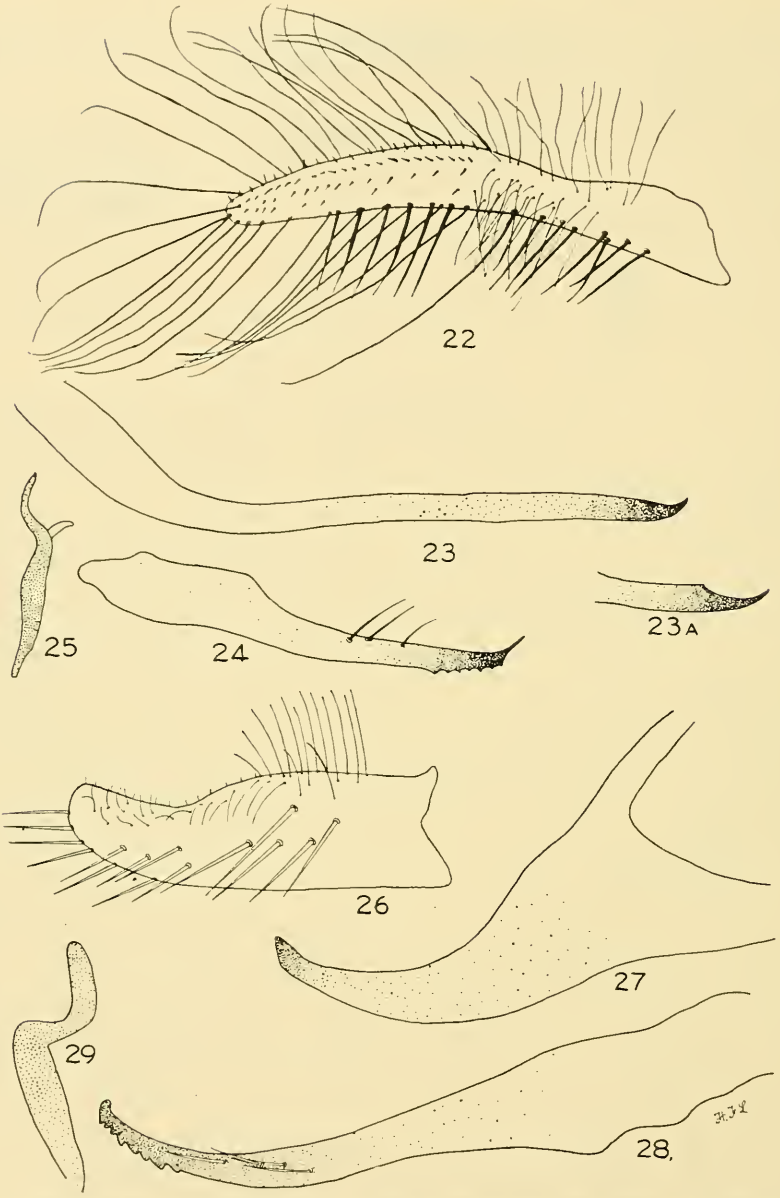
All veins from R_{1b} to Cu_2 reach the margin of the tegmen, and an appendix is therefore never present. (An appendix is formed when the terminations of the veins, instead of attaining the tegmen margin, are united by a sub-marginal vein (Text-fig. 5, sub) which connects the ends of some or all of the veins, leaving a veinless area or appendix between it and the margin.)

The principal variations in the tegmen venation of *Austroasca* will be pointed out as each species is dealt with later. One feature, however, may be mentioned here. In all the specimens I have seen, the basal part of the tegmen is covered with a layer of wax-like material which gives the tegmen a "mealy" appearance. Specimens which have been stored in preserving fluids containing alcohol do not show this layer, since it has been dissolved.

The Hind Wing. (Text-fig. 5.)

The venation is again characteristic. Near the base the combined vein C + Sc forms a thickened anterior margin to the wing, making a kind of "shoulder". It terminates suddenly near the end of this "shoulder". The remainder of the wing margin is very thin and difficult to observe.

Six long veins occur, R, M, Cu_1, Cu_2, 1A + 2A, and 3A. The tips of all these veins are united by a sub-marginal vein (Text-fig. 5, sub) and hence none of them reaches the wing margin. Between the sub-marginal vein and the wing margin is a large



Text-figures 22-29.—*A. terrae-reginae* and *A. viridigrisea* (re-drawn from Paoli).

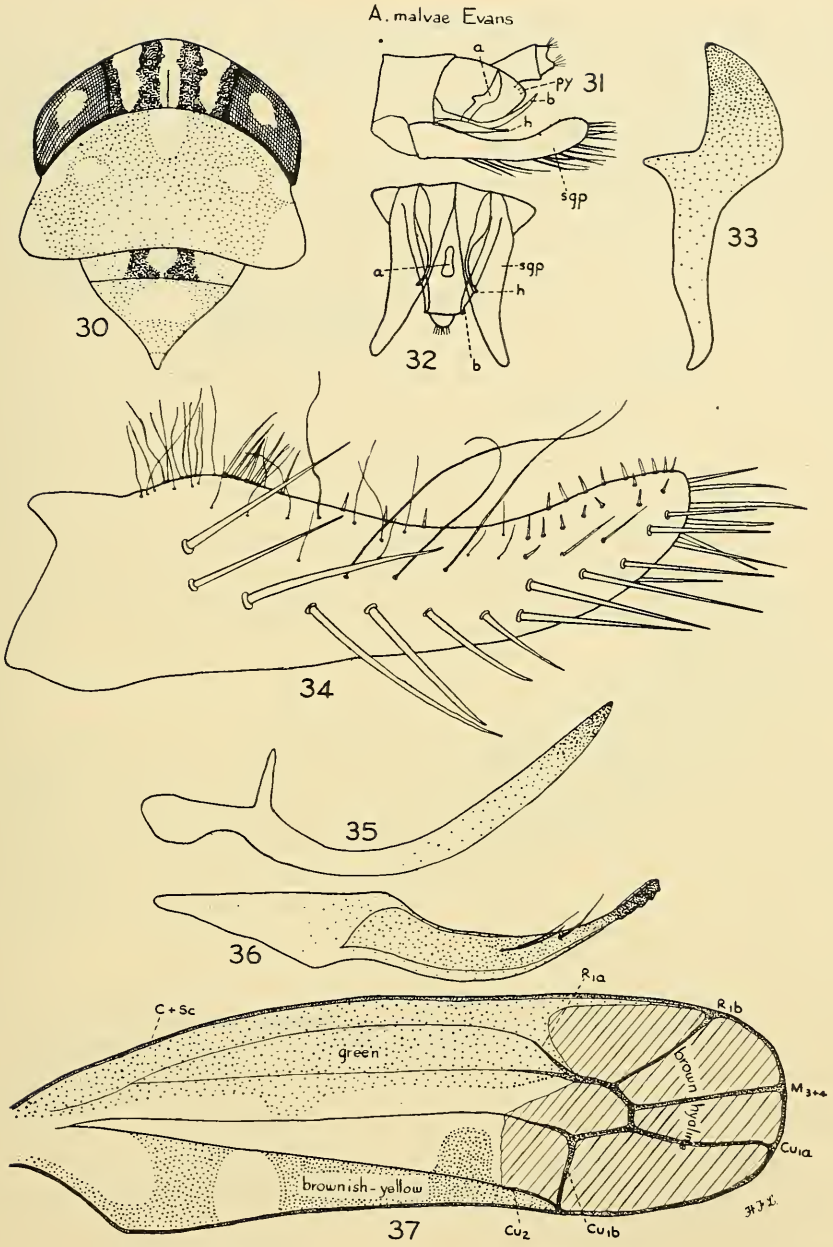
22-25, *A. terrae-reginae*.—22, subgenital plate; 23, brachone; 23A, tip of brachone showing concave notching; 24, harpagone; 25, aedeagus.

26-29, *A. viridigrisea*.—26, subgenital plate; 27, brachone; 28, harpagone; 29, aedeagus.

veinless area. 1A + 2A, before joining the sub-marginal vein, forks into 1A and 2A. A single, large, sub-rectangular apical cell is always present, closed by the sub-marginal vein. Pre-apical closed cells never occur.

The Legs. (Text-fig. 1.)

The first two pairs of legs are of the generalized cicadellid type and need no comment. The hind legs are long. Their femora bear a few strong spines distally. The somewhat flattened tibiae bear strong spines in two or three series, more particularly on the distal halves. The basal half of each tibia has a ventral comb of short bristles.



Text-figures 30-37.—*A. malvae* Evans.

30, Crown, pronotum and scutellum; 31, male genitalia (lateral view); 32, male genitalia (ventral view); 33, aedeagus; 34, subgenital plate; 35, brachone; 36, harpagone; 37, tegmen.

The Abdomen.

This is typical of the Cicadellidae generally.

The Genitalia.

The female genitalia (Text-figs. 9, 10, 11, 15) follow the generalized homopterous pattern and as this has been adequately discussed by Snodgrass (1935) little more need be added. Only slight variations occur among the species of *Austroasca.* The female genitalia are always large, prominent, and heavily bristled.

The male genitalia are highly specialized and are characteristic. In discussing them I use the terminology which Snodgrass (1935) adopted for his generalized description of the male genitalia of the Homoptera, adding new terms for those structures only which are peculiar to the Empoasciti, and giving these Greek names so as to be in harmony with his terminology.

The aedeagus excepted, all elements of the male genitalia are paired, each member of a pair being the mirror image of its fellow. The genitalia proper are so enclosed as to be visible in prepared sections only.

From the lateral margins of the ninth abdominal dorsum there extends downwards and posteriorly a pair of large lobes. The combined structure thus formed by the dorsum and its lobes is called the *pygophore* (py, Text-figs. 31, 39, 46, 54, 60, 69), and it encloses dorsally and laterally the genitalia proper.

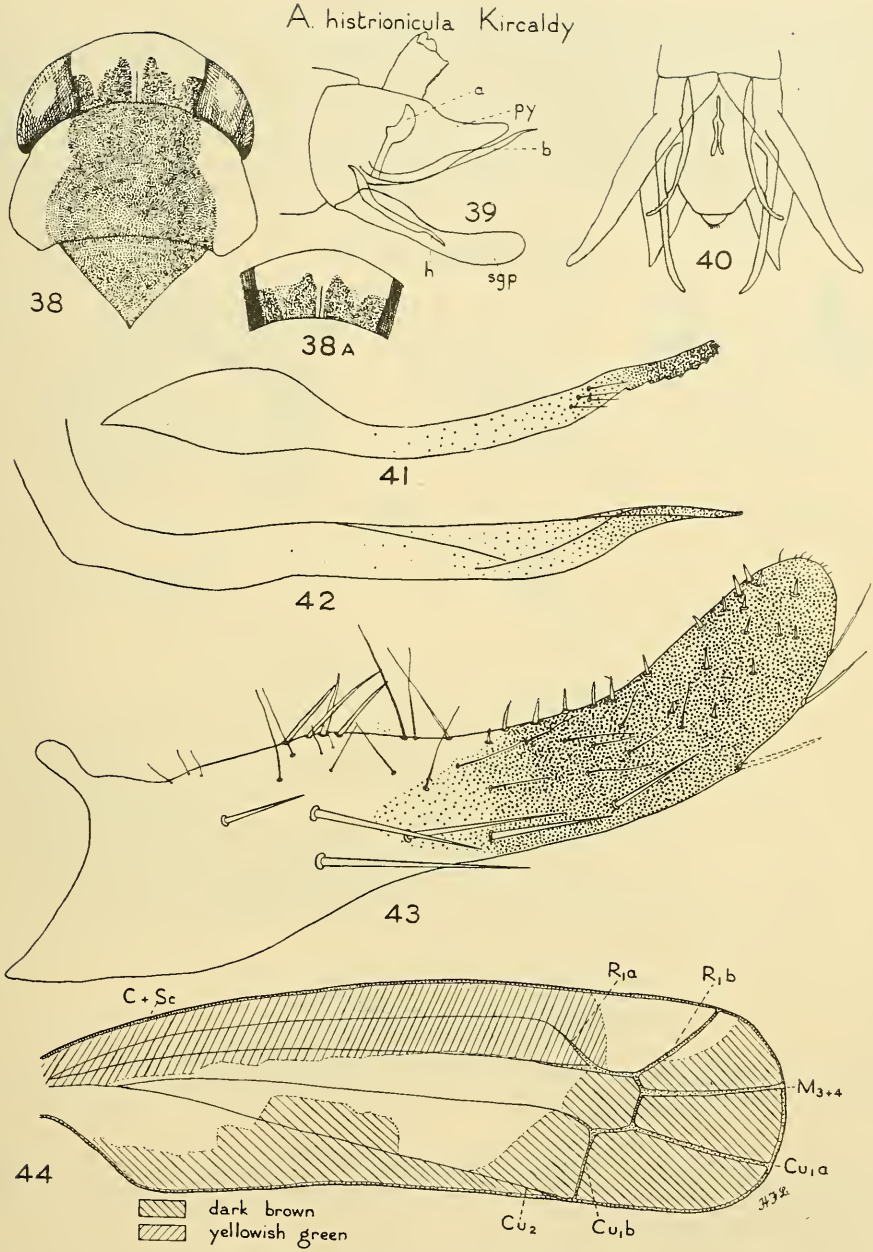
From the ninth abdominal sternum there grow out two large, elongate, carinate lobes which extend posteriorly to form the floor of the genital atrium. These are the sub-genital plates (sgp, Text-figs. 6, 7, 14, 31, 39, 46, 54, 60, 69). In *Austroasca* their tips are always upturned. They are always more or less heavily bristled, their chaetotaxy being characteristic for each species. From two to four types of setae may be present. Long, strong, thick, pointed bristles always occur. These are the ensiform bristles. Along the apical half of the dorsal margin there is usually a row of very short, stout bristles, the marginal setae. Similar setae may also be scattered over the outer surface of the apical parts of the sub-genital plates. Sometimes there occur very long bristles, thick at the base and then rapidly tapering, ending in long flagella. These are the flagellate bristles: they attain their greatest development in *A. terrae-reginae* (Text-fig. 57). They occur to a lesser extent in *A. alfalfae* (Text-fig. 51). Finally, thin scattered hairs of medium length may occur in various parts, but more especially towards the base (Text-figs. 26, 34, 51, 57).

The genitalia proper consist of an aedeagus and two or three pairs of claspers. The lower pair of claspers are the harpagones (h, Text-figs. 6, 14, 31, 39, 46, 54, 60, 69). These are usually short and stout, and are always strongly sclerotized. Their bases bear strong muscular attachments, the muscles controlling them being in the eighth abdominal segment. Their muscular attachments readily distinguish them from other members of the genitalia. They terminate in denticulations on the ventral side only. Just before the denticulations begin, a small, variable number of strong bristles is found. The position and number of the bristles, and the shape and number of the denticulations are specific characters (see Text-figs. 24, 36, 41, etc.).

From the lateral walls of the pygophore there arises internally a pair of prominent accessory structures whose purpose is to aid the harpagones during copulation. These have no muscular attachments but are always strongly sclerotized, particularly towards their apices. They are usually referred to as "lateral processes of the pygophore". As these must be repeatedly referred to in descriptions, and as the above expression is somewhat lengthy and indefinite, I propose to call them brachones (that is, arms). They are always much larger and more conspicuous than the harpagones, vary greatly, in different species, in shape, length and curvature, and in themselves are often sufficient for specific determination. They may be long and slender (Text-figs. 17, 23, 42), sail-like with broad bases and tapering tips (Text-figs. 27 and 63), almost straight (Text-fig. 17) or strongly curved (Text-figs. 49 and 63). Their tips may be merely tapered (Text-figs. 17 and 35) or may be sculptured in various ways (Text-figs. 23A and 49). In *A. bractigera* they are in the form of wide flat plates notched along the apical margin (Text-fig. 72). They are one of the most plastic units of the anatomy of the Empoasciti.

The aedeagus consists of a basal, more or less straight, attached portion and a free dorsal portion. This latter consists of a pair of lobes whose size, shape and curvature vary considerably in different species (Text-figs. 33, 56, 65).

The two terminal segments of the abdomen, segments X and XI, together comprise what is known as the anal tube. From its base, in most genera, there descends into



Text-figures 38-44.—*A. histrionicula* Kirkaldy.

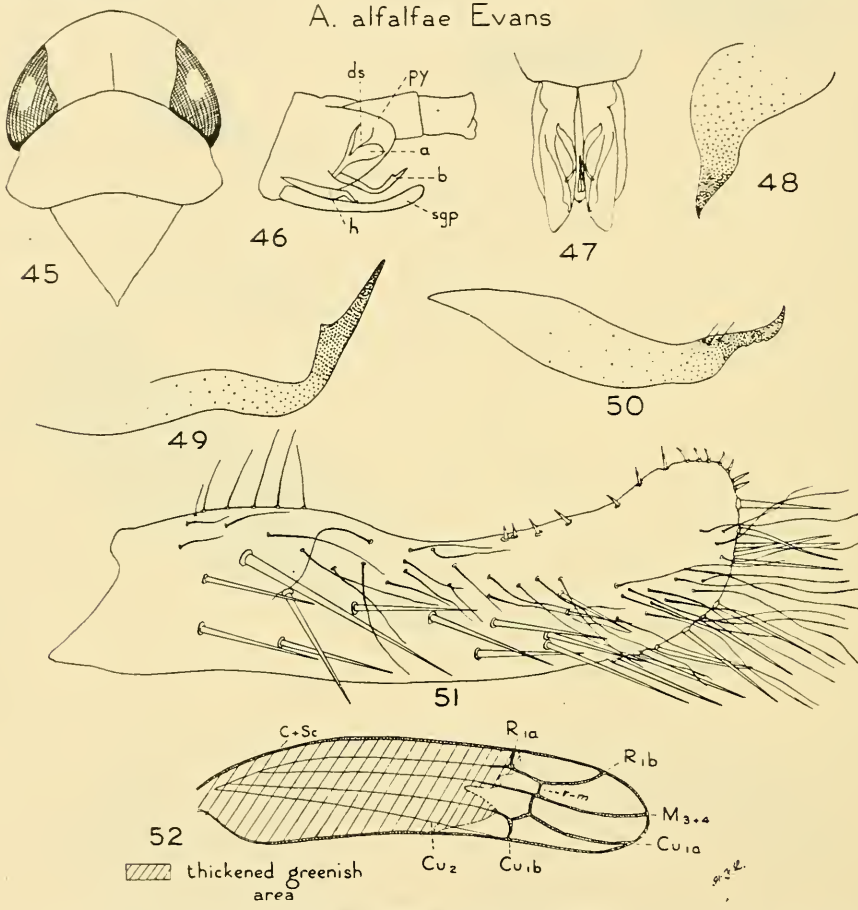
38, crown, pronotum and scutellum; 38A, variation in crown markings; 39, male genitalia (lateral view); 40, male genitalia (ventral view); 41, harpagone; 42, brachone; 43, subgenital plate; 44, tegmen.

the genital atrium a pair of strong, usually curved, hooks. These are developed from the tenth abdominal dorsum and serve, in those genera possessing them, as a third pair of claspers. These are the dorsal hooks. They are greatly reduced in *Austroasca*, where they are either vestigial or entirely absent. When present, they are very small, bluntly-pointed protuberances (ds, Text-fig. 46, and Text-figs. 19, 48, 62).

Diagnosis of Austroasca, gen. nov.

Genotype, *Austroasca viridigrisea* Paoli (1936).

The general morphological characters of the Empoasciti are shared by all its genera. Those characters which separate *Austroasca* from its allies are: The crown is always wide relative to the distance between its anterior and posterior margins; it is broadly, roundedly produced, the extent of the production never being great. In no known species is a C.I. of thirty or more found. Both male and female genitalia are heavily bristled, ensiform bristles being always present and obvious. Dorsal hooks are either vestigial or absent.



Text-figures 45-52.—*A. alfalfae* Evans.

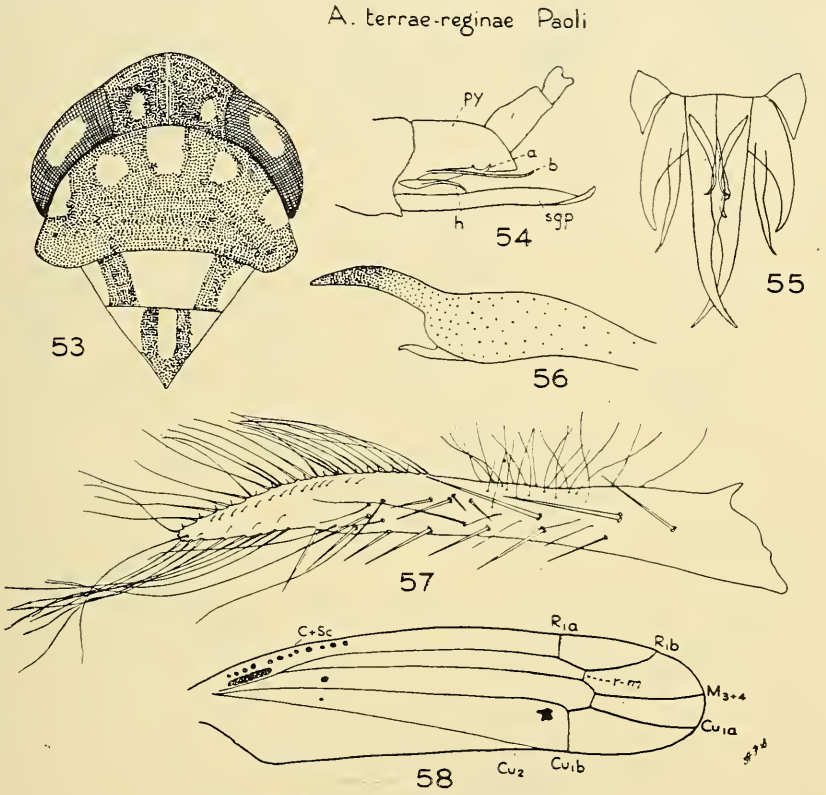
45, crown, pronotum and scutellum; 46, male genitalia (lateral view); 47, male genitalia (ventral view); 48, dorsal hook; 49, brachone; 50, harpagone; 51, subgenital plate; 52, tegmen. Note R and M distinct and presence of r-m.

In its affinities *Austroasca* most closely approaches the *obtusa* group of species of Fieber's genus, *Kybos*. In both, the crowns are broadly, roundedly produced and the genitalia are heavily bristled. It differs greatly in the weakly developed or absent dorsal hooks which, in *Kybos*, are prominent. *Kybos* is a North American genus. It is probable that when the homopterous fauna of south-east Asia and Indonesia is better known, more closely related genera will be found in these areas.

Characters Used in the Classification of Species.

With the small number at present known it is relatively easy to separate the species of *Austroasca*, shortly after death, by colour differences. As the insects dry, however,

great changes in the original colours occur. Blue and green (the latter a very common colour in the Empoasciti) become a nondescript grey, and yellow tends to whiten. White marks, originally present, may be lost, while a white pattern, not present in life, may develop through various causes. The only colours permanent under all conditions are black and brown. Specimens stored in liquids turn white except for such brown or black marks as were originally present. As has been the experience in other parts of the world, the discovery of new species will make even more difficult, and ultimately impossible, specific separation on a colour basis alone.



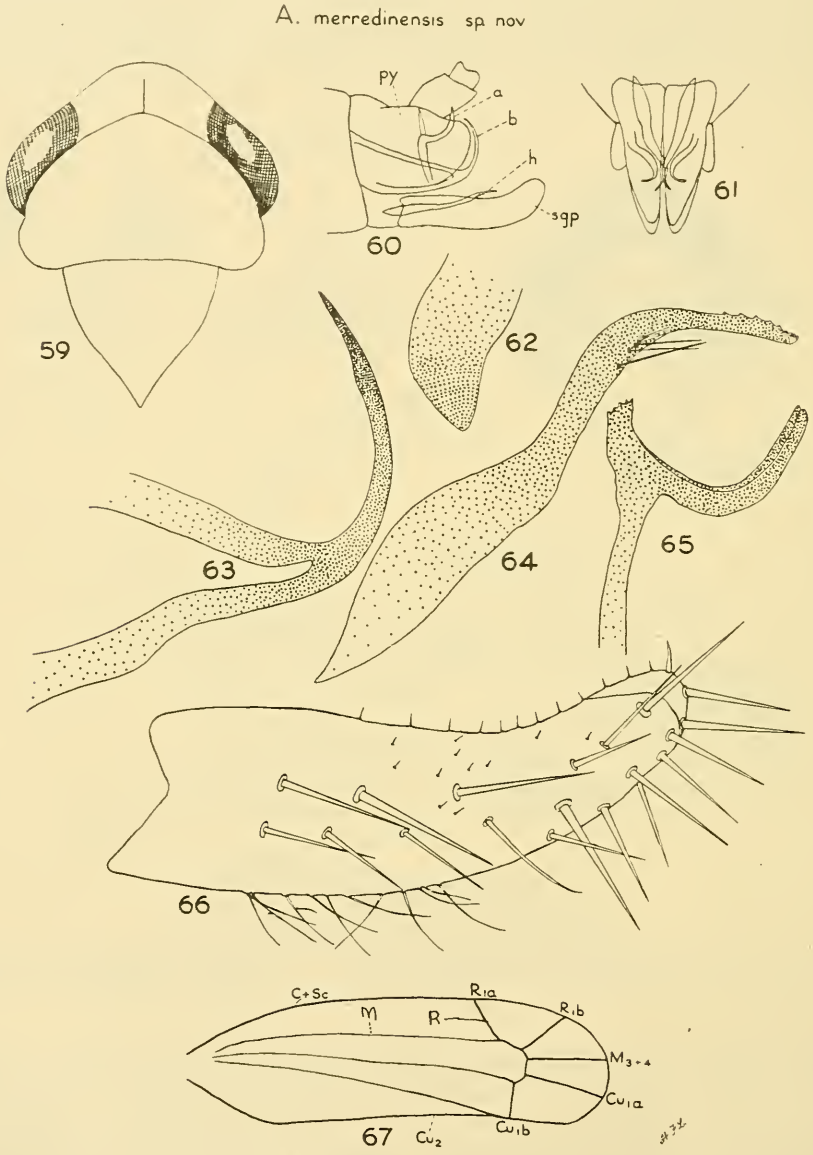
Text-figs. 53-58.—*A. terrae-reginae* Paoli.

53, crown, pronotum and scutellum; 54, male genitalia (lateral view); 55, male genitalia (ventral view); 56, aedeagus; 57, subgenital plate. Note great development of flagellate bristles; 58, tegmen showing location of spot in cell Cu_1 and presence of r-m. R and M separate veins.

For satisfactory determination of species, evanescent characters such as colour (black and brown excepted) must therefore give way to characters which, irrespective of the method or duration of preservation, will remain unchanged. Such stable characters must be morphological, and are to be found in the venation of the tegmen, the Coronal Index, and the male genitalia. Of these, the latter are of first importance. When viewed laterally and ventrally, the general arrangement of the parts, and the shape of each part, are characteristic for each species. Useful confirmatory evidence is provided by the detailed structure of the brachone and harpagone, and the chaetotaxy of the subgenital plate.

Adoption of these characters implies that new species shall not be described from females alone. In the absence of good characters, identification of known female forms is difficult; to set up new species without being able to separate them at any time from the described forms is poor taxonomy. Where the species is of economic importance,

both sexes will occur together; if the would-be identifier has no males in the material, the remedy is obvious. To help the worker who may have female material only, I have included separate keys for each sex, but the makeshift nature of the key for females must be borne in mind.



Text-figures 59-67.—*A. merredinensis*, sp. nov.

59, crown, pronotum and scutellum; 60, male genitalia (lateral view); 61, male genitalia (ventral view); 62, dorsal hook; 63, brachone; 64, harpagone; 65, aedeagus; 66, subgenital plate; 67, tegmen.

A few words on the description of new species of the Empoasciti may not be out of place here. To define the species clearly, figures are of much more value than verbal descriptions. Apart from what else it contains, a description which does not figure the male genitalia as a whole from both the lateral and ventral aspects, and separate details of the structure of the parts of the genitalia, cannot be regarded as adequate. Without

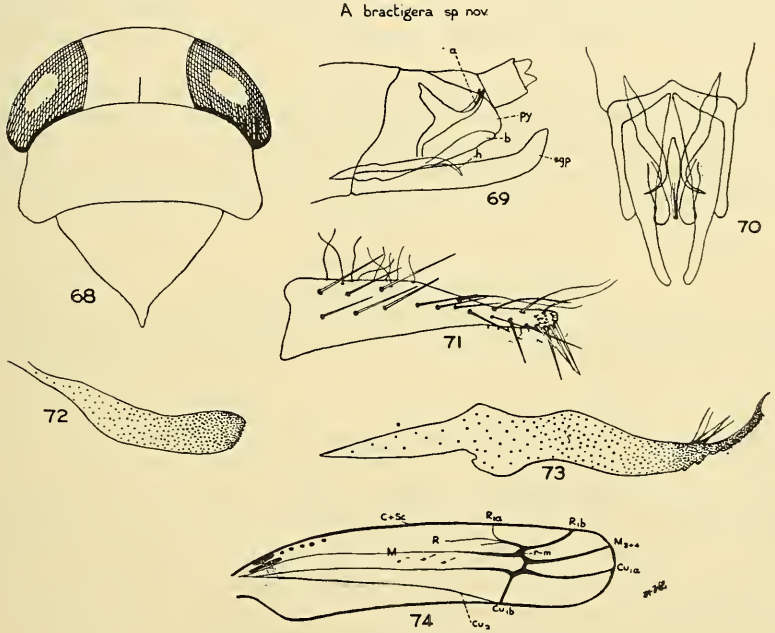
these figures, future identification is uncertain; with them, no question can ever arise as to what species is referred to.

Methods of Study and Techniques Used.

The Coronal Index is first found as explained above. This limits the number of possible species to which the specimen may belong, and this number is further limited by the nature of the tegmen venation.

The next step consists in the preparation of the male genitalia so that the parts can be clearly seen. After giving various methods a trial, I have finally standardized on the following, which meets all my requirements:

If the insect has been freshly killed, or has been stored in a liquid medium, the terminal five or six segments of the abdomen are removed. This is done with fine needles, made by using the smallest entomological pins, with the heads cut off, in metal holders. In dried specimens, the same segments may be removed with a small pair of very sharp scissors.



Text-figures 68-74.—*A. bractigera,* sp. nov.

68, crown, pronotum and scutellum; 69, male genitalia (lateral view); 70, male genitalia (ventral view); 71, subgenital plate; 72, brachone (note characteristic shape and denticulations); 73, harpagone; 74, tegmen.

The sections are put in 20 per cent. caustic potash solution and left therein until they have cleared as is shown by all the elements of the genitalia becoming plainly visible. No heat should be applied, as this usually produces distortion. Dried insects clear more rapidly than those which have been stored in preserving fluids. The latter may take two or three days.

When cleared, the section is removed to distilled water for fifteen minutes, the surplus segments providing a means of manipulating it with either needles or needle-pointed forceps without damaging or causing distortion of, the parts of the genitalia. At the end of this time, it is transferred first to 90 per cent. alcohol for ten minutes and then to a one per cent. solution of basic fuchsin in 95 per cent. alcohol for ten minutes. The staining is not essential but is desirable since, in pale-coloured specimens, some of the structures may become invisible during subsequent treatment.

From the stain, the section is put in absolute alcohol for ten minutes. From this it is removed to a drop of cedar-wood oil in a hollow-ground slide where it is moved to a lateral position so that the two harpagones and the two brachones are superimposed. Fine needles are used to arrange the section in this position, and movement is prevented by means of small fragments of glass placed round it. Using a ×10 ocular and a ×10 objective, a careful drawing of the genitalia is made.

The section is then turned so that its ventral surface is uppermost, kept in position as before, and drawn.

These drawings having been completed, the section is washed in xylol, and then placed in a drop of "Sira" or other permanent mountant on a microscope slide, where it is carefully dissected under a binocular. This is best done by rotation the genitalia till the ventral side is uppermost and then dividing the section in two by inserting a needle point at the base of the subgenital plates and carefully separating them with another needle. The membranes will be found to tear much more easily than the sclerotized parts of the genitalia. A cover slip is then applied.

From the slide so prepared, exact drawings can be made of all elements of the genitalia. For this work, I find a ×10 ocular and a ×40 objective satisfactory, fine details being checked by changing to a ×25 ocular, thereby getting a magnification of 1,000.

All the figures in this paper have been made from my own drawings of the actual insects and sections prepared as above, except Text-figures 14–19, which were drawn from the prepared genitalia of the type, and Text-figures 22–28, which are redrawn from Paoli (1936). For accuracy, these latter leave little to be desired. I have used a camera lucida for the drawings. By doing them myself, I am able to guarantee accuracy of detail.

Notes on Discarded Species, Misidentifications, and Synonymy.

Empoasca athertoni (Evans, 1941).

This is not a member of any genus of the Empoasciti. Lacking the necessary knowledge, I am not qualified to place it in its correct genus. It appears, as the following structural details show, to belong to the tribe Jassini of Evans (1947).

The face is very wide and short, its width being nearly twice its length.

The crown is extremely wide relative to the very short distance between its anterior and posterior margins, and the ocelli are on it near the anterior margin.

The tegmen has a large appendix, and shows little reduction in venation. In addition to the veins normally present in the empoascit tegmen, R_s, M_{1+2}, and a distinct Anal vein occur. All veins are strong and clearly evident in the basal part of the tegmen.

The hindwing also has a much more complete venation. In addition to the veins normally present in the empoascit hindwing, the following occur: Sc is a separate vein; R_{2+3}, R_{1+5}, M_{1+2}, and M_{3+4} are all present, as are both Cu_1 and Cu_2. There are three apical cells closed by the submarginal vein which terminates at the second Anal vein. These cells are cell R_{2+3}, cell M_{1+2}, and cell M_{3+4}.

The male genitalia are distinctive. The subgenital plates are very short and stout, while the aedeagus is very similar to that of members of the genus *Jassus*, and quite unlike that of any known genus of the Empoasciti.

"*Empoasca terrae-reginae*" for *E. viridigrisea* Paoli.

In 1941, Evans identified as *Empoasca terrae-reginae* Paoli a green leaf-hopper reported to be abundant in lucerne, on tomatoes and other vegetables, and on weeds, in both Queensland and New South Wales. At the same time he gave a partial description of the insect (Evans, 1941).

Amongst the material examined by me was a number of specimens identified by him as *E. terrae-reginae*. I carefully compared these and his description with Paoli's original description and figures of *E. viridigrisea* (Paoli, 1936). As the specimens and description agreed in every detail with Paoli's account, I came to the conclusion that Evans' "*E. terrae-reginae* Paoli" was, in fact, *E. viridigrisea* Paoli.

A number of specimens of this insect, including two identified as "*E. terrae-reginae*", together with a number of prepared genitalia, were submitted to the British Museum authorities with the request that they be compared with Paoli's type of *E. viridigrisea*. (All the specimens bore numbers only.)

They confirmed my opinion that the insects were *E. viridigrisea* Paoli and added, "we consider it identical with a species referred to by Dr. J. W. Evans as *Empoasca terrae-reginae* Paoli in *Proc. Roy. Soc. Queensland*, 52, p. 11, 1941".

This misidentification has been perpetuated since that date in the literature of economic entomology. The species must now revert to its correct name, *A. viridigrisea* Paoli, 1936.

Empoasca maculata Evans (1942*a*).

A study of Paoli's original description of *Empoasca terrae-reginae* (Paoli, 1936) leaves no doubt that *E. maculata* is a synonym for this species.

The subgenital plates, alone (see Text-figs. 22 and 57), are so highly characteristic as to be sufficient in themselves, but all other parts of the genitalia of *maculata* are identical with those of *terrae-reginae*. Both are yellow insects and each has a small brown spot on the tegmen. I figure the drawings of Paoli of both this species and his *viridigrisea*, and, in an appendix, include my translations of his descriptions so that the facts can be checked by anyone interested.

It is peculiar that this synonymy should ever have arisen since, as late as 1939, J. H. Smith (1939), in the Entomological Section of the Annual Report of the Queensland Department of Agriculture and Stock, was well aware that the Queensland cotton jassid was *E. terrae-reginae*, for he writes: "The cotton jassid, *E. terrae-reginae* Paoli, proved more serious than for some time past, and many areas were heavily infested late in the season. Work on this pest at the Biloela Research Station is a joint project between the plant breeder and the entomologist and strain resistance is a feature of present investigations."

It may be noted in passing that Paoli's type of *terrae-reginae* came from Biloela, where it was attacking cotton. The cotton jassid therefore reverts to its original name, *A. terrae-reginae* Paoli.

Empoasca pulcherrima Evans (1924*b*).

Having read Kirkaldy's original description of his *Cicadula histrionicula* (Kirkaldy, 1906), I was convinced that *E. pulcherrima* was a synonym for this species.

Specimens of *pulcherrima* were therefore sent to Mr. C. E. Pemberton, the Entomologist of the Hawaiian Sugar Planters' Association in Hawaii, asking him to compare them with Kirkaldy's type. His reply is as follows: "In comparing the specimens [of *E. pulcherrima*] with our type of *E. histrionicula* Kirk., I find no difference. Your three specimens vary slightly in colour pattern on the dorsum. The specimen in the center matches our specimen almost exactly. Though our specimen has lost its tegmina, the wings are still present, and the venation seems to match exactly the venation of your specimens. Your specimens are faintly larger; but I do not consider the difference significant. . . . I am strongly inclined to believe that your specimens are actually *E. histrionicula* Kirk."

Since *pulcherrima* corresponds exactly with Kirkaldy's description, this name must be discarded and the species revert to its original name of *histrionicula* Kirk.

Empoasca fabae Harris.

This insect has been recorded (Anon., 1944-1945) as attacking tomato plants in Queensland. This reference has been carefully checked and it appears that no identification of the insect was ever made. In view of the host plant, and the locality from where it was reported, it is virtually certain that the insect was *A. viridigrisea* Paoli, its general colour and pattern having much in common with those of the North American species, though the different shapes of the crown in each would easily differentiate them.

There is no evidence to suggest that *E. fabae*, or any other exotic species, occurs in any part of Australia.

THE GENUS AUSTROASCA, ITS SUBDIVISIONS, AND RELATIONS BETWEEN THE SPECIES.

The eight known species of *Austroasca* all share alike in the common heritage of the Empoasciti. Seven of the species, however, resemble each other much more closely than any one of them does the eighth.

The aberrant member of the genus is *A. bancrofti*, of which I have seen five specimens only. This is the only species of which I have had no material for microscopic preparations. Fortunately the tegmen and the genitalia of the type (male) have been separately mounted. Of the remaining specimens, two are complete females and two are females which have lost their abdomens.

For this species I erect the subgenus *Paolia* and distinguish it from the subgenus *Austroasca* s.str. as follows:

SUBGENUS PAOLIA, NOV.

The average size is considerably greater than that of species of *Austroasca* s.str.

The sutures of the head are complete and easily seen.

The venation of the tegmen is unique. R, instead of occupying its normal position (see R, Text-figs. 4, 37, 44, 52, 58, 67 and 74), runs parallel, and very close, to the costa (see R, Text-fig. 13), until about half-way along the tegmen, where it unites with the costa. It soon turns posteriorly and then apically uniting with M. The combined vein R + M gives off the branch R_{1a} to the costal margin and then forks into R_{1b} and M_{3+4}. In contrast to the venation of *Austroasca* s.str., where the cross-vein m-cu connects M_{3+4} only with Cu_1, in this subgenus it connects R + M with Cu_1 so that the three veins R_{1b}, M_{3+4}, and m-cu are all in contact at one point. This has been brought about by the basad movement of m-cu, its resulting increase in length making it as long as Cu_{1b}, though in *Austroasca* s.str. it is nearly always shorter, and usually very much shorter, than Cu_{1b}.

The genitalia apparently differ in certain respects from those of *Austroasca* s.str. A normal pygophore either has not been developed or has been damaged in mounting. A torn fragment (shown dotted in Text-fig. 14) may be part of a pygophore lobe.

The subgenital plates are much more weakly bristled than in other species of the genus, while the harpagones appear to lack bristles.

Unfortunately the spatial relation between the parts cannot be known at present. The genitalia of the type have been mounted after partial dissection, and Text-figure 14 is a reconstruction made from drawings, all on the same scale, of the separate parts. The possibility of serious error is obvious when such a procedure is adopted, and whether the position of the species in the subgenus is confirmed, whether it is shown to be merely an aberrant form within the genus, or whether its complete removal from *Austroasca* s.lat. is necessary, the future study of new material alone can decide. In putting it in a separate subgenus, it can be later eliminated, if necessary, without any alteration to *Austroasca* s.str.

While the seven remaining species of *Austroasca* form a more or less homogeneous group, three well-defined subgroups, based primarily on variation of the tegmen venation, can be distinguished. The variation in the venation can be correlated with the degree of specialization of the genitalia. When so grouped, genetic relationships are made clear and, at the same time, there is some indication of the evolutionary level attained by the various species.

I believe that the most generalized forms occur in the *viridigrisea* subgroup and that these probably most closely approach the austroascan ancestor in structure. In the tegmen of this group the combined vein R + M is present, r–m is therefore lacking, and R_{1a} meets the costal margin of the tegmen obliquely (Text-figs. 4 and 67). The subgroup contains two species, *viridigrisea* and *merredinensis*. Both species exhibit similar characters in the genitalia. The subgenital plates (Text-figs. 26 and 66) are short, wide, and possess relatively few strongly-developed ensiform bristles. The harpagones (Text-figs. 28 and 64) are relatively short and stout, and their denticulations are of similar pattern. Both have wide sail-like brachones (Text-figs. 27 and 63) with

broad two-pronged bases and tapering, curved, simple tips, while the free dorsal lobes of the aedeagus are curved in an open arc (Text-figs. 29 and 65).

The *histrionicula* subgroup is equally distinctive. It contains the species *histrionicula* and *malvae*. The tegmen venation is similar to that of the *viridigrisea* subgroup except that R_{1a} is vestigial, appearing as a mere thickening of R near where R_{1a} should fork. R_{1a} is not present as a distinct vein and does not reach the costal margin (Text-figs. 37 and 44). It may be fortuitous that the tegmina of both species show a similar colour pattern, and that the colours and pattern on the body generally are not unlike. The genitalia show that this subgroup has attained a higher evolutionary level than the first. The chaetotaxy of the subgenital plates (Text-figs. 34 and 43) is of a similar pattern and is of a more complex nature than that of the *viridigrisea* subgroup. A few flagellate bristles, though not well developed, are present. The harpagones are of a similar structure (Text-figs. 36 and 41). but it is in the brachones (Text-figs. 35 and 42), the most plastic feature of the genitalia of the Empoasciti, that the greatest changes have occurred. The broad two-pronged base has been lost, though the spur in *malvae* may be a vestige of a prong. The brachones are now slender and cylindrical, the terminal halves being straight with simple tapering tips. The aedeagus (Text-figs. 33 and 39) is very similar in each, the dorsal lobes assuming the form of short, thick, crescents.

The highest evolutionary development is to be found in the *terrae-reginae* subgroup, consisting of *terrae-reginae*, *alfalfae* and *bractigera*. In the tegmina, the cross-vein r-m is present since R and M retain their separate identities (Text-figs. 52, 58 and 74). R_{1a} meets the costal margin perpendicularly, though it may be difficult to see, as is the case in *bractigera*. The genitalia show the peak of evolution attained by known species of the genus. The chaetotaxy of the subgenital plates is obviously of the same pattern (Text-figs. 51, 57 and 71). All four types of bristles occur. There is a tendency towards the development of an abundance of long flagellate bristles which are so strongly developed in *terrae-reginae* that it can be identified by this character alone. The harpagones (Text-figs. 24, 50 and 73) have become short and stout, each terminates in a spine, and each bears a small number only of short stout bristles. The brachones (Text-figs. 23, 23A, 49 and 72) have undergone further modification, since there is now a tendency for their terminations to be sculptured. They are always strongly notched in *alfalfae*, saw-like, apically, in *bractigera*, and very often concavely notched in *terrae-reginae*. Text-figures 55, 47 and 70 show that the general arrangement of parts is similar in the three species.

Based on the above facts, I arrange the species in the following evolutionary scale. Of the known species I regard *viridigrisea* as the most generalized, followed in succession by *merredinensis*, *malvae*, *histrionicula*, *bractigera*, and *alfalfae*, with *terrae-reginae* as the most specialized species.

In view of the small number of known species, these ideas must be tentative, but, at the same time, the facts are suggestive.

Conclusion.

In this study I have conscientiously tried to apply those principles which I regard as essential to the satisfactory revision of any group. I have done much painstaking research, including a thorough study of types, and of all the literature bearing on the subject, more especially the original descriptions. I have given complete re-descriptions of all species needing it, together with, I hope, adequate illustrations. Finally, I have tried to make keys which will enable any entomologist who is prepared to familiarize himself with the characters used, and to make careful microscopic preparations, to ascertain what species he is identifying (if known), or to determine definitely whether it is an undescribed one. I believe I have laid a foundation on which those who follow can build with confidence.

Note: In Table 1 is shown the number of specimens of each species examined and the locations where these were collected; in Table 2 a list of the known food plants of each species is given.

TABLE 1.

Showing Numbers of Specimens Studied and Districts where These were Collected.

	A. viridigrisea.			*A. terraereginae* 1.			*A. alfalfae* 2.			*A. histrionicula* 3.			*A. malvae* 4.			*A. merredinensis* 5.			*A. bancrofti* 6.			*A. bractigera* 7.		
	♂	♀	Total.	♂	♀	Total.	♂	♀	Total.	♂	♀	Total.	♂	♀	Total.	♂	♀	Total.	♂	♀	Total.	♂	♀	Total.
Queensland—																								
No district	1	2	3	—	—	—	1	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ayr.. ..	15	16	31	—	—	—	10	8	18	—	—	—	4	4	8	—	—	—	—	—	—	—	—	—
Biloela ..	4	7	11	2	4	6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bowen ..	10	12	22	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Boyne River	—	—	—	6	5	11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Brisbane ..	—	—	—	—	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Brookfield	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Callide ..	1	3	4	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cambooya	1	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Charters Towers ..	4	5	9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Eidsvold ..	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	3	—	—	—
Gatton ..	1	1	2	—	—	—	—	—	—	2	2	4	2	4	6	—	—	—	—	—	—	—	—	—
Gayndah ..	3	5	8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Gracemere	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Horne Hill	—	—	—	—	—	—	2	2	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Humphrey	—	—	—	10	15	25	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Indooroopilly	1	3	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Jandowae ..	2	1	3	3	3	6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Kilmore ..	—	—	—	2	4	6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Kingaroy ..	—	2	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Kongaroy ..	2	2	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Mimgary ..	—	—	—	2	1	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Mundubbero	—	—	—	1	5	6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pentland ..	2	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Rockhampton	—	—	—	—	—	—	—	4	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Toowong ..	—	—	—	—	—	—	—	—	—	1	3	4	—	—	—	—	—	—	—	—	—	—	—	—
Yamala ..	—	—	—	1	3	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Yeeroongpilly	1	—	1	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
New South Wales—																								
Bellbrook	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bolwarra ..	2	3	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Branxton ..	1	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Camboyne	1	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cabramatta	—	1	1	—	—	—	3	9	12	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Dundas ..	—	3	3	—	—	—	3	6	9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Dungog ..	—	2	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Gunnedah	1	2	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Maitland ..	—	7	7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Millthorpe	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Mount Keira	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1
Mudgee ..	4	5	9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Narellan ..	8	8	16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Nemingha	1	2	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Paterson ..	7	3	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pitt Town..	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Prospect ..	12	11	23	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Raworth ..	5	4	9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Roslyn ..	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Seaham ..	1	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Sydney ..	1	4	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	2	—	—	—
Tamworth	3	5	8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Wauchope	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Wilberforce	3	4	7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Windsor ..	1	2	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Wingham	1	4	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

TABLE 1.—*Continued.*

Showing Numbers of Specimens Studied and Districts where These were Collected.—Continued.

	A. viridigrisea.			*A. terrae-reginae* 1.			*A. alfalfae* 2.			*A. histri-onicula* 3.			*A. malvae* 4.			*A. merred-inensis* 5.			*A. ban-crofti* 6.			*A. brac-tigera* 7.		
	♂	♀	Total.	♂	♀	Total.	♂	♀	Total.	♂	♀	Total.	♂	♀	Total.	♂	♀	Total.	♂	♀	Total.	♂	♀	Total.
Victoria—																								
Nathalia ..	—	5	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
South Australia—																								
Athelstone..	1000	1000	2000	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Berri ..	11	12	23	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Marion ..	11	15	26	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Mitcham ..	18	25	43	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Renmark ..	6	8	14	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Western Australia—																								
Bridgetown	2	2	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Kenwick ..	5	11	16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Manjimup	2	3	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Merredin ..	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	17	27	—	—	—	—	—	—
Perth ..	6	5	11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Wyndham	12	14	26	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Tasmania—																								
No species known																								
Grand totals	1174	1239	2413	27	40	67	20	32	52	3	5	8	6	8	14	10	17	27	1	4	5	1	—	1

Key to genus Austroasca *nov.*

m-cu connecting M_{3+4} with Cu_1; R in normal position .... subgenus *Austroasca*
m-cu connecting R + M with Cu_1 (Text-fig. 13); R abnormally close to C .... subgenus *Paolia*

Subgenus *Austroasca* nov. Males.

1. Crown conspicuously marked with brownish-black 2
   Crown not marked with brownish-black 3
2. (1) Four brown marks on crown in form of separate longitudinal bands touching anterior margin (Text-fig. 30) ..... *malvae* Evans (1942*b*)
   Two brown marks on crown either roughly U-shaped or subquadrangular, not touching anterior margin (Text-figs. 38, 38A) ..... *histrionicula* Kirkaldy (1906)
3. (1) Brachone with wide base (Text-figs. 27, 63) 4
   Brachone with narrow base 5
4. (3) Termination of brachone long, slender and much recurved (Text-fig. 63) .... *merredinensis*, sp. nov.
   Termination of brachone short, thick and curved (Text-fig. 27) .... *viridigrisea* Paoli (1936)
5. (3) Brachones expanding to form broad plates, toothed on distal margins (Text-fig. 72) .... *bractigera*, sp. nov.
   Brachone slender 6
6. (5) Brachone strongly angled, tip deeply notched (Text-fig. 49) ..... *alfalfae* Evans (1941)
   Brachone almost straight (Text-fig. 23); tip sometimes concavely notched (Text-fig. 23A) ..... *terrae-reginae* Paoli (1936)

Subgenus *Austroasca* nov. Females.

1. Crown conspicuously marked with brownish-black 2
   Crown not marked with brownish-black 3
2. (1) Four brown marks on crown in form of separate longitudinal bands touching anterior margin (Text-fig. 30) ..... *malvae* Evans (1942*b*)
   Two brown marks on crown either roughly U-shaped or subquadrangular, not touching anterior margin (Text-fig. 38, 38A) ..... *histrionicula* Kirkaldy (1906)
3. (1) Cross-vein r-m present in tegmen 4
   Cross-vein r-m absent in tegmen 6
4. (3) Tegmen with a small brown spot in cell Cu_1 near forking of Cu_{1b} (Text-fig. 58) .... *terrae-reginae* Paoli (1936)
   Tegmen without such a spot 5

5. (4) Crown distinctly, obovately produced C.I. = 23 (Text-fig. 45) .... *alfalfae* Evans (1941)
Crown very little produced C.I. = 10 (Text-fig. 68) ..... *bractigera*, sp. nov.
6. (3) R_{1a} directed towards base of tegmen (Text-fig. 67). Brownish insects .....
..... *merredinensis*, sp. nov.
R_{1a} directed towards apex of tegmen (Text-fig. 4). Greenish or greyish insects .....
..... *viridigrisea* Paoli (1936)

Subgenus *Paolia* nov.

Head yellow with three oval black marks, two on crown, and a median one high on face
..... *A.* (*Paolia*) *bancrofti* Evans (1939)

TABLE 2.

Recorded Host Plants of Species of Austroasca.

Species.	Breeding and Feeding on.	Feeding Only.
viridigrisea	Potato. Tomato. Lucerne. French bean. Rock melon. *Solanum nigrum* L. *Chenopodium album* L. *Malva parviflora* L. *Amaranthus viridis* L. *Citrullus vulgaris* Schrad. Tobacco. Silver beet.* Cotton.* *Trianthema portulacastrum* L.* *T. decandra* L.* *Ricinis communis* L.*	*Cynodon dactylon* Richard. Celery. *Portulacca oleracea* L. *Bidens pilosa* L.* *Tribulus terrestris* L.*
merredinensis	*Atriplex* sp.	
malvae	*Malva parviflora* L.* *Abutilon* sp.	
histrionicula	*Sida subspicata* F. v. M. *S. rhombifolia* L.*	Cotton.*
alfalfae	Poona pea (*Vigna sinensis* L.).* *Pisum sativum* L.* Lucerne.* Cotton.* *Crotalaria* sp.* French bean.	Potato.*
terrae-reginae ..	Cotton. *Sida corrugata* L.* *Abutilon* sp.*	*Amaranthus viridis* L.* *Chenopodium carinatum* R.Br.* *Clerodendron tomentosum* R.Br.*
bancrofti	No hosts recorded.	No hosts recorded.
bractigera	No hosts known.	No hosts known.

* Information from May, 1950.

AUSTROASCA (AUSTROASCA) VIRIDIGRISEA PAOLI (1936).

(Text-figures 1–11, 24–29.)

Empoasca viridigrisea Paoli, *Mem. Soc. Ent. Ital.*, 15, 1936: 12–13.

Empoasca terrae-reginae Evans, *Proc. Roy. Soc. Queensland*, 52, 1941: 11.

Suggested common name, the vegetable jassid. *Length.*—Male: Average of 1,174 specimens, 3·8 mm.; max. 4·0 mm., min. 3·5 mm. Female: Average of 1,239 specimens, 3·9 mm.; max. 4·2 mm., min. 3·8 mm. *Colour*: Green with white markings.

Head.—Crown: C.I. = 13 (Text-fig. 1). Anterior margin gently curved. Emerald green with narrow, irregular median, white stripe, four lateral white spots, one on

anterior margin close to each eye, and one posterior to each of these. Coronal suture incomplete. *Face*: Shape typical (Text-fig. 2). Yellowish-green with white, irregular, narrow, median white stripe from vertex to level of antenna bases. The pattern varies considerably, some specimens showing more white than others. Two white bands, one from below each ocellus, and directed outwards. *Antennae* typical, scape and pedicel green, third segment and remainder of antenna dark green (Text-fig. 3). *Ocelli* two, high on face, one between median and each eye, each in centre of yellowish-white, circular spot. *Eyes* dark brown.

Thorax.—Pronotum (Text-fig. 1): Anteriorly yellowish-green becoming translucent and paler posteriorly; an irregular median white spot, and four lateral white spots, two on each side. All spots on anterior margin. *Scutellum* (Text-fig. 1): Emerald green, yellowish laterally. A complex, characteristic, white median mark (Text-fig. 1A) and a long, white, irregular stripe along each lateral margin. The median mark varies little in shape; in a few specimens it is not forked.

Wings.—Tegmen (Text-fig. 4): Basal four-fifths yellowish and opaque, almost concealing venation, which is typical. Apical fifth brownish to colourless hyaline. Veins green and obvious in clear apical area. *Hind Wing* (Text-fig. 5) typical, colourless hyaline, veins prominent and green. *Legs* typical, green, tending to peacock blue distally. Pretarsi dark brown.

Abdomen.—Typical of genus. Dorsal surface green, ventral surface yellow to yellowish-green. *Genitalia* deep green (Text-figs. 6 and 7). *Subgenital plate* (Text-fig. 26) short and broad, with about fifteen stout ensiform bristles and about fourteen long thin hairs on dorsal edge near base. *Harpagone* (Text-figs. 8 and 28): About eight teeth and four stout bristles. *Brachone* (Text-fig. 27) subtriangular with broad base, rapidly tapering to a blunt point; termination curved. *Aedeagus* (Text-fig. 29): Free dorsal part curved in an open arc.

Type in British Museum.

Type locality.—Bowen, near Pomodori, Queensland, Australia, October 20, 1931 (D. O. Atherton).

Host plants.—See Table 2.

Austroasca (Austroasca) merredinensis, sp. nov.

(Text-figures 59–67.)

Length.—Male: Average of 10 specimens, 3·9 mm.; max. 4·0 mm., min. 3·9 mm. Female: Average of 17 specimens, 4·4 mm.; max. 4·5 mm., min. 4·3 mm. *Colour*: General colour light brownish, showing no pattern. (Specimens have been preserved in alcohol.)

Head.—Crown: C.I. = 27. Anterior margin bluntly angularly produced, brownish (Text-fig. 59). *Face* typical, brownish. *Antennae* typical, brownish. *Ocelli* high on face. *Eyes* bleached to white by alcohol.

Thorax.—Pronotum: Anterior margin bluntly angled so as to be more or less parallel with anterior margin of crown (Text-fig. 59). *Scutellum* (Text-fig. 59) brownish.

Wings.—Tegmen (Text-fig. 67) light brown to colourless hyaline. Venation typical. *Hind Wing* colourless, venation typical. *Legs* brownish, typical.

Abdomen brownish, typical. *Genitalia* (Text-figs. 60 and 61). *Subgenital plate* (Text-fig. 66) short and broad. About 20 strong ensiform bristles; lower margin with a fringe of about twelve thinnish bristles about half the length of the strongest central ensiform bristle. Apical two-thirds of upper margin with marginal setae. Apex of plate terminating in a concavity. *Harpagone* (Text-fig. 64) short and stout, apical part curved with about eight or nine denticulations. Setae in two rows: an outer row of three strong bristles and an inner row of three or four bristles not so long as outer bristles. *Brachone* (Text-fig. 63) wide at base, rapidly tapering to a long, thin, very recurved tip, terminating in a sharp point. *Aedaegus* (Text-fig. 65): Free dorsal part curved in an open arc.

Type material.—Male holotype; tegmen and dissected genitalia mounted; remainder of body in alcohol.

Type material in Coll. Division of Entomology, C.S.I.R.O., Canberra, A.C.T.

Type locality.—Merredin, Western Australia, April 3, 1940. "On Saltbush" (C. F. H. Jenkins).

Host plant.—*Atriplex* sp.

Austroasca (Austroasca) malvae Evans.

(Text-figures 30-37.)

Empoasca malvae Evans, *Proc. Roy. Soc. Queensland*, 54, 1942: 49. (Note: The numbers 3 and 6 in Evans' figures should be transposed.)

Length.—Male: Average of six specimens, 3 mm.; max. 3·1 mm., min. 2·9 mm. Female: Average of eight specimens, 3·5 mm.; max. 3·7 mm., min. 3·3 mm. *General Colour* greenish-yellow with brown markings.

Head.—Crown: C.I. = 19 (Text-fig. 30). Pale green with four irregular longitudinal brown stripes, one bordering each eye. Coronal suture incomplete. *Face* normal, yellowish with a broad, median, irregular, longitudinal, white stripe. *Antennae* normal, greenish. *Ocelli* close to eyes, one in each lateral pale green band on lower part of corono-facial angle. *Eyes* brown.

Thorax.—Pronotum (Text-fig. 30) generally light brown with median greenish-white mark immediately posterior to median pale green band of crown and a white mark near each antero-lateral margin. Between each of these and the median mark is a sub-oval white mark. Posterior median section translucent and greenish yellow; posterior lateral lobes pale green. *Scutellum* (Text-fig. 30) yellowish-brown with a median white oval spot continued posteriorly as a median greenish-white stripe to suture, where it expands to a large sub-oval white blotch. On either side of median white blotch on anterior of scutellum is a dark band. Tip of scutellum pale green.

Wings.—Tegmen (Text-fig. 37): Apical third brown hyaline, a wide greenish area along costal margin between that margin and Cu_1. Area posterior to Cu_2 largely brownish-yellow except the two whitish translucent areas shown. Area between Cu_1 and Cu_2 chiefly whitish translucent. Veins greenish-white. *Hind Wing* normal. *Legs* normal, green.

Abdomen normal greenish. Most of posterior of each tergite occupied by a large brown area, the anterior being yellowish-green. Posterior of ninth tergite with an almost black transverse band. Ventral surface yellowish-green. *Genitalia* pale green (Text-figs. 31 and 32). *Subgenital plate* (Text-fig. 34) long, broad at base and gently tapering. About 25 strong ensiform bristles. Near centre of plate are three flagellate bristles, while a few shorter such bristles occur above these near the upper margin. Terminal fifth of upper margin with marginal setae. Near base of plate and on upper margin is a group of long hairs followed by six to seven short ensiform-like bristles. *Harpagone* (Text-fig. 36) short and stout with between five and six denticulations and four bristles. *Brachone* (Text-fig. 35) short, slender, curved and simple, with an upward-directed spur near base. *Aedeagus* (Text-fig. 33): Free dorsal part in form of a thick crescent.

Type.—Male mounted on point, in Coll. Queensland Museum. HÓ5233.

Type locality.—Gayndah, Queensland, April 7, 1942. "On *Sida subspicata*" (A. May).

Austroasca (Austroasca) histrionicula Kirkaldy (1906).

(Text-figures 38–44.)

Cicadula histrionicula Kirkaldy, *Haw. S.P. Exp. Sta. Entom. Bull.*, 1, part 9: 361.

Empoasca histrionicula Myers, *Bull. Ent. Res.*, 18, 1928: 311.

Empoasca pulcherrima Evans, *Proc. Roy. Soc. Queensland*, 54, 1942: 49. (Note: The numbers 3 and 6 in Evans' figures should be transposed.)

Length.—Male: Average of three specimens, 2·7 mm.; max. 2·75 mm., min. 2·7 mm. Female: Average of five specimens, 2·8 mm.; max. 2·9 mm., min. 2·7 mm. *Colour* yellowish-green with conspicuous brown markings.

Head.—Crown: C.I. = 17 (Text-fig. 38). Slightly produced, light green, most of its area occupied by two large U-shaped almost contiguous dark brown marks. These

marks vary considerably in shape. Frequently they are U-shaped, the arm of the U nearer the median line being longer, but in many specimens the colour "overflows" so as to make the marks roughly subquadrangular, as is the case in Kirkaldy's type (Text-fig. 38A). *Face* typical. Fronto-clypeus lemon yellow, ante-clypeus and labrum light green. *Antennae* green. *Ocelli* high on face, each nearer the eye than median line. *Eyes* dark brown.

Thorax.—Pronotum (Text-fig. 38) with a broad, median, velvety, brown band; laterally, pale green. *Scutellum* (Text-fig. 38) wholly dark brown.

Wings.—Tegmen normal, pale yellowish-green with large dark brown area (Text-fig. 44). *Hind Wing* normal. *Legs* normal, yellowish-green.

Abdomen.—Normal, yellowish in colour, a large subtriangular brown area covering most of the terga. Tergum of ninth segment brownish-black, a narrow yellow lateral band on posterior of eighth tergite intervening between the two brown areas. Sternal surface entirely yellow. Anal tube wholly dark brown. *Genitalia* (Text-figs. 39 and 40): In both sexes the basal half is yellowish, the terminal half brown, intensifying to black at the tips (Text-fig. 43). *Subgenital plate* (Text-fig. 43) long, basal third wide, apical two-thirds tapered with upper and lower margins subparallel; nine or ten ensiform bristles present. Terminal half of upper margin with marginal setae. On upper margin near base are three or four small hairs followed by four or five small ensiform-like bristles and three or four flagellate type bristles. *Harpagone* (Text-fig. 41): Basal third wide, apical two-thirds slender and almost straight. Nine to ten denticulations, four or five small slender bristles in two series. *Brachone* (Text-fig. 42) strongly elbowed at base, then straight, more or less cylindrical, tapering suddenly to a point, twisted. *Aedeagus* (*a*, Text-fig. 39): Free dorsal part in form of a thick crescent.

Type.—Female mounted on point. In Coll. Haw. Sug. Planters' Assn., Honolulu, Hawaii.

Type locality.—Bundaberg, Queensland. Collected by Koebele and Perkins' expedition in 1904.

Austroasca (Austroasca) bractigera, sp. nov.

(Text-figures 68–74.)

Length.—Holotype male, 3·6 mm. (only specimen known). *Colour* yellow.

Head.—Crown (Text-fig. 68) extremely slightly produced; C.I. = 10. Bright yellow with faint white stripe on coronal suture, which is incomplete. *Face* normal and yellowish. *Antennae* normal, brownish-yellow, flagellum brown. *Ocelli* two, close to eyes, and level with top of post-frontal suture. *Eyes* brownish-black.

Thorax.—Pronotum (Text-fig. 68) robust; yellow possibly marked with white on anterior margin. *Scutellum* yellow with apparently two white lateral bands and a terminal white patch.

Wings.—Tegmen (Text-fig. 74) normal, brownish-yellow and hyaline. Cross vein r-m present, R_{1a} weakly developed; near base in cell Sc is a series of five circular protuberances, and two elongated raised patches formed by the union of a number of similar protuberances. *Hind Wing* colourless; venation normal, veins white. *Legs* normal, yellow.

Abdomen.—Yellow dorsally and ventrally, white laterally. *Genitalia* (Text-figs. 69, 70) yellow. *Subgenital plate* (Text-fig. 71) long, the distal half very narrow with dorsal and ventral margins subparallel. Ensiform bristles in two series; near apex are three or four well-developed flagellate bristles; marginal setae also present. *Harpagone* (Text-fig. 73) short and robust; about thirteen denticulations terminating in a curved spine; four to five bristles; base rugged. *Brachone* (Text-fig. 72): In its shape the brachone of this species is quite unique. It is short and from a narrow base opens out into a broad flat plate with its apical margin notched like a saw. The brachone, alone, will at once identify this species. *Aedeagus* (*a*, Text-fig. 69): The aedeagus is relatively large. Its attached basal part is narrow but soon widens and gives off a second strong point of attachment. The two free lobes are curved in an open arc.

Type.—Holotype male, mounted on card; genitalia separately mounted. In Coll. Department of Agriculture, Sydney, New South Wales.

Type locality.—Only one specimen, the type, is known. This came from Mt. Keira, New South Wales, and bears the label "Mt. Keira, New South Wales, at light 3.12.1949. C. E. Chadwick".

Austroasca (Austroasca) alfalfae Evans.

(Text-figures 45–52.)

Empoasca alfalfae Evans, *Proc. Roy. Soc. Queensland*, 52, 1941: 11.

Length.—Male: Average of 20 specimens, 2·75 mm.; max. 2·85 mm., min. 2·7 mm. Female: Average of 32 specimens, 3·6 mm.; max. 3·8 mm., min. 3·4 mm. *Colour* yellowish-green.

Head.—Crown: C.I. = 23. Obovately produced, yellowish-green (Text-fig. 45). *Face* normal, yellowish-green. *Antennae* normal, green. *Ocelli* two, one much nearer each eye than median line, near upper limit of face. *Eyes* dark brown.

Thorax.—Pronotum (Text-fig. 45) yellowish-green apparently unmarked with white. *Scutellum* yellowish-green with indefinite white markings, green towards lateral margins.

Wings.—Tegmen (Text-fig. 52): Venation normal; the erect vein R_{1a} is a characteristic of this and the next species. Cross-vein r-m present. Basal two-thirds of tegmen thickened, yellowish-green and translucent; apical third colourless hyaline. *Hind Wing* normal, veins pale green. *Legs normal*, yellowish-green.

Abdomen.—Normal, yellowish-green darkening towards posterior end. *Genitalia* (Text-figs. 46, 47) green. *Subgenital plate* (Text-fig. 51) relatively short, its upper and lower margins subparallel. About fifteen ensiform bristles, the uppermost near the base much longer and stronger than the others. Apical half of upper margin with marginal setae. A series of six or seven hairs on upper margin near base. Scattered over the "body" of the plate are long flagellate hairs which are very abundant towards its lower apical region. *Harpagone* (Text-fig. 50) short and stout, terminating in a spine-like point, with three or four denticulations, and with three short stout bristles. *Brachone* (Text-fig. 49) slender and strongly angled upwards about half-way along its length, where it is narrowest. It then widens for half the remainder of its length and is then notched strongly, terminating in a long, stout-pointed portion. *Aedeagus*: Free dorsal lobes somewhat ovate. *Dorsal hook* (Text-fig. 48 and *ds*, fig. 46): an extremely small dorsal hook can be seen under a magnification of 1,000.

Type.—Male, mounted on point in Coll. Queensland Museum, Ho. 5225.

Type locality.—Lockyer, Queensland, Australia, November 6, 1939 (D. O. Atherton), "On lucerne".

Austroasca (Austroasca) terrae-reginae Paoli.

(Text-figures 53–58 and 22–25.)

Empoasca terrae-reginae Paoli, *Mem. Soc. Ent. Ital.*, 15, 1936: 13–14.

Empoasca maculata Evans, *Pap. Proc. Roy. Soc. Tasmania*, 1942: 27.

Suggested common name, the cotton jassid.

Length.—Male: Average of 27 specimens, 3·3 mm.; max. 3·6 mm., min. 3·0 mm. Female: Average of 40 specimens, 4·0 mm.; max. 4·2 mm., min. 3·9 mm. *Colour* yellow with white markings.

Head.—Crown (Text-fig. 53) distinctly produced in a blunt angle. C.I. = 27. Yellow with median, longitudinal, narrow, irregular white stripe, and two sub-oval lateral white marks, midway between eyes and coronal suture. *Face* normal, yellow with broad, white, median, longitudinal stripe and two white stripes from middle of upper part of face directed diagonally towards lower margin of each eye. In many specimens the three stripes are united above to form a broad arrow. Frontal and epicranial sutures obvious. *Antennae* normal, brownish-yellow. *Ocelli* two, one very close to each eye on upper part of face. *Eyes* black.

Thorax.—Pronotum (Text-fig. 53) long, about twice crown length, yellow, with five white marks close to anterior margin, one median and two laterally. These five marks

vary greatly in size and shape but their number and position are constant. *Scutellum* (Text-fig. 53) yellow with a large subrectangular median white blotch between suture and anterior margin of scutellum, lateral margins white. Posterior to suture is a small elongate median white blotch; the two anterior lateral parts of this area are white.

Wings.—Tegmen (Text-fig. 58) normal, colourless hyaline with a small brown irregular spot in cell Cu_1 near the forking of Cu_{1b}. The colour of the spot varies from dark brown to yellowish and its shape is very variable. Its area and position are constant. In cell Sc and near the base of the tegmen is a line of small, circular, colourless protuberances varying in number between twelve and sixteen. Posterior to these is a small raised area formed by the union of from seven to nine such protuberances. A larger protuberance commonly occurs in cell M and a smaller one posterior to it in cell Cu_1. Cross-vein r-m present; R_{1a} perpendicular to costal margin. *Hind Wing* normal, colourless, veins white. *Legs* normal, yello v.

Abdomen.—Normal, dorsally yellow, ventrally yellowish-white. *Genitalia* (Text-figs. 54, 55) yellow, highly characteristic. *Subgenital plate* (Text-fig. 57) extremely long and narrow, its length being approximately ten times its greatest width. About twelve well-developed ensiform bristles. Near its apex ventrally is a number of extremely long flagellate bristles, while a row of similar but somewhat shorter bristles occur along the terminal half of the upper margin, which bears marginal setae in the same region. Towards the base and on and near the upper margin is a group of long thin hairs. The flagellate bristles are so long as to give the plates a hairy appearance even to the naked eye. *Harpagone* (Text-fig. 24) short and stout, terminating in a spine; seven to eight denticulations; three short stout bristles. *Brachone* (Text-fig. 23) extremely long and slender, slightly angled about one-quarter from its base, then straight with a small upcurved tip. Many specimens show a concave notching at the tip (Text-fig. 23A). *Aedeagus* (Text-fig. 56). Free dorsal part curved in an open arc.

Type.—Genitalia dissected and mounted separately, in Coll. British Museum.

Type locality.—Biloela, Queensland, Australia, January 4, 1932 (D. O. Atherton), "From cotton".

Austroasca (Paolia) bancrofti Evans.

(Text-figures 12–19.)

Empoasca bancrofti Evans, *Pap. Proc. Roy. Soc. Tasmania*, 1938: 40.

Length.—Male: One specimens (the type), 4 mm. (Evans' measurement). Female: Two specimens, 5·1 mm., 5·2 mm. (two specimens have the abdomens missing but are adjudged as females on other evidence). *Colour* yellowish with brown markings.

Head.—Crown (Text-fig. 12): C.I. = 12–13. Bright yellow with two oval blackish spots, one posterior to each ocellus. Coronal suture complete. *Face* normal in shape, but differs from all other species in having the coronal, frontal and epicranial sutures all complete and well defined; bright yellow with median, oval, black spot just above level of antenna bases. *Antennae* normal; scape and pedicel yellow; third segment and flagellum brown. *Ocelli* two, orange in colour, one between each eye and median line. *Eyes* black.

Thorax.—Pronotum (Text-fig. 12) yellowish with large, median, transverse, crescentic brown area, the whole finely white pollinose. *Scutellum* (Text-fig. 12) yellow medially with two lateral brown areas and a median apical brown spot.

Wings.—Tegmen (Text-fig. 13): Venation unique; R runs parallel to and very close to C + Sc, uniting with the latter about half-way along the costal margin. It then turns sharply posteriorly and after a bend unites with M, the combined vein R + M continuing on, giving off the branch R_{1a} and eventually forking into R_{1b} and M_{3+4}, thereby eliminating the cross-vein r-m. The cross-vein m-cu, by moving basad, has lengthened, and its anterior termination meets R_{1b} and M_{3+4} at the one point. Along the costal margin is a blue-black band which fills the whole of the area between C and M from the base of the tegmen to the point where R combines with M. A similar blue-black area extends along the posterior margin to the union of Cu_2 with that margin. Scattered over the basal half of the tegmen is a number of small circular protuberances, colourless

in the colourless part and black when these occur in the blackened areas. The remainder of the tegmen is milky white and translucent. *Hind Wing* not studied in detail for reasons given above. Milky white and translucent, veins white. *Legs* normal, yellowish.

Abdomen.—Normal; dorsal surface yellow with median row of brown spots extending along its whole length, two similar rows of lateral brown spots, one on each side of each tergum; ninth tergum and anal tube entirely brown. *Genitalia* yellow (Text-figs. 14, 15). Female genitalia as in genus; male genitalia abnormal. Text-fig. 14 has been reconstructed as explained above. *Pygophore* appears to be quite abnormal, there being no true pygophore as generally understood. This is possibly due to defects in preparation of the material. *Subgenital plate* (Text-fig. 18) short and tapering. Near lower basal margin are five ensiform bristles; after a gap there follow twelve small ensiform bristles and six small bristle-like hairs near the apex; marginal setae, flagellate bristles and fine hairs appear to be missing. *Harpagone* (Text-fig. 16) large, stout, twisted, but apparently of a simple type; the end is broadly rounded with five blunt teeth; there is no sign of bristles. *Brachone* (Text-fig. 17) long, slender, curved at the tip. *Dorsal hook* (Text-fig. 19), although much smaller than in other genera of the Empoasciti, is larger than in any other species of *Austroasca* s.lat. Its tip bears a V-shaped ridge and it is strongly sclerotized. *Aedeagus* has been torn in the type genitalia and its shape cannot be made out.

Type material.—Holotype male mounted on pin. Genitalia and tegmen mounted separately. In Coll. Division of Entomology, C.S.I.R.O., Canberra, A.C.T.

Type locality.—Eidsvold, Queensland, Australia (T. Bancroft). In view of the paucity of material (I have not yet seen a complete male) the status of this species must be somewhat conjectural. The complete sutures of the head and the abnormal tegmen venation are features common to the five specimens examined, but no certainty can be arrived at until I have thoroughly examined and dissected a complete male. Only in this way will it be possible to determine the exact nature of the parts of the genitalia and their spatial relationship. When I have had the opportunity of so doing, certain of the above statements may need modification.

Appendix.

Translations of Paoli's descriptions of *A. viridigrisea* and *A. terrae-reginae.*

A. VIRIDIGRISEA.

"Colour of body (when dry) greyish green, with almost colourless tegmina; eyes very pale.

Head with vertex rounded in the male (in the female?), its length not much more than half the width between the eyes (7:12), with its posterior margin somewhat incurved.

Tenth abdominal segment rather short, the ventral surface with a sprinkling of very short spines united into comb-like groups; processes of the anal tube [dorsal hooks] very short in the form of small protuberances, weakly sclerotized.

Aedeagus strongly curved in the free terminal part.

Genital laminae [subgenital plates] short and broad with the ensiform bristles moderately dispersed; on the upper margin is a group of rather numerous (about 12) long bristles, the remainder bearing short bristles; sternal surface with a fringe of medium length bristles about half as long as the width of the lamina.

Upper styli [brachones] well protected, concealed, wide at the base, then rapidly narrowing and curving, sharp at the apices.

The lower styli [harpagones] wide at the base, then gradually tapering and recurved with 4–5 lateral bristles and 8–9 teeth at each apex.

The abdominal apodemes appear to be missing, since, in the one preparation that I was able to make, and that comprising almost the entire abdomen, these could not be traced.

Body length of the male (when dry) mm. 1·9–2, including the wings 2·8–2·9.*

* These measurements are much smaller than in any specimen I have seen.—*Author.*

Habitat: Bowen, Queensland (Australia) near Pomodori. (Sent by D. O. Atherton.)

I have seen three males in the British Museum Collection. These are labelled:

Bowen, Q. 20.10.31, D.O.A.
Queensland. R. Veitch.
Host: Tomato, D. O. Atherton.

Type in British Museum.

Observations: This species, by the reduction of the upper styli and the probable lack of abdominal apodemes is most closely allied to *E. decedens* Paoli, but the aedeagus is not sclerotized nor curved at an angle at the tip."

A. TERRAE-REGINAE.

"Body wholly pale yellow (when dry) with colourless tegmina; eyes almost black, ocelli brownish.

Head anteriorly rounded in the male, slightly more produced in the female; the length of the vertex is a little more than half the width between the eyes. The long pronotum is one and a half times the length of the head with its posterior margin a little incurved.

The tenth abdominal segment has its ventral surface uniformly covered with spines for the whole of its length; the processes of the anal tube [dorsal hooks] are short, bent into straight teeth incurved at the apices. The free slender part of the aedeagus is curved in an arc.

Laminae [sub-genital plates] long, straight, with the greatest width near the basal part, and narrowing towards the apices; the ensiform bristles are of two kinds; those near the apices are fine, about 4–5 times as long as the width of the lamina, and terminate in flagella; towards the base they assume the normal form, but are always fairly long; both kinds overlap in the medial region; the upper margin bears rather slender bristles but these are shorter than those of the lower margin; in the basal half, marginal setae are lacking on the upper margin. The sternal surface bears short setae situated almost in the middle of the distal half; these become thin and very long on the basal half.

The elongated upper genital styli [brachones] are almost straight with a slight curve very near their apices; sometimes, at the curve the style shows a slight concavity.

The lower genital styli [harpagones] gradually taper with 2–3 big bristles at the distal half and 7–8 teeth near the tip, which is prolonged into a sharp point.

Abdominal apodemes not seen through scarcity of material.

Length of body of male mm. 2·3; including the wings mm. 2·8; of the female 2·1–2·3; including the wings 2·8–2·9.

Habitat: Biloela, Queensland (Australia), from D. O. Atherton. I have seen 2♂ and 2♀ collected from cotton, 4th January, 1932 (British Museum). These are labelled:

Biloela,
4.1.32,
From Cotton,
D. O. Atherton,
Queensland.

Type in British Museum.

Observations: In some characters, such as size and pale coloration, this species shows affinities with *E. facialis* Jac., but more particularly through the long straight laminae bearing abundant and long bristles. The scarcity of material has prevented my examining other features such as the presence and shape of the abdominal apodemes but *the characters indicated above are so specialized that they are sufficient for the precise determination of the species.*" *

* The italics are mine.—*Author.*

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EXPLANATION OF PLATE XV.

Left.—Portion of stem of black nightshade (*Solanum nigrum*), × 0·8. Plant has been killed by feeding of *A. viridigrisea*.

Right.—Typical damage done by feeding of *A. viridigrisea*. 1. Leaf of *Amaranthus viridis*. The black specks are the execreta of the insects. 2. Leaf of *Malva parviflora* (small-flowered mallow). 3. Leaf of *Medicago sativa* (lucerne). 4. Leaf of *Apium graveolens* (celery). 5. Leaf of *Citrullus vulgaris* (pie-melon).

MISCELLANEOUS NOTES ON AUSTRALIAN DIPTERA. XV.

TABANUS, HETEROPSILOPUS.

By G. H. Hardy.

[Read 28th November, 1951.]

Synopsis.

In family Tabanidae two new synonyms are given for *Tabanus imperfectus* Walker, and the characters are discussed. In Dolichopodidae, a key is given for the genus *Heteropsilopus* and new synonymy is recorded.

Genus Tabanus, subgen. Dolichapha Enderlein.

Hardy, 1948, *Proc. Roy. Soc. Queensland*, 59: 169–178.

The subgenus is defined in the above reference, and it covers the *Tabanus circumdatus*-complex and the closely allied *imperfectus*-complex, both of which have become so involved in literature that no author seems to have a clear understanding of the components. The typical *circumdatus* form is light brown, and the typical *imperfectus* form is blackish, but varying in the amount of lighter brown which is more or less confined to the base of the abdomen. Specimens in collections show a wide range between these colours and, as shown below, the shape of the frontal callus cannot be considered fully reliable for specific identification.

There seems to be no hope of disentangling the confusion brought about in these species without field experience, and the collection from each type locality of sufficient specimens to cover all variations that may occur there, for study whilst in a fresh condition. Especially is the male required, from which sex has to be established the specific status in each locality. I anticipate that the species passing under the name *imperfectus* in Tasmania, which has no enlargement of facets in the eye of the male, will be found to differ from the mainland form which apparently has enlarged facets, but this character may be subspecific in status.

Tabanus imperfectus Walker.

T. imperfectus Walker, 1848, *List Dipt. Brit. Mus.*, 1: 179.—Ricardo, 1915, *Ann. Mag. Nat. Hist.*, (8) 16: 278.—? White, 1915, *Proc. Roy. Soc. Tasmania*, 11.

T. dubiosus Ricardo, 1915, *Ann. Mag. Nat. Hist.*, (8) 16: 284 (*dubiosa* in error).

T. indefinitus Taylor, 1918, *Rec. Austr. Mus.*, 12: 68.

Synonymy.—Walker's type of *imperfectus* was described by Ricardo as having an enlarged callus taking up "the whole of the anterior half of the forehead" and no extension of the callus was seen by her. She records it from New South Wales.

T. dubiosus Ricardo, based on Queensland specimens, at the same time recorded from Katoomba, New South Wales, is said to have the callus almost reaching the eyes, oblong, the linear extension ending in a point.

T. indefinitus Taylor, also from the Blue Mountain area, is said to have its callus as wide as the frons and with a short extension. The type shows the callus agreeing with the description, and yet corresponding with two specimens from Katoomba the callus of which is open to varied interpretations explained below. In Australian collections specimens standing under the three names are certainly one species.

These two Katoomba specimens were caught early in November, 1949, and, although not long emerged, already had their frons abraded, being bare of vestiture over a wide area. The apparent callus is therefore large, somewhat gothic-arched in shape, ending in a point two-thirds towards the summit. The lower half of the frons is almost completely occupied by this pseudocallus and the arching extension is in no way divided from it. When judged to be abraded, and seeking the true outline, one can

imagine a slender process arising from a practically eye-to-eye oblong callus, or even an oblong without a process. Even this may be reduced to a squarish or roundish object, well separated from the eyes, a view justified by the evident but very minute hair-pits scattered over the surrounding area.

After collecting various extra specimens at Katoomba, and after re-examining the material used by Taylor, I considered that both Ricardo and Taylor were deceived by appearances, due to the condition of the specimens they studied, all specimens from the Blue Mountain area being but one species.

T. imperfectus White, described from Mangalore, Tasmania, shows a wide variety of pseudocalli on specimens available for study, but it is doubtful if it be truly conspecific with the mainland form.

Characters.—A dark, hairy-eyed species, with the apical markings of each segment ashy-white, faintly yellowish at times, the colour merging into a central white spot on a blackish-brown abdomen; the sides of the first two segments are often lighter brown. The true callus is probably small, well separated from the eyes, but the frons becomes so readily denuded that the callus becomes ill-defined and it is not known if a true extension occurs. Minute hair-pits scattered over the surface will denote that abrasion has taken place, forming a pseudocallus. The vestiture of the frons is mainly dark greyish with some brown staining over the central area. Apparently on specimens that are old when caught, the frons slightly collapses, becoming parallel sided, but normally the frons widens slightly towards the antennae.

Remarks.—Taylor refers to golden hairs in the abdominal spots and margins. These are slightly yellowish on his type, so I presume Taylor examined them under artificial light to see them as golden.

Hab.—In literature the species is recorded from Queensland to Tasmania. It occurs at Katoomba, New South Wales, rather sparingly, specimens being taken from November, 1949, through the summer months, but only 14 were captured over the period. In the summer 1950–51 only three were seen. The collecting area is around a swamp on Katoomba Creek, which supports *Scaptia auriflua* Don., *S. patula* Walk. and *S. brevicornis* Macq., all in small numbers, but no male of a *Tabanus* was seen there. Another *Tabanus* occurs and seems to be a rare undescribed species of subgenus *Cydistomyia.*

Genus Heteropsilopus Bigot, 1859.

The limits of the genus are not certainly known. *Chrysosoma interruptum* Becker and *C. caelicum* Parent, differing only in having the third antennal segment at least one and a half times longer than broad and with a terminally placed arista, probably belong here, but the following key contains only those with typical antennae.

Key to species of genus Heteropsilopus.

1. Anterior tarsi combined are 2½ times longer than the tibia ..... *jacquelinei* Parent.
   Anterior tarsi combined are less than twice the length of the tibiae 2
2. First posterior tarsus as long as the four following segments combined 3
   First posterior tarsus shorter 4
3. Abdomen rarely with yellow above, then limited to the anterior margins of the first two segments. Male with intermediate tarsi fringed with hook-shaped cilia .... *cingulipes* Walker.
   Abdomen with conspicuous yellow parts at least basally. Male with a cuticular apical spur on the first segment of the intermediate tarsus ..... *brevicornis* Macquart.
4. First posterior tarsus as long as the three following segments combined. Anterior tarsi combined only 1⅓ the length of tibia. Male intermediate tarsi with the two apical segments peculiarly formed ..... *ingenuus* Erichson.
   First posterior tarsus as long as the two following segments combined. Anterior tarsi combined 1½ length of tibia. Male with a broadened fifth segment on the intermediate tarsi ..... *trifasciatus* Macq.

In this key the proportional lengths of tarsal segments are those given in descriptions, but slight variations may be found on specimens from different regions. It has yet to be shown that the two names in couplet 4 are not based on the one species.

HETEROPSILOPUS CINGULIPES Walker.

Psilopus cingulipes Walker, *Ent. Mag.*, 2, 1835: 472.—*Sciapus plumifera* Becker, *Cap. Zool.*, 1, 1922: 206.

Synonymy.—That Becker's species should prove conspecific with that of Walker is quite unexpected, but the evidence is based on field observations, leaving no doubt concerning this synonymy. Collecting around my laboratory at Katoomba, I found not only were the two forms present, but also during the latter half of December all grades between them in colour variations were present. The species occurred in enormous numbers, persisting through the summer in diminishing quantities.

In various collections, where specimens come from mainly low-land areas, the dominant type is the clear winged *cingulipes*, but the dark winged form also occurs there. From the Blue Mountains come (*a*) specimens with wings clear and faintly marked; (*b*) two bands formed but isolated from the costa, and these bands when interrupted centrally may become four spots on the wing; (*c*) the two bands, though reaching the costa, do not join together, varying to join together as in Becker's illustration. The third band, which is normally small and interrupted, also varies in density of colour and in the amount of area covered.

Other parts are similarly variable, the anterior coxae varying from pale yellow, almost white, to intensely yellow, and usually they are fuscous coloured on the anterior side. The abdomen may be entirely metallic, varying to mainly yellow below, this yellow spreading above along the anterior border of the first two segments.

In December, 1950, five specimens with lightly marked wings were kept, each in a separate glass tube; one died, the other four had developed full and dense colour markings five days afterwards.

On this evidence it would seem that the synonymy given by me in 1935 is mainly correct, the exception being that doubtfully placed *Chrysosoma metallicum* Parent, 1932, a female now removed. Some mainland specimens have been referred to as *trifasciatus* Macq. and most of these are *H. ingenuus* Erich., but probably some belong to the present species, the two being very alike in characters.

Characters.—On the male the intermediate tarsi contain easily overlooked cilia, forming a row of bent-over, hook-shaped hairs, about 20 of these hairs to the millimetre. The row forms a fringe reaching the tibia, on which it peters out by narrowing down to very small hairs. Other characters are given in the key.

Notes.—On the above evidence it may be assumed that other species are similarly variable in coloration to a greater or less extent and that these variations are found mainly during the early part of the season in which they occur. There are apparent trends to regional variations which also must be taken into account.

HETEROPSILOPUS TRIFASCIATUS Macquart.

Psilopus trifasciatus Macquart, 1849.—*Chrysosoma metallicum* Parent, 1932.

Synonymy.—Macquart's type, redescribed by Parent as having the first segment of the posterior tarsi equal to the length of the two following segments combined, conforms to *C. metallicum*, which feature suggests the above synonymy. The type of the latter is a female, whereas Macquart's type is a male, of which Parent gives the tarsal drawing that does not conform with *H. ingenuus* Erich., and is perhaps due to slight damage.

Hab.—Macquart gives Tasmania as type locality in his fourth supplement, but Sydney is likely to be the true locality.

HETEROPSILOPUS INGENUUS Erichson.

Psilopus ingenuus Erichson, 1842.—*Scapius chalceus* White, 1916.

Synonymy.—The type of *chalceus*, a female specimen, may be the present species with duller colour and less wing marking than is normally found. It was captured early in the season.

Characters.—On the male the apical segments of the intermediate tarsi are peculiarly formed, the shape being illustrated by Parent under the name *gloriosus*,

which is a synonym. The smaller size and the extension of the apical band along the costa to the wing tip (as illustrated for *trifasciatus* by Macquart) will serve to distinguish the form from *cingulipes*.

Hab.—The species is definitely known from Tasmania, Victoria, and the Blue Mountains of New South Wales. It was found in moderate number at Katoomba in December, 1950, but became scarce in the following month. One specimen had as prey a species of *Simulium*.

HETEROPSILOPUS BREVICORNIS Macquart.

Synonymy.—Parent's remarks about the type state that the middle tarsi are not ornamented, and this was supplemented later in a letter which stated that he could not dissociate the name from the present form. There is need for more clarity in references, but it seems that *Scapius chalceus* White, 1916, must be removed from the synonymy.

HETEROPSILOPUS JACQUELINEI Parent.

Sciopus jacquelinei Parent, *Ann. Soc. Sci. Bruxelles*, (B) 52, 1932: 169.

Characters.—Presumably the intermediate tarsi are simple on the male, the first segment being described as one and a half times the length of the following segments combined. The description was based on a unique male from Canberra and has not been recognized in collections available to me.

LINNEAN MACLEAY FELLOWSHIPS ACCOUNT.

BALANCE SHEET at 28th February, 1951.

LIABILITIES.	£	s.	d.	ASSETS.	£	s.	d.	£	s.	d.
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	18,470	1	0	Debentures:						
				Metropolitan Water, Sewerage and Drainage Board, at cost	14,606	14	9			
				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			
								53,184	9	9
				Current Assets—						
				Commonwealth Savings Bank				285	11	3
	£53,470	1	0					£53,470	1	0

INCOME ACCOUNT. Year Ended 28th February, 1951.

	£	s.	d.		£	s.	d.
To Salaries of Linnean Macleay Fellows	1,056	14	4	By Interest	1,931	8	3
„ Payroll Tax	3	18	9				
„ Balance, being Surplus Income transferred to General Account	327	9	6				
„ Capital Account	543	5	8				
	£1,931	8	3		£1,931	8	3

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 28th February, 1951, 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 28th February, 1951, as shown by the books. Certificates of the investments have been inspected.

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

Sydney, 20th March, 1951.

A. B. Walkom,
Hon. Treasurer.

2nd March, 1951.

BACTERIOLOGY ACCOUNT.

BALANCE SHEET at 28th February, 1951.

LIABILITIES.	£	s.	d.	ASSETS.	£	s.	d.	£	s.	d.
Accumulated Funds—				Fixed Assets—						
Amount bequeathed by Sir William Macleay	12,000	0	0	Commonwealth Loans, at cost	17,320	0	0			
Accumulated Income Capitalized	6,120	0	0	Debentures: Metropolitan Water, Sewerage and Drainage Board, at cost	800	0	0			
	18,120	0	0					18,120	0	0
Income Account at 28th February, 1951	1,171	12	6	Current Assets—						
				Commercial Banking Company of Sydney Ltd.	616	1	5			
				Commonwealth Savings Bank	555	11	1			
								1,171	12	6
	£19,291	12	6					£19,291	12	6

INCOME ACCOUNT. Year Ended 28th February, 1951.

	£	s.	d.		£	s.	d.
To Salary	470	16	8	By Balance from 1949–50	3,077	14	11
„ Travel Allowance	300	0	0	„ Interest	584	7	11
„ Equipment and Repairs	48	2	6	„ Donations	650	0	0
„ Field Expenses	14	16	0				
„ Expenses	6	15	2				
„ Capital Account	2,300	0	0				
„ Balance to 1951–52	1,171	12	6				
	£4,312	2	10		£4,312	2	10

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 28th February, 1951, 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 28th February, 1951, as shown by the books. Certificates of the investments have been inspected.

A. B. Walkom,
Hon. Treasurer.

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

Sydney, 20th March, 1951.

2nd March, 1951.

ABSTRACT OF PROCEEDINGS.

ORDINARY MONTHLY MEETING.

28th March, 1951.

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

Library accessions amounting to 28 volumes, 246 parts or numbers, 32 bulletins, 12 reports and 58 pamphlets, total 376, had been received since the last meeting.

PAPERS READ (by title only).

1. A *Septoria* Disease of *Euphorbia peplus* L. By Dorothy E. Shaw.

2. Serological Studies of the Root-nodule Bacteria. IV. Further Analysis of Isolates from *Trifolium* and *Medicago*. By Hilary F. Purchase, J. M. Vincent and Lawrie M. Ward.

3. Preservation Techniques for Scarabaeid and other Insect Larvae. By P. B. Carne.

ORDINARY MONTHLY MEETING.

26th April, 1951.

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

The President announced that the Council had elected the following office-bearers for the 1951–52 session: Vice-Presidents, Dr. G. D. Osborne, Dr. Lilian Fraser, Dr. R. N. Robertson and Mr. D. J. Lee; Honorary Treasurer, Dr. A. B. Walkom; Honorary Secretary, Dr. W. R. Browne.

Dr. T. Clive Backhouse, D.P.H., D.T.M. & H., F.R.A.C.P., Sydney University, was elected an Ordinary Member of the Society.

Library accessions amounting to 22 volumes, 139 parts or numbers, 26 bulletins and 19 pamphlets, total 206, had been received since the last meeting.

PAPERS READ.

1. The Anatomy and Morphology of the Operculum in the Genus *Eucalyptus*. Part I. The Occurrence of Petals in *Eucalyptus gummifera* (Gaertn.) Hochr. By J. L. Willis.

2. Some Notes on *Athrotaxis*. By Charles G. Elliott. (*Communicated by Dr. Patrick Brough.*)

3. The Paramphistomes (Trematoda) of Australian Ruminants. Part I. Systematics. By P. H. Durie.

Short addresses were given by Professor Emmons (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.

ORDINARY MONTHLY MEETING.

27th June, 1951.

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

Mr. A. S. Fraser, M.Sc., Sydney University, Mr. H. B. Kerr, B.Sc.Agr., Croydon, Dr. B. J. F. Ralph, B.Sc., A.A.C.I., University of Technology, Sydney, and Mrs. C. E. Seccombe, B.A., Bellevue Hill, were elected Ordinary Members of the Society.

The President offered congratulations to the following members: 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, being the first occasion on which the scholarship has been awarded to a woman; and Dr. A. R. Woodhill, on obtaining the D.Sc. degree of the University of Sydney.

Library accessions amounting to 23 volumes, 144 parts or numbers, 33 bulletins, 13 reports and 14 pamphlets, total 227, had been received since the last meeting.

PAPERS READ.

1. A Review of the Australian Species of *Sarcochilus* (Orchidaceae). By H. M. R. Rupp.

2. Australian Rust Studies. VIII. *Puccinia graminis lolii*, an Undescribed Rust of *Lolium* spp., and Other Grasses in Australia. By Professor W. L. Waterhouse.

3. On *Trombicula minor* Berlese, 1905. By Carl E. M. Gunther.

4. Studies on Australian Marine Algae. VI. New Geographical Records of Certain Species. By Valerie May.

5. The Marine Algae of Brampton Island, Great Barrier Reef, off Mackay, Queensland. By Valerie May.

6. The Evolution of the Radio-medial Area in the Wings of the Muscoidea Acalyptrata (Diptera). By H. F. Lower.

An address was given by Dr. Baas-Becking, a distinguished Netherlands botanist, entitled "A Biologist Looks at the Problem of Waste".

ORDINARY MONTHLY MEETING.

25th July, 1951.

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

Mr. B. R. Hewitt, Kempsey, N.S.W., was elected an Ordinary Member of the Society.

The President announced that Dr. F. V. Mercer had been elected a member of Council in place of Dr. R. N. Robertson, who had resigned.

The President referred to the death of Dr. Robert Broom, who had been a Corresponding Member of the Society since 1902, on 6th April, 1951, aged 84.

The President offered congratulations to Dr. Janet Harker, F.R.E.S., on obtaining the Ph.D. degree of the University of Manchester, and to Dr. G. F. Humphrey, on the award of the Ph.D. degree of the University of Sydney.

Library accessions amounting to 17 volumes, 116 parts or numbers, 4 bulletins, 2 reports and 13 pamphlets, total 152, had been received since the last meeting.

PAPERS READ.

1. A Mite from a Beehive on Singapore Island (Acarina: Laelaptidae). By Carl E. M. Gunther.

2. *Celaenopsoides* Gunther, 1942: A Synonym of *Ophiomegistus* Banks, 1914 (Acarina: Parasitidae). By Carl E. M. Gunther.

3. The Development of Bryozoan Faunas in the Upper Palaeozoic of Australia. By Joan Crockford (Mrs. Beattie).

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

ORDINARY MONTHLY MEETING.

29th August, 1951.

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

Messrs. E. S. Lowery, M.A., Northmead, N.S.W., and D. K. McAlpine, Bronte, N.S.W., were elected Ordinary Members of the Society.

The President announced that Dr. A. R. Woodhill had been elected a Vice-President for the remainder of the current session in place of Dr. R. N. Robertson, who had resigned from the Council.

Library accessions amounting to 7 volumes, 73 parts or numbers, 44 bulletins and 3 reports, total 127, had been received since the last meeting.

PAPERS READ.

1. Succinoxidase of Potato Tuber. By Adele Millerd.

2. Controlled Pollination of *Eucalyptus*. By L. D. Pryor.

3. A Genetic Analysis of some *Eucalyptus* Species. By L. D. Pryor.

4. Investigations on the Preferences shown by *Aëdes* (*Stegomyia*) *aegypti* Linn., and *Culex* (*Culex*) *fatigans* Wied., for Specific Types of Breeding Water. By Tom Manefield.

5. The Nomenclature of *Heteronychus sanctae-helenae* Blanchard (Coleoptera: Scarabaeidae: Dynastinae). By E. B. Britton. (*Communicated by P. B. Carne.*)

NOTES AND EXHIBITS.

Miss Kathleen M. I. English exhibited an introduced slug, *Testacella haliotidea. Testacella*, a carnivorous snail slug, was discovered in considerable numbers in Adelaide Botanic Gardens in 1931. In 1949, they were recorded from a garden in Geelong, Victoria, where they had been noticed for some years. Distribution: Europe and Canary Is. References: *Wild Life*, xi, pp. 506 and 516 (Nov., 1949); xii, p. 84 (Feb., 1950).

Mr. A. Musgrave exhibited specimens of the Giant Orb-weaver, *Nephila maculata* (Fabricius, 1793), a member of the Family Eperidae (= Argiopidae) from the North Coast of New South Wales. Three females of this species have been forwarded to the Australian Museum, Sydney, during the past decade. Two of these were sent by Dr. G. H. Hewitt of Bellingen, Bellinger River, and were collected about 12th January, 1941, and the 2nd February, 1951 (the last from Repton near the mouth of the river). The third specimen came from Glenreagh, a little north of Bellingen, and was collected by Mr. D. Thompson, 11th June, 1950. The spider has a wide range from Africa, through India to China and the Pacific Islands. In Australia it has only been recorded from Queensland, so that these records from the Bellingen district extend the range of the spider further south.

On behalf of Professor P. D. F. Murray, Mr. A. N. Colefax exhibited specimens of young turtles from the Great Barrier Reef. These had been stained with alizarin, and cleared, in order to show the development of the bony skeleton. All of the bony elements were bright red, and were in strong contrast to the remaining tissues which remained unstained, though transparent. Fixed, but otherwise untreated specimens, were also shown by way of comparison.

ORDINARY MONTHLY MEETING.

26TH SEPTEMBER, 1951.

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

Miss Helen P. Lancaster, B.Sc., University of Sydney, was elected an Ordinary Member of the Society.

The President referred to the death on 19th September, 1951, of Mr. Edwin Cheel, who had been a member of the Society since 1899, a member of Council from 1925 to 1940, and President, 1930–31; also to the death, on 30th August, 1951, of Professor T. Harvey Johnston, a member of the Society since 1907.

The President announced that the Council is prepared to receive applications for Linnean Macleay Fellowships tenable for one year from 1st January, 1952, from qualified

candidates. Applications should be lodged with the Hon. Secretary not later than Wednesday, 7th November, 1951.

Library accessions amounting to 9 volumes, 155 parts or numbers, 36 bulletins, 3 reports and 13 pamphlets, total 216, had been received since the last meeting.

PAPER READ.

The Life-history of a Penaeid Prawn (*Metapenaeus*) breeding in a Coastal Lake (Tuggerah, New South Wales). By Muriel C. Morris and Isobel Bennett.

Addresses were given 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.

NOTES AND EXHIBITS.

Mr. A. J. Bearup exhibited a blood-film of an Australian gecko, *Phyllurus platurus* (Shaw), collected at Glen Davis by Mr. R. Palmer on 6th August, 1951, showing chromatin bodies and vacuoles similar to those described by Chatton and Blanc as *Pirhaemocyton tarentolae*. The film also showed haemogregarines and microfilariae. The adult filarial worms were found in the mesentery supporting the liver.

Dr. F. V. Mercer exhibited a lantern slide of a caterpillar, which had been collected by Miss K. English, on a dried branch of *Eucalyptus eugenioides*, exhibiting mimicry of its surroundings to a remarkable degree. The most striking feature of the mimicry was the similarity between the top of the head and the broken end of the twig.

ORDINARY MONTHLY MEETING.

31st October, 1951.

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

Miss Isobel I. Bennett, Crow's Nest, N.S.W., and Mr. G. H. Packham, Earlwood, 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, 1952, from qualified candidates. Applications should be lodged with the Hon. Secretary not later than Wednesday, 7th November, 1951.

Library accessions amounting to 22 volumes, 116 parts or numbers, 5 reports and 5 pamphlets, total 148, had been received since the last meeting.

PAPERS READ.

1. Remarks on some Australian *Laius* Guér. (Col. Malachiidae). By Walter Wittmer. (*Communicated by J. W. T. Armstrong.*)

2. A Critical Consideration of c-mitosis with Reference to the Effects of Nitrophenols. By Mary M. Hindmarsh, Linnean Macleay Fellow in Botany.

NOTES AND EXHIBITS.

Miss M. Hindmarsh exhibited a film of mitosis in the reproductive cells of the Grasshopper. The development of the phase contrast microscope has made possible observations on living cells and this technique has been employed in making this film.

Dr. R. N. Robertson exhibited a preparation of plant mitochondria which had been extracted from tissue of red beet and an electron micrograph of mitochondria taken by Dr. E. H. Mercer.

Mr. A. N. Colefax exhibited a device for the rapid moulding of metal foil containers for paraffin embedding. Attached to a wooden base is a rectangle of 18g. flat brass the size of the blank, and a small block of brass the size and shape of the desired container.

The lead foil is first rubbed on the flat plate to imprint the size of the latter on it, cut to size with a pair of scissors, and then moulded, by the fingers, around the brass block. This gives a one-piece container with the usual triangular flaps at the ends.

Speed of production is high, and it is recommended that several sizes of blanking plate and block be mounted on the one base, in order to cover a range of containers commonly used in embedding.

Mr. D. J. Lee gave a short summary of recent observations and the importance of entomological work in connection with outbreaks of myxomatosis and encephalitis in Eastern Australia.

ORDINARY MONTHLY MEETING.

28th November, 1951.

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

Professor L. G. M. Baas-Becking, Ph.D., D.Sc., Botany Department, Sydney University, and Mr. Colin L. Macdonald, Lewisham, N.S.W., were elected Ordinary Members of the Society.

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 1952.

The President also announced that a series of eight broadcast lectures on "The Nature of the Universe", by Fred Hoyle, will be broadcast by the National Station on the first eight Friday nights in 1952, i.e., 4th January to 22nd February, 1952, at 7.30 p.m.

Library accessions amounting to 20 volumes, 168 parts or numbers, 24 bulletins and 3 reports, total 215, had been received since the last meeting.

PAPERS READ.

1. Miscellaneous Notes on Australian Diptera. XV. *Tabanus*, *Heteropsilopus*. By G. H. Hardy.

2. A Revision of Australian Species previously referred to the Genus *Empoasca* (Cicadellidae, Homoptera). By Harold F. Lower.

3. The Use of Excised Shoots in Linseed Investigations. By H. B. Kerr.

The President referred to the 60th anniversary (on 7th December, 1951) of the death of the Society's benefactor, Sir William Macleay, and historic personal relics were exhibited.

A welcome was extended to a party of scientists from the Danish research frigate "Galathea"; and a lecture was given by Dr. Anton Bruun, leader of the expedition, 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.

LIST OF MEMBERS.

(15th December, 1951.)

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.
1912 Aurousseau, Marcel, B.Sc., c.o. Mr. G. H. Aurousseau, 16 Woodland Street, Balgowlah, N.S.W.

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.
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), Bradley Street, Cobar, N.S.W.
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, B.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.
1947 Bradhurst, Miss Peggy Joan, B.Sc., 25 Belgium Avenue, Roseville, N.S.W.
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, 34 Kent Road, Rose Bay, N.S.W.
1911 Browne, William Rowan, D.Sc., Department of Geology, Sydney University.
1943 Bryan, Clement, B.A., Intermediate High School, Corowa, N.S.W.
1949 Burden, John Henry, 1 Havilah Street, Chatswood, N.S.W.
1931 *Burges, Professor Norman Alan, M.Sc., Ph.D., Botany School, Sydney University.
1920 Burkitt, Professor Arthur Neville St. George Handcock, M.B., B.Sc., Medical School, Sydney University.

1949 Campbell, Mrs. Emily Mary, 22 Madeline Street, Hunter's Hill, N.S.W.
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.Sc. (Melb.), Department of Entomology, Imperial College of Science and Technology, Prince Consort Road, London, S.W.7, England.
1905 Carne, Walter Mervyn, 7 De Villiers Avenue, Chatswood, N.S.W.
1936 *Chadwick, Clarence Earl, B.Sc., Entomological Branch, Department of Agriculture, Farrer Place, Sydney.
1947 Christian, Stanley Hinton, Malaria Survey, Banz, Central 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., P.O. Box 13, Bright, Victoria.
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, B.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., Department of Geology, Sydney University.
1950 Crawford, Lindsay Dinham, B.Sc., 4 Dalton Avenue, West Hobart, Tasmania.

1945 Davis, Mrs. Gwenda Louise, B.Sc., New England University College, Armidale, N.S.W.
1948 Davison, Miss Daphne Claire, M.Sc., 9 Brissenden Avenue, Collaroy, N.S.W.
1950 Day, Alan Arthur, 13 Besborough Avenue, Bexley, 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.
1927 *Dixson, Sir William, "Merridong", 586 Gordon Road, Killara, 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.

1948 Ealey, Eric H. M., 18 Ray Road, Epping, N.S.W.
1941 Edwards, Eric Thomas, Ph.D., M.Sc.Agr., National Press Pty. Ltd., 126-130 Phillip Street, Sydney.
1949 Elliott, John Henry, 8 Shellcove Road, Neutral Bay, N.S.W.
1947 Endean, Robert, M.Sc., 15 Milton Avenue, Eastwood, N.S.W.
1930 English, Miss Kathleen Mary Isabel, B.Sc., 1 Mt. Morris Street, Woolwich, N.S.W.

1947 Fenton, Miss Enid Grace, 45 Cecil Street, Gordon, N.S.W.
1948 Fraser, Ian McLennan, 131 Fox Valley Road, Wahroonga, N.S.W.
1948 Fraser, Miss Judith A., M.Sc., 14 Milray Avenue, Wollstonecraft, N.S.W.
1930 Fraser, Miss Lilian Ross, D.Sc., "Hopetoun", 25 Bellamy Street, Pennant Hills, N.S.W.

1950 Garden, Miss Joy Gardiner, B.Sc.Agr., Botanic Gardens, Sydney.
1935 *Garretty, Michael Duhan, D.Sc., "Surrey Lodge", Mitcham Road, Mitcham, Victoria.
1944 Greenwood, William Frederick Neville, c.o. Colonial Sugar Refining Co. Ltd., Lautoka, Fiji.
1946 *Griffiths, Mrs. Mabel, B.Sc. (*née* Crust), 2 Carden Avenue, Wahroonga, N.S.W.
1936 Griffiths, Mervyn Edward, M.Sc., Australian Institute of Anatomy, Canberra, A.C.T.
1939 *Gunther, Carl Ernest Mitchelmore, M.B., B.S., D.T.M., D.T.M. & H. (England), Bulolo Gold Dredging Limited, Bulolo, Territory of Papua–New Guinea.

1950 Hallinan, John Michael, "Quirindi", 65 Dunmore Street, Bexley, N.S.W.
1928 Hamilton, Edgar Alexander, 16 Hercules Street, Chatswood, N.S.W.
1917 Hardy, George Huddleston Hurlstone, "The Gardens", Letitia Street, Katoomba, N.S.W.
1947 Harker, Janet Elspeth, M.Sc., Ph.D., F.R.E.S., c.o. Zoological Department, The University, Manchester 13, England.
1932 Harris, Miss Thistle Yolette, B.Sc., 14 Pacific Street, Watson's Bay, N.S.W.
1947 Henderson, David Leonard Wylie, L.S.M.I.S., "Berida", R.M.B. 420, Bourke, N.S.W.
1951 Hewitt, Bernard Robert, c.o. Box 177, Kempsey, 2C, N.S.W.
1930 Heydon, George Aloysius Makinson, M.B., Ch.M., Flat 5, 79 O'Sullivan Road, Rose Bay, N.S.W.
1938 Hill, Miss Dorothy, M.Sc., Ph.D., Department of Geology, University of Queensland, Brisbane, Queensland.
1943 Hindmarsh, Miss Mary Maclean, B.Sc., Botany School, University of Sydney, N.S.W.
1930 Holmes, Professor James Macdonald, Ph.D., B.Sc., F.R.G.S., F.R.S.G.S., Department of Geography, Sydney University.
1943 Horowitz, Benzoin, Eng.Agr.S., Dr.Agr.Sc. (Cracow, Poland), C.S.I.R.O., c.o. Waite Institute, Private Mail Bag, Adelaide, South Australia.
1932 Hossfeld, Paul Samuel, M.Sc., 132 Fisher Street, Fullarton, South Australia.
1942 Humphrey, George Frederick, M.Sc., Ph.D., Department of Biochemistry, Sydney University.

1917 Jacobs, Ernest Godfried, "Cambria", 106 Bland Street, Ashfield, N.S.W.
1938 Jacobs, Maxwell Ralph, D.Ing., M.Sc., Dip.For., Commonwealth Forestry Bureau, Canberra, A.C.T.
1947 Johnson, Lawrence Alexander Sidney, B.Sc., 178 Beecroft Road, Cheltenham, N.S.W.
1945 Johnston, Arthur Nelson, B.Sc.Agr., Hawkesbury Agricultural College, Richmond, N.S.W.
1937 Jones, Mrs. Valerie Margaret Beresford, M.Sc. (*née* May), Mooloolabel Esplanade, Narrabeen, N.S.W.
1930 Joplin, Germaine Anne, B.Sc., Ph.D., Bureau of Mineral Resources, Canberra, F.4, A.C.T.
1948 Jopling, Alan Victor, B.Sc., B.E., 86 Alfred Road, Brookvale, N.S.W.
1933 Judge, Leslie Arthur, 87 Eastern Road, Turramurra, N.S.W.

1949 Keast, James Allen, B.Sc., Australian Museum, College Street, Sydney.
1951 Kerr, Harland Benson, B.Sc.Agr., 41 Badminton Road, Croydon, N.S.W.
1937 Kesteven, Geoffrey Leighton, D.Sc., c.o. F.A.O. of United Nations, Milawa Mansions, Para atit Road, Bangkok, Siam.
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VOL. 76.

Genera and Subgenus.

Species.

LIST OF PLATES.

PROCEEDINGS, 1951.

CORRIGENDUM.

The following lines were omitted under the heading "Notes and Exhibits" at the meeting of the Society on 26th July, 1950, and should be inserted in the PROCEEDINGS, Vol. lxxv, 1950, p. xxvii, following line 22:

Mr. A. K. O'Gower exhibited the eggs, larvae and pupae of cat fleas and pointed out the possibility of high infestations in domestic situations from the presence of cats. Two collections were made at a Dulwich Hill joinery works during the last week of June and early July. The situations examined were the sleeping sites of two cats. Four such sites were found, each being less than one square yard in area. From these collections a total of some 500 eggs together with more than 8,000 larvae resulted.

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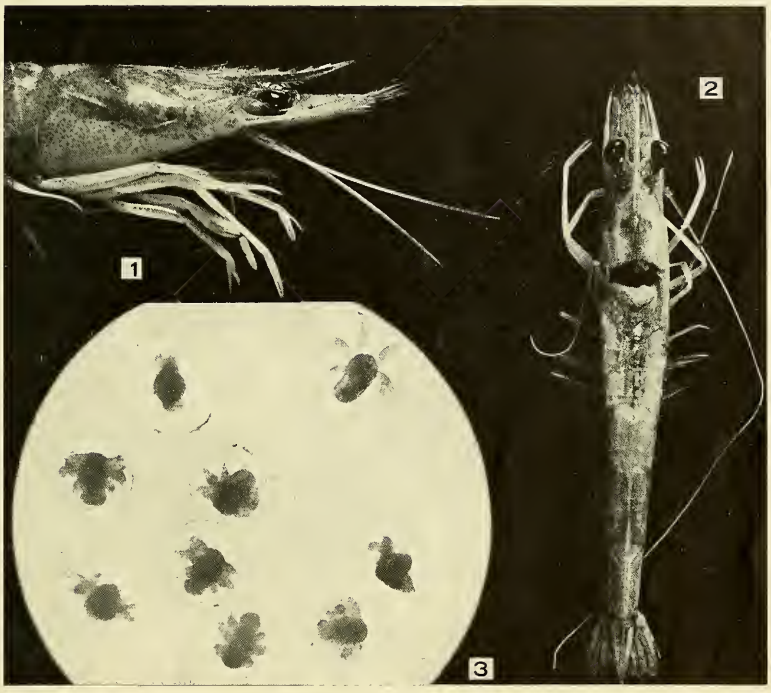
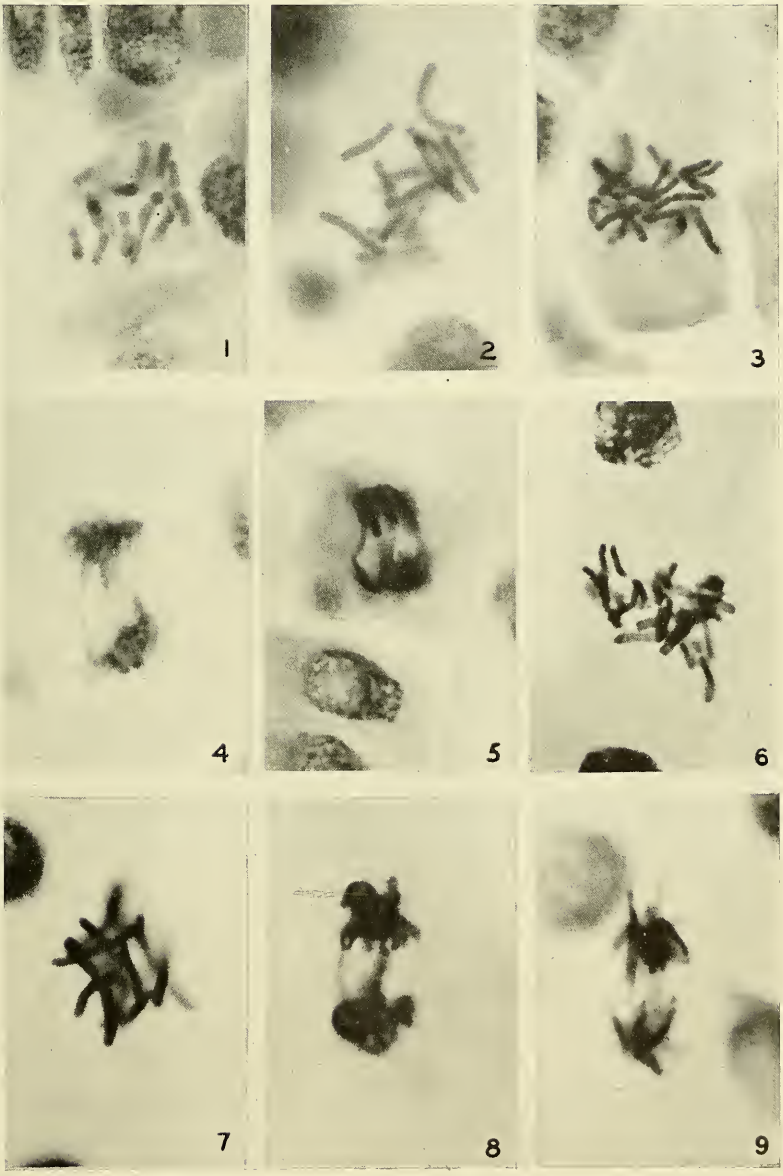
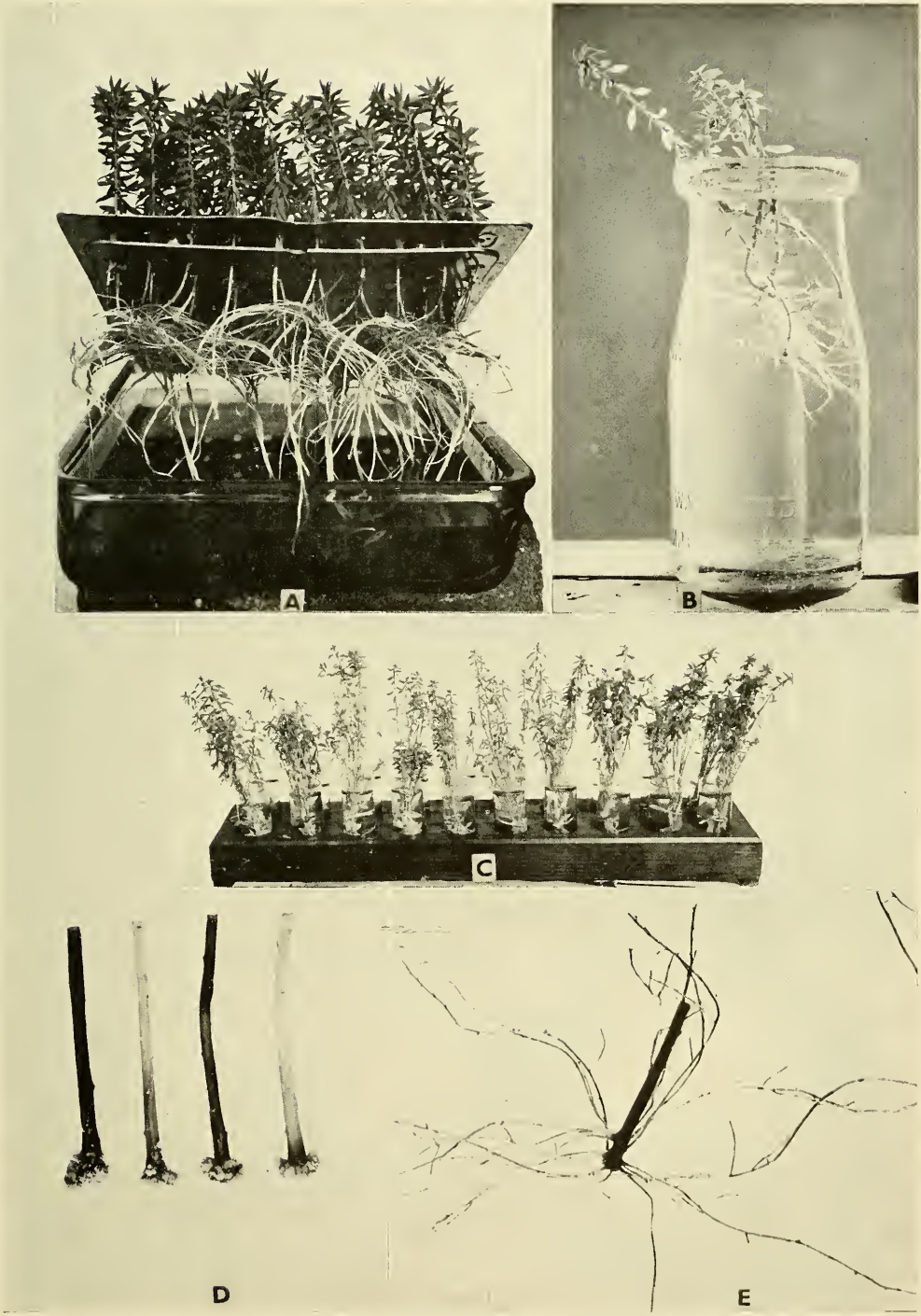
(1951.)



Penaeid Prawn (*Metapenaeus*, n. sp.).

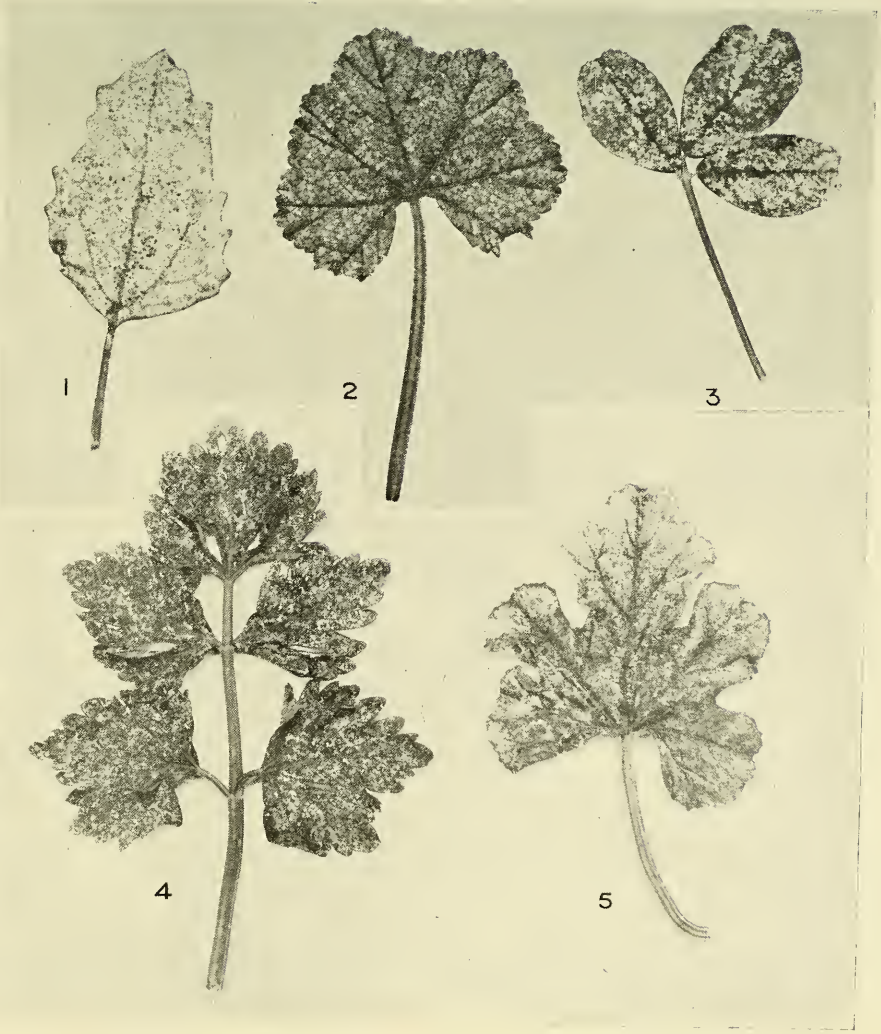


Effect of 2,4-dinitrophenol on Onion root tip cells.



Use of Excised Shoots in Linseed Investigations.

Portion of stem of black night shade (*Solanum nigrum*).



Typical damage done by feeding of *Austroasca viridigrisea*.

(Issued 31st May, 1951.)

Vol. LXXVI.
Parts 1-2.

Nos. 353-354.

THE

PROCEEDINGS

OF THE

LINNEAN SOCIETY

OF

NEW SOUTH WALES

FOR THE YEAR

1951.

Parts 1–2 (pp. i–xx; 1–48).

CONTAINING THE PROCEEDINGS OF THE ANNUAL GENERAL MEETING AND PAPERS READ IN MARCH-APRIL.

With five plates.
[Plates i-v.]

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PROCEEDINGS, LXXVI, PARTS 1-2, 1951.

CONTENTS.

Corrigendum.

The following lines were omitted under the heading "Notes and Exhibits" at the meeting of the Society on 26th July, 1950, and should be inserted in the PROCEEDINGS, Vol. lxxv, 1950, p. xxvii, following line 22:

Mr. A. K. O'Gower exhibited the eggs, larvae and pupae of cat fleas and pointed out the possibility of high infestations in domestic situations from the presence of cats. Two collections were made at a Dulwich Hill joinery works during the last week of June and early July. The situations examined were the sleeping sites of two cats. Four such sites were found, each being less than one square yard in area. From these collections a total of some 500 eggs together with more than 8,000 larvae resulted.

(*Issued 17th September, 1951.*)

Vol. LXXVI.
Parts 3-4.

Nos. 355-356.

THE

PROCEEDINGS

OF THE

LINNEAN SOCIETY

OF

NEW SOUTH WALES

FOR THE YEAR

1951.

Parts 3–4 (pp. 49–157).

CONTAINING PAPERS READ IN JUNE-AUGUST.

With six plates.
[Plates vi-xi.]

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1875–76	I*	3 0	3 0	5 0	7 6	1899	XXIV	12 6	12 0	10 0	10 6
1877	II	4 0	4 0	4 0	—	1900	XXV	8 0	10 6	10 6	17 6
1878	III	5 0	5 0	6 0	7 6	1901	XXVI	10 0	9 0	5 0	17 6
1879	IV	6 0	6 0	8 0	6 6	1902	XXVII	7 0	7 6	7 6[3]	15 0
1880	V	6 6	—	7 6	7 6	1903	XXVIII	9 0	12 6	14 0	15 0
1881	VI	6 0	10 0	10 0	—	1904	XXIX	10 0	7 6	9 0	10 0
1882	VII	7 6	10 0	5 0	10 0	1905	XXX	6 0[4]	10 0	12 6	8 0[5]
1883	VIII	10 0	5 0	7 0	8 0	1906	XXXI	12 6	12 6	12 6	15 0
1884	IX	8 0	12 0	25 0	25 0	1907	XXXII	8 0	8 6	15 0	18 0
1885	X	12 0	7 6	15 0	17 6	1908	XXXIII	7 0	9 0	14 0	12 6
1886	I†	10 6	12 0	13 0	12 6	1909	XXXIV	12 0	17 0	14 0	16 6
1887	II	7 0	8 0	12 0	27 0	1910	XXXV	11 0	11 0	7 0	12 6
1888	III	15 0	24 0	20 0	18 0	1911	XXXVI	9 6	9 6	9 6	10 0
1889	IV	11 0	16 0	19 0	11 0	1912	XXXVII	8 6	25 0	12 6	15 0
1890	V	11 0	9 0	9 0	9 0	1913	XXXVIII	14 0	7 6	6 0	13 0
1891	VI	10 0	9 6	17 0	7 6	1914	XXXIX	13 0	17 0	25 0	19 0
1892	VII	6 6	4 6	8 0	8 0	1915	XL	17 0	12 6	10 0	11 0
1893	VIII	5 0	11 0	6 0	9 0	1916	XLI	10 0	12 0	15 0	19 0
1894	IX	12 0	12 0	13 0	8 0	1917	XLII	14 0	9 0	12 6	16 6
1895	X	15 0	8 6	10 0[1]	12 0	1918	XLIII	20 0	14 0	21 0	19 0
1896	XXI	9 0[2]	6 6	7 6	27 6	1919	XLIV	12 6	11 6	17 6	13 0
1897	XXII	10 0	8 6	9 0	12 6	1920	XLV	10 9	7 6	9 0	11 0
1898	XXIII	3 0	6 0	12 0	14 0	1921	XLVI	9 0	8 0	7 6	9 6

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INDEX TO VOLUMES I-L OF THE PROCEEDINGS [Issued 15th February, 1929]. Pp. 108. Price 5s.

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plate; covered with sparse short plain setae. Metapodal plates roughly triangular, their apices behind coxae iv, their bases at the lateral margins of the body; with a few short plain setae over the bases and the adjacent integument.

Coxa i bearing a stout tapering plain seta, 160μ long, projecting straight forward from a shoulder on the anteromedial angle; a shorter, stout seta projecting medially, and a group of five stout setae on the lateral side. Coxa ii with one stout seta towards its anterior margin and a group of six posteriorly. Coxa iii with one anterior and five posterior setae. Coxa iv with four stout setae. Six segments in each leg, but the last two segments in leg i fused, and partly fused in the other three legs. Legs short, very stout, normally curved postero-ventrally; i, 500μ; ii, 525μ; iii and iv, 600μ long. Postero-ventral aspect of last five segments of each leg with a thickened plate. All segments with several stout sharp setae; no spurs on any leg. Tarsus i longer than the others, straighter and more slender; tarsi ii, iii and iv short, stout, curved. A large caruncle, but no claws, on each tarsus (Text-fig. 2).

Epistome only visible from above when proboscis projected; a small, translucent semicircle (Text-fig. 5). Mandibles with three segments, scissors-shaped, the medial fixed blade with a row of minute teeth; a small flagellum at the lateral side of the base of the blades (Text-fig. 3). Hypostome bifid, each half bearing three short stout forward-pointing setae; lingula bifid, each point bearing three small rounded projections on its medial surface (Text-fig. 4). Palpi of five segments, with a few fine setae on segments iii and iv; terminal segment rounded, with one short sharp stout seta on its disto-medial aspect, and covered with several fine straight setae.

Type at the British Museum; paratype at the School of Public Health and Tropical Medicine, University of Sydney.

PROCEEDINGS, LXXVI, PARTS 3-4, 1951.

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(*Issued 15th January, 1952.*)

Vol. LXXVI.
Parts 5-6.

Nos. 357-358.

THE

PROCEEDINGS

OF THE

LINNEAN SOCIETY

OF

NEW SOUTH WALES

FOR THE YEAR

1951.

Parts 5-6 (pp. 157-225; xxi-xxxvii).

CONTAINING PAPERS READ IN SEPTEMBER-NOVEMBER, ABSTRACT OF PROCEEDINGS, LIST OF MEMBERS AND INDEX.

With four plates.
[Plates xii-xv.]

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1923* ..	XLVIII	2 6	12 0	16 0	13 6	2 0	—
1924* ..	XLIX	2 0	13 6	12 6	10 0	2 0	—
1925* ..	L	2 0	12 0	8 9	14 6	2 0	—
1926* ..	LI	2 0	13 6	9 6	15 0	2 0	—
1927* ..	LII	2 6	10 6	14 0	12 3	2 0	—
1928 ..	LIII	2 0	8 6	8 9	10 0	9 0	2 0
1929 ..	LIV	2 0	6 3	8 6	11 0	12 6	2 0
1930 ..	LV	2 0	10 0	8 9	8 6	16 3	2 0
1931 ..	LVI	2 0	8 0	7 0	7 3	8 9	2 0

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1933 ..	LVIII	8 0	11 9	8 6	1947 ..	LXXII	8 3	12 0	18 6
1934 ..	LIX	6 6	8 6	10 9	1948 ..	LXXIII	13 0	20 0	25 0
1935 ..	LX	7 9	10 3	11 3	1949 ..	LXXIV	23 6	23 6	23 6
1936 ..	LXI	6 6	7 0	9 9	1950 ..	LXXV	23 6	23 6	23 6
1937 ..	LXII	6 0	9 3	8 9					
1938 ..	LXIII	6 3	11 6	9 9					
1939 ..	LXIV	12 3	12 3	8 9					
1940 ..	LXV	11 9	10 6	8 0					
1941 ..	LXVI	6 6	9 3	9 6					
1942 ..	LXVII	9 0	12 3	6 9					
1943 ..	LXVIII	5 6	6 9	8 3					
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PROCEEDINGS, LXXVI, PARTS 5-6, 1951.

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